Strength of Habitat and Landscape Metrics in Predicting Golden-Headed Lion Tamarin Presence or Absence in Forest Patches in Southern Bahia, Brazil

Becky E. Raboy[1,2,6], Leonardo G. Neves[2,3], Sara Zeigler[4], Nicholas A. Saraiva[1,5], Nayara Cardoso[2,3], Gabriel Rodrigues dos Santos[2], Jonathan D. Ballou[1], and Peter Leimgruber[1]

[1] Department of Conservation and Science, National Zoological Park, Smithsonian Institution, P.O. Box 37012-MRC 5503, Washington, DC 20013, U.S.A.

[2] Instituto de Estudos Socioambientais do Sul da Bahia, Rua Araujo Pinho, no. 72, Centro, Ilhéus, BA, 45653-145, Brazil

[3] Departamento de Ciências Biológicas, Universidade Estadual de Santa Cruz, Rodovia Ilhéus/Itabuna, km 16, 45662-000, Ilheus, BA, Brazil

[4] Department of Geography, University of Maryland, 2181 Lefrak Hall, College Park, MD 20742, U.S.A.

[5] ONG Pivot Maranhão, Rua dos Pescadores, 02, Bairro Cacimba Redonda, 65585-000, Paulino Neves, MA, Brazil

ABSTRACT

We investigated the effects of forest fragmentation on golden-headed lion tamarins (*Leontopithecus chrysomelas*) by qualitatively and quantitatively characterizing the landscape throughout the species range, conducting surveys, and exploring predictive models of presence and absence. We identified 784 forest patches that varied in size, shape, core area, habitat composition, elevation, and distance to neighboring patches and towns. We conducted 284 interviews with local residents and 133 playback experiments in 98 patches. Results indicated a reduction in the western portions of the former species range. We tested whether *L. chrysomelas* presence or absence was related to the aforementioned fragmentation indices using Monte Carlo logistic regression techniques. The analysis yielded a majority of iterations with a one-term final model of which Core Area Index (percent of total area that is core) was the only significant type. Model concordance ranged between 65 and 90 percent. Area was highlighted for its potential predictive ability. Although final models for area lacked significance, their failure to reach significance was marginal and we discuss potential confounding factors weakening the term's predictive ability. We conclude that lower Core Area Index scores are useful indicators of forest patches at risk for not supporting *L. chrysomelas*. Taken together, our analyses of the landscape, survey results, and logistic regression modeling indicated that the *L. chrysomelas* metapopulation is facing substantial threat. The limited vagility of lion tamarins in nonforest matrix may lead to increasingly smaller and inbred populations subject to significant impact from edge effects and small population size. Local extinction is imminent in many forest patches in the *L. chrysomelas* range.

Abstract in Portuguese is available at http://www.blackwell-synergy.com/loi/btp

Key words: Atlantic forest; fragmentation; *Leontopithecus chrysomelas*; lion tamarins; logistic regression; Monte Carlo methods; predictive models.

FOREST LOSS AND HABITAT FRAGMENTATION in tropical ecosystems can have negative consequences for local biodiversity, causing population declines and species extinctions (Fahrig 2003). Fragmented landscapes may be particularly unfavorable to forest-specialists that rarely use habitats surrounding forest fragments (Gascon *et al*. 1999). Effects of fragmentation may be immediate or sometimes evident only after substantial time has passed (Brooks *et al*. 1999).

Lion tamarins (genus: *Leontopithecus*) exemplify a primate genus acutely threatened by habitat loss and fragmentation. Lion tamarins are endemic to the Atlantic Forest, one of the more threatened tropical forests in the world and a global biodiversity hotspot (Olson & Dinerstein 1998, Myers *et al*. 2000). The Atlantic forest now constitutes several thousand fragments totaling 8 percent of its former extent as reported by Tabarelli *et al*. (1999). Lion tamarin metapopulation sizes have declined in response (Rylands *et al*. 2002) and all four species are listed as Endangered or Critically Endangered (IUCN 2008).

Southern Bahia is a region of the Atlantic Forest where forest conversion and habitat fragmentation have been changing the landscape dramatically (Morellato & Haddad 2000). Diverse forms of land use have contributed to this pattern. The long-term survival of golden-headed lion tamarins (*Leontopithecus chrysomelas* Kuhl, 1820), resident to Southern Bahian forests (Fig. 1 inset), is at risk (Rylands *et al*. 2002). Shade-cocoa agroforests form the majority of habitat in the eastern portion of the *L. chrysomelas* geographic range, linking patches of mature and regenerating forests (Fig. 1A). Although still prevalent, the amount of shade-cocoa forest has been declining since the 1980s due to a weakening local cocoa industry (Alger & Caldas 1994, Saatchi *et al*. 2001). The western portion of the *L. chrysomelas* range is predominantly used for cattle ranching, consisting of small and isolated forest fragments. Selective logging, rubber tree, eucalyptus, coffee, and palm oil plantations have also contributed to forest loss and degradation across the *L. chrysomelas* range (Mori *et al*. 1983, Rylands *et al*. 1991–1992, Chomitz *et al*. 2005).

Leontopithecus chrysomelas use many forest types including mature, shade-cocoa, secondary and edge habitat to obtain their principal trophic resources: fruit, nectar, insects, and small vertebrates (Raboy & Dietz 2004). Despite a general use of forest habitats for
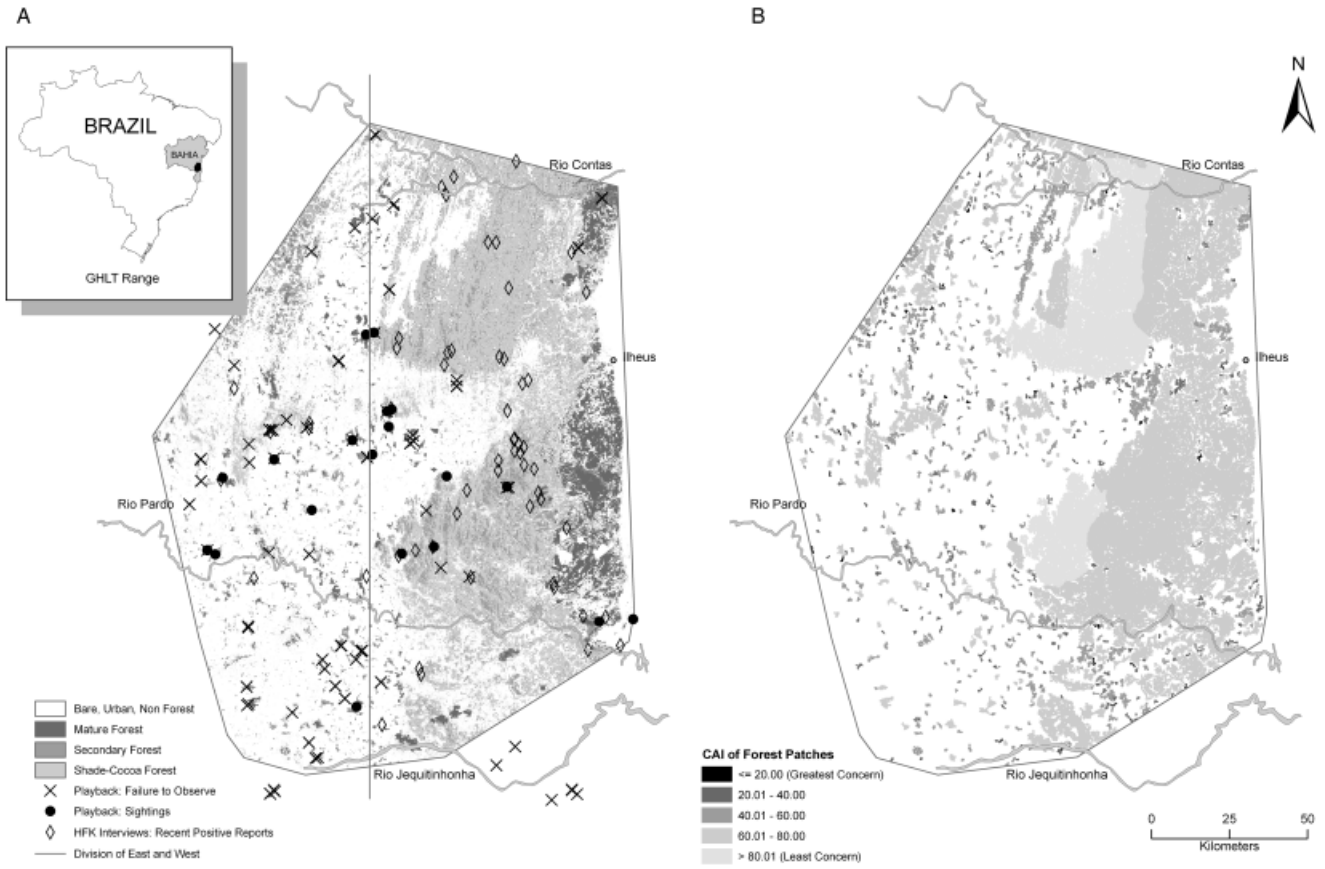
FIGURE 1. Map of the Atlantic forest of Brazil showing location of the southern Bahia study region and the formerly recognized *L. chrysomelas* geographic range (see inset). The left map (A) shows four land cover types within the *L. chrysomelas* range and the survey results. The right map (B) shows a gradation of CAI scores for the 784 study fragments. Patches with lower percentages for CAI (darker) have a greater likelihood of not containing *L. chrysomelas* presently or in the near future.

food, the tamarins specialize on mature and shade-cocoa forest to find tree holes for sleeping at night (Raboy *et al*. 2004). The extent to which they settle and reproduce successfully within degraded habitats remains unclear and may vary depending on the landscape characteristics. Threats to forest primates resulting from severe fragmentation and increased edge effects may include changes in the physical structure of forests, resource availability, and predator complexes (Marsh 2003). Moreover, small and isolated fragments may contribute to demographic instability, inbreeding depression, and population decline of resident fauna (Mills & Smouse 1994, Lacy 2000).

The objective of our study was to understand the current state of the landscape in the *L. chrysomelas* range and the effect that forest fragmentation has had on the species. We characterized the degree of habitat fragmentation in the *L. chrysomelas* geographic range, conducted an extensive population survey including direct (playback/observation) and indirect (expert interviews) techniques, and explored predictive models of presence and absence from forest patches using Monte Carlo logistic regression randomization techniques. Specifically, we tested whether *L. chrysomelas* presence or absence is related to a range of habitat fragmentation indices including area, isolation, and distance measures.

METHODS

CHARACTERIZATION OF THE LANDSCAPE.—To define the recognized geographic range of *L. chrysomelas* we created a map of 152 published and confirmed records of *L. chrysomelas* presence between 1850 and 1999 (compiled by Prado *et al*. 2003b), and calculated a minimum convex polygon (MCP; Fig. 1 inset) containing these locations using Hawths Tools extension (Beyer 2004) for ARC-GIS 9.2 (ESRI, Redlands, CA, U.S.A.). All landscape analyses were restricted to this MCP area.

We collapsed 12 Southern Bahia land cover categories from Landau *et al*. (2003a) into two classes: forest (mature forest, secondary forest, shade-cocoa forest), and nonforest (Fig. 1A). We smoothed the raster dataset using a circular kernel with a three-cell radius (ARC-GIS 9.2). Wide road clearances can be barriers to small mammal movement (Oxley *et al*. 1974), especially for arboreal species in tropical rainforests and those that avoid open spaces (Goosem 1997). We therefore considered the highways and large paved roads (Landau *et al*. 2003b) as patch dividers. We utilized spatial clustering to delineate separate and uniquely coded forest patches. The landscape contained 8940 isolated patches from which we removed patches < 40 ha, the smallest reported home range for

L. chrysomelas (Rylands 1989), assuming these would not support populations. Herein the patch dataset refers to the restricted sample of 784 patches ≥40 ha.

We calculated 12 patch metrics listed in Table 1. The first four metrics, AREA, SHAPE, CAI, and NN, were calculated in Fragstats 3.3 (McGarigal *et al.* 2002) and the last eight, EASTING, NORTHING, HI_ELEV, MOD_ELEV, CITY COUNT, MAT, SEC, and COCOA, were derived from our own GIS analyses in ArcGIS 9.2 using published datasets (Prado *et al.* 2003a). Patches were classified as eastern or western to roughly follow the landscape division between shade-cocoa and cattle ranching. The median UTM easting coordinate of patch centroids (418887 m; South American 69, UTM Zone 24 South) was used as the division between those patches belonging to the east and west.

POPULATION SURVEY INTERVIEWS.—Although some patches reached sizes of > 10,000 ha, the majority of the patches in the MCP landscape were small (94% were < 1000 ha) and thus we focused on sampling these. Firstly, we stratified sampling by location and size class. We divided the rectangular extent of our MCP shapefile into nine regions of equal extent forming a 3×3 grid of the region. Then we categorized patches in each region into four size classes: 40–100, 100–300, 300–1000, and > 1000 ha. Secondly, from each grid we randomly selected 5 percent of the patches from the first two size classes, 10 percent of the third size class and 20 percent of the largest size classes for visitation to have roughly equal representation of *N* for each size class. Survey patches were visited between October 2004 and October 2005 by a field team, locating selected patches using GPS devices with Superintendência do Desenvolvimento do Nordeste cartographic (at 1:100,000 scale) and GIS maps. We approached patches as closely as possible by available roads. As we neared the study patch we asked the people we encountered where we could find community members with good forest knowledge to serve as interviewees. Individuals identified themselves or referred us to other friends, relatives or co-workers. For the first part of the interview, interviewees were asked to identify and discuss pictures of six primates and six other mammals from the region, some locally extinct. We asked interviewees to identify the animals in the pictures with common names and whether or not they had seen them in the forest. We inquired about group sizes, vocalizations, or other species-specific behaviors. Forest knowledge (FK) scores were assigned to each interviewee on a scale of 1–10 at the conclusion of the interview based on the responses provided in the first part of the interview. The score 10 represented the greatest comprehension of the small mammal and primate community of Southern Bahia and was assigned to someone who correctly identified all photos and described correct information for the species. Scores were lowered when interviewees could not identify all photos, confused species, or otherwise conveyed incorrect information. Interviews with FK scores ≥5 were considered as high FK (HFK) scores. This was later used as a filter in data analysis to eliminate potentially inaccurate observations. For the second part of the interview, we proceeded with specific questions regarding *L. chrysomelas*, inquiring about their presence in specific fragments and in the region in general, time since last viewing, presence of infants, and whether or not they had ever seen lion tamarins crossing roads or fields.

Unpredictable field conditions made it difficult to determine *a priori* interview sample sizes per study patch. Many areas in the west were sparsely populated, and encountering interviewees was difficult.

POPULATION SURVEY PLAYBACKS.—We conducted playbacks of *L. chrysomelas* long calls in forest patches to determine presence or absence between November 2005 and November 2007. Lion tamarins use long calls to maintain intergroup spacing (Ruiz-Miranda & Kleiman 2002) thus playing back recordings of long calls is an effective method to survey them (Pinto & Rylands 1997, Kierulff & Rylands 2003). Resident lion tamarins respond with similar calls, aggressive vocalizations or by approaching the source location of the playback. Vocalizations were recorded from captive animals in the Smithsonian National Zoological Park and wild animals from a previous study in Una Biological Reserve using a Marantz stereo cassette recorder (PMD 430; Marantz America Inc., Mahwah, NJ, U.S.A.) and Sennheiser directional microphone (ME88; Senheiser Electronic Corporation, Old Lyme, CT, U.S.A.). Vocalizations were played back on a Saul Mineroff speaker/amplifier (SME-AFS; Mineroff Electronics Inc., Elmont, NY, U.S.A.) using a Panasonic Discman (SL-SX470; Panasonic Corporation, Secaucus, NJ, U.S.A.).

After an initial effort to sample the same patches that we had selected and visited for our interviews, we modified our methods to allow for the selection of alternative sampling locations in cases

TABLE 1. *Explanation of patch variables used.*

Variable	Explanation
AREA	The area of the patch (m²)
SHAPE	Patch perimeter divided by the minimum perimeter possible for a maximally compact patch of the corresponding patch area
CAI	The percentage of a patch that is core area (defined by the area of the region in the patch that was > 100 m from the patch perimeter).
NN	Nearest neighbor distance measured as the Euclidean distance from a patch's edge to the edge of the nearest patch (m)
EASTING	The eastward measured distance of the patch centroid in UTM coordinates (South American 69, Zone 24S)
NORTHING	The northward measured distance of the patch centroid
HI_ELEV	The percent of area 800 m elevation or greater in a patch
MOD_ELEV	The percent of a patch that is contained within 1 km buffer of the 400 m elevation contours
CITY_COUNT	The number of towns occurring within a 20 km radius of the patch centroid
MAT	The percent of mature forest in a patch
SEC	The percent of secondary forest in patch
COCOA	The percent of shade-cocoa forest in patch

where it was extremely difficult to reach the forest or when permission to enter private property was not obtainable. To the extent possible, we substituted the locations with patches of similar area and relative location. In addition to visiting the aforementioned patches falling within the focal MCP area, three trips were taken beyond the MCP borders to test the limits of the species range after receiving additional indication from informants about the likelihood of finding lion tamarins. These data points are included in our descriptive account of the species landscape in the results section, but were not used in predictive modeling.

In open forest, we walked *ca* 50 m into the forest to start the transect and continued walking perpendicular to the forest edge, traveling deeper into the fragment. We followed trails or dirt roads if available. Approximately every 100 m for 1 km we played two long calls in each of four directions (North, South, East, and West), waited 5 min, and repeated the process. In less penetrable forests, we cut a trail at least 1 d before the sampling period or ran the transect superficially along the border, entering *ca* 25 m into the forest every 100 m to play back calls. Previous lion tamarin playback studies indicated that wild golden lion tamarins (*L. rosalia*) responded well to playbacks at a distance up to 100 m but not beyond (Kierulff & Rylands 2003).

Observers were trained to recognize the sounds of *L. chrysomelas* moving through the trees and their vocalizations during training sessions with habituated groups tracked on a daily basis by other researchers. When traveling between playback points, observers continued to look and listen for tamarins. When observed, the time of observation was noted. When accessible, we obtained GPS coordinates for each point in the transect.

Playbacks were not conducted during steady rain or wind. Transects were walked between 0600 and 1600 h, the period *L. chrysomelas* are most likely to be awake (Raboy & Dietz 2004). If presence was not established during the first playback session at a given location, the playback process was repeated at least once more at that location on a different day.

COMPILATION OF INTERVIEWS AND PLAYBACKS.—We created an algorithm to assign presence or absence to study patches based on multiple results from interviews and playbacks. If a playback transect was positive for any repetition of the transect, the patch containing it was assigned positive. If all repetitions of a playback transect were negative with no information from interviews, the patch was assigned negative. Otherwise, if the positive to negative ratio of the sum of HFK interviews and playback repetitions was ≥ 1 the patch was assigned positive. If the ratio was < 1, the patch was assigned negative. For example, if three interviews were conducted for a particular patch yielding one positive and two negative responses and two repetitions of a playback transect were conducted for that same patch that were both negative, then we would calculate as follows: $(1+0)/(2+2) = 1/4$, which is < 1 and thus the patch would be categorized as negative.

LOGISTIC REGRESSION.—We used multiple logistic regression to explore which habitat and landscape factors best predicted presence and absence in the surveyed patches according to our compiled sur-

TABLE 2. *Correlation matrix for terms considered in initial model.*

Variable	AREA	SHAPE	CAI	NN	EASTING	HI_ELEV
AREA	1.000					
SHAPE	0.897[a]	1.000				
CAI	0.362[a]	0.415[a]	1.000			
NN	-0.199[a]	-0.322[a]	-0.234[a]	1.000		
EASTING	0.373[a]	0.451[a]	0.227[a]	-0.287[a]	1.000	
HI_ELEV	0.199[a]	0.181	0.228[a]	-0.128	0.024	1.000

[a]Significant at $P < 0.05$.

vey results ($N = 98$ patches). We considered the 12 parameters outlined in Table 1 as potential predictive variables and thus starting terms in our model. We performed univariate logistic regression analyses on each of these variables and those with $P > 0.25$ were eliminated from the starting model (Hosmer & Lemeshow, 2000). Six variables, AREA, SHAPE, CAI, NN, EASTING, HI_ELEV, remained as potential starting terms. We determined the correlation matrix for the remaining terms. SHAPE and AREA were highly correlated ($r = 0.90$, $P < 0.05$), while the rest of the correlations ranged between 0.02 and 0.45 (Table 2). Variance inflation factors (VIF) were ≤ 1.30 for all terms except AREA (5.45) and SHAPE (6.24). Given that VIFs < 10 likely indicate the absence of problematic correlation among the predictors, all six terms were maintained.

To run the logistic regression, we used Monte Carlo techniques to subsample the absence data points. Monte Carlo sampling of datasets can be useful in attributing statistical validity to complex biological processes and when datasets are small or imbalanced (Manly 1991). Specifically we created an analysis data set consisting of all presence data points ($N = 25$) and 25 randomly selected absence data points (from a pool of 73 possible absence data points). Multiple analysis datasets were generated in SAS 8.02 (SAS Institute Inc., Cary, NC, U.S.A.), each with a different random selection of 25 absence points. To evaluate the capacity to process multiple initial starting terms, an exploratory analysis data set (50 iterations) was created using backwards stepwise selection on six terms with criterion to remove set at $P > 0.20$. Eighteen percent of runs yielded models that lacked validity and > 40 percent of runs were insignificant. The two most prominent variables were CAI and AREA. Fourteen iterations yielded a significant one-term CAI final model. Three iterations had significant one-term AREA or two-term final model with AREA included. Therefore, to increase the capacity of the logistic regression tests to generate significant results, only CAI and AREA were used as starting terms in a second round of the randomization process, which we iterated 500 times. Results were divided into the four categories of final results: one-term CAI, one-term AREA, two-term, or zero-term (models that lacked validity) models. For each of the first three categories, the mean and distributions were obtained for the likelihood ratio chi-square value, its corresponding P-value, overall model concordance, and rates of false positive and negatives. These methods were used to explore the relative importance of several independent variables on lion tamarin

TABLE 3. *Mean ± SD in landscape and habitat metrics in the East and West of MCP.*

Patch Statistics	East	West	P-value	All Fragments
N	392	392	–	784
AREA (ha)	1914 ± 13,056	231 ± 504	ns	1073 ± 9282
SHAPE	2.8 ± 2.7	2.2 ± 0.9	ns	2.5 ± 2.1
CAI (%)	46 ± 16	46 ± 14	ns	46 ± 15
NN (m)	443 ± 569	909 ± 950	$P <$ 0.0001[a]	550 ± 816
MAT (%)	18 ± 30	25 ± 27	$P <$ 0.001[b]	23 ± 29
SEC (%)	26 ± 19	55 ± 30	$P <$ 0.01[a]	41 ± 29
COCOA (%)	47 ± 33	13 ± 28	$P <$ 0.01[a]	30 ± 35
MOD_ELEV (%)	15 ± 32	52 ± 46	$P <$ 0.0001[a]	33 ± 44
HI_ELEV (%)	0.08 ± 0.83	0.5 ± 3.6	ns	0.3 ± 2.6
CITY COUNT	6 ± 2	4 ± 2	$P <$ 0.01[b]	5 ± 2
%MCP Forested	51	15	–	37

[a]Mann–Whitney *U* test;

[b]*T*-test.

presence or absence and to serve as a basis with which to develop more complex statistical analyses in the future.

RESULTS

CHARACTERIZATION OF LANDSCAPE.—The forest patches varied in size, shape, percent of core area, habitat composition, elevation and distance to nearest neighboring patches and towns (Table 3). Ninety-four percent of the patches were < 1000 ha, and 52 percent were < 100 ha in size. Twelve patches reached sizes of > 10,000 ha. The shape of patches ranged from compact (tightly formed, approximating a circle) to complex (irregular edges, multiple projections). Patches in the west contained mostly secondary habitat and were isolated by non-forest matrix. Eastern patches consisted mainly of shade-cocoa, were the largest in size, and were sometimes only separated from their nearest neighboring patch by a road. Western patches were more likely to contain areas of 400 m or higher elevation and had lower density of cities near patch centroids. The east half of the MCP study area was 51.0 percent forested whereas the west was 14.9 percent (Table 3).

POPULATION SURVEY.—We conducted 284 interviews. FK scores range was 1–10 (mean = 6.7, SD = 1.55, N = 272), and 90.4 percent were rated as HFK. The large number of HFK interviews reflected our methods of selecting individuals believed *a priori* to have good forest knowledge by fellow community members, such as hunters. Half (50.3%) of HFK interviews were positive for *L. chrysomelas* in the east (N = 165), whereas only 27.2 percent were positive in the west (N = 81; Fig. 1). In reference to habitat type, 69.2 percent of the HFK respondents that responded to this question (N = 91) described the habitats in which they had seen lion tamarins as mature forest (using the terms 'good' or 'shade-cocoa') while 16.5 percent of people described *L. chrysomelas* as using degraded habitats (using the terms 'secondary' and 'capoeira'). The remaining 14.3 percent described the habitat as 'forested' without description of the level of anthropogenic pressure. We conducted 133 playback experiments in 52 locations within the MCP area and nine outside (Fig. 1A). The number of repetitions per location ranged from 1 to 11 with a modal value of 2.3. Only 25.4 percent of all locations were positive for *L. chrysomelas*. Half of these documented *L. chrysomelas* on the first repetition of the transect and half on subsequent passes. In the east, 32.0 percent of locations were positive for *L. chrysomelas* while 21.1 percent were positive in the west. The geographic coordinates of positive sightings are presented in supporting information Table S1.

Compiling the results from interviews and playbacks, we assigned 25 patches as '*L. chrysomelas* present' and 73 as '*L. chrysomelas* absent'. This represented 12.5 percent of the 784 patches in the MCP area.

LOGISTIC REGRESSION.—The Monte Carlo logistic regression randomization analysis yielded 481 iterations with 1-term final models, 18 two-term models and one zero-term model (Table 4). The majority (N = 413; 82.6%) of iterations had one-term CAI final models and were the only significant type of final model (95% of iterations were significant; Fig. 2). The one-term CAI, one-term AREA and two-term models overall concordance range was 65–90 percent with modal values of 70–75 percent for the one-term variables and 75–80 percent for the two term models (Fig. 2). The one-term AREA models had better predictive ability in determining presence than did CAI models (Fig. 3). CAI ranged between 25 and 50 percent risk of false negatives and positives; however, the median was lower for negative than positive (Fig. 3). AREA had a much higher predictive ability for presence (15–35%) than absence (30–40 %; Fig. 3).

DISCUSSION

THE *L. CHRYSOMELAS* LANDSCAPE.—The landscape in the MCP area showed great complexity and habitat heterogeneity. The forest, which once covered the entire area of the *L. chrysomelas* range (Galindo-Leal & Camara 2003), is now considerably fragmented.

TABLE 4. *Mean results for three types of final logistic regression models.*

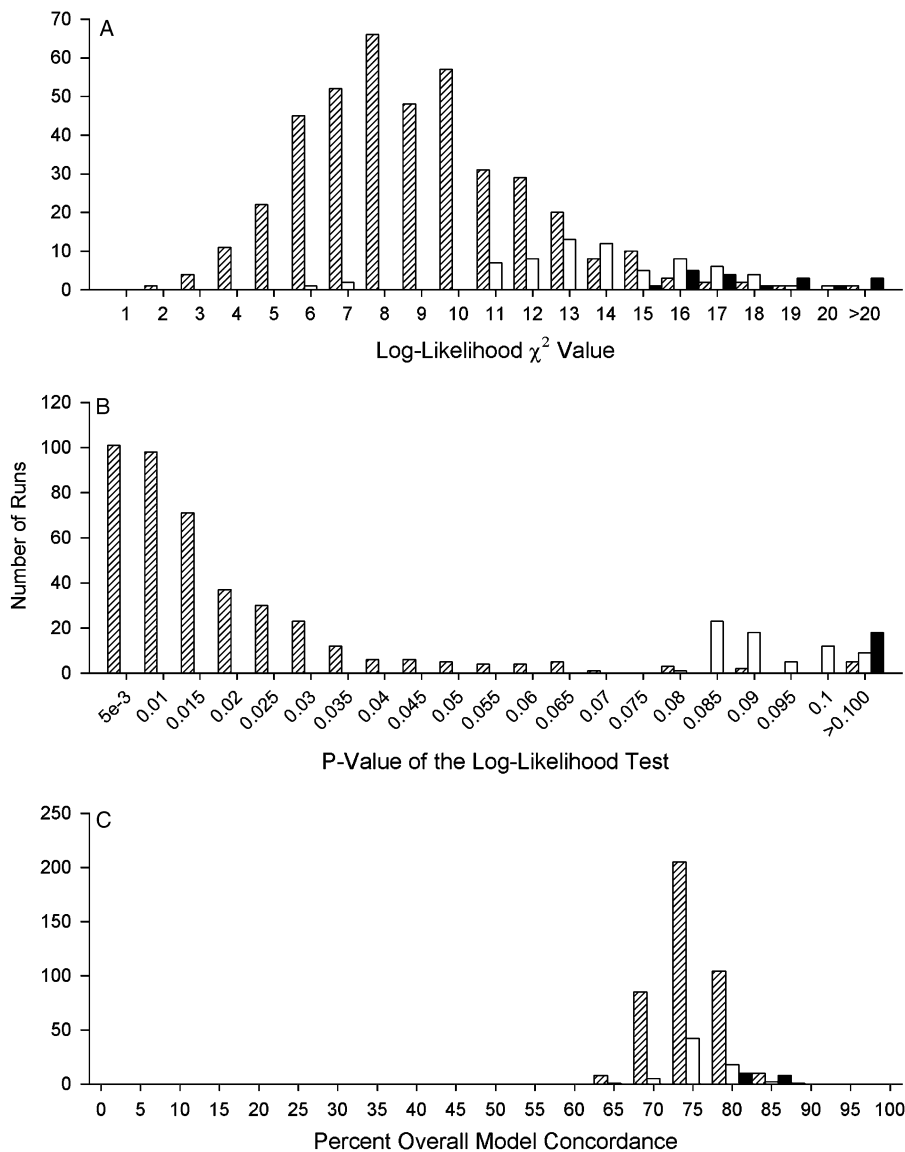| Model	*N* iterations	Chi-square	P-value	Concordance (%)	False positive (%)	False negative (%)
1-term CAI	413	8.5	0.016	72.8	36.3	34.3
1-term AREA	68	13.4	0.093	73.4	17.5	39.3
2-term	18	17.4	0.181	79.6	22.5	33.0

FIGURE 2. Frequency histograms for (A) log-likelihood ratio, (B) the *P*-value associated with the log-likelihood test, and (C) overall model concordance for the three types of final models for the randomization runs (hatched: one-term CAI; white: one-term AREA; and black: two-term).

Forests were comprised of different habitat types and occurred both as contiguous expanses and isolated from one another. In our study, patch size varied from small to large spanning low elevations to those exceeding 800 m. Land use included mature, shade-cocoa, and degraded forests as well as urban development, pasture and other types of agriculture. For many of the independent variables assessed for the 784 fragments, variation around the mean was exceptionally high. Our maps depicting the extreme fragmentation of southern Bahia (Fig. 1) are similar to those documented in other regions of the Atlantic forest that contained more than a thousand small fragments (Ranta *et al.* 1998). The east and west of the *L. chrysomelas* range have been described by researchers as markedly different in climate, degree of fragmentation, and habitat composition (Pinto & Rylands 1997). When dividing forest patches of the

L. chrysomelas landscape systematically by the north-south divide based on median easting of patch centroids, some clear differences were found. In the west, lion tamarins were less likely to be seen by our survey team or by interviewees. Distance to nearest patches on the west was nearly twice that of the east. The west was also more likely to have areas of high altitude.

Habitat composition differed between the east and west as well. Western patches contained more degraded habitat than any other type whereas the eastern patches contained mostly shade-cocoa. The sizes of patches were not significantly different between the east and west. However, the east had extremely large variability around the mean in contrast to the west. In the east, extensive areas of contiguous forest were interspersed with small isolated fragments whereas the west had mostly small isolated fragments. Using climate
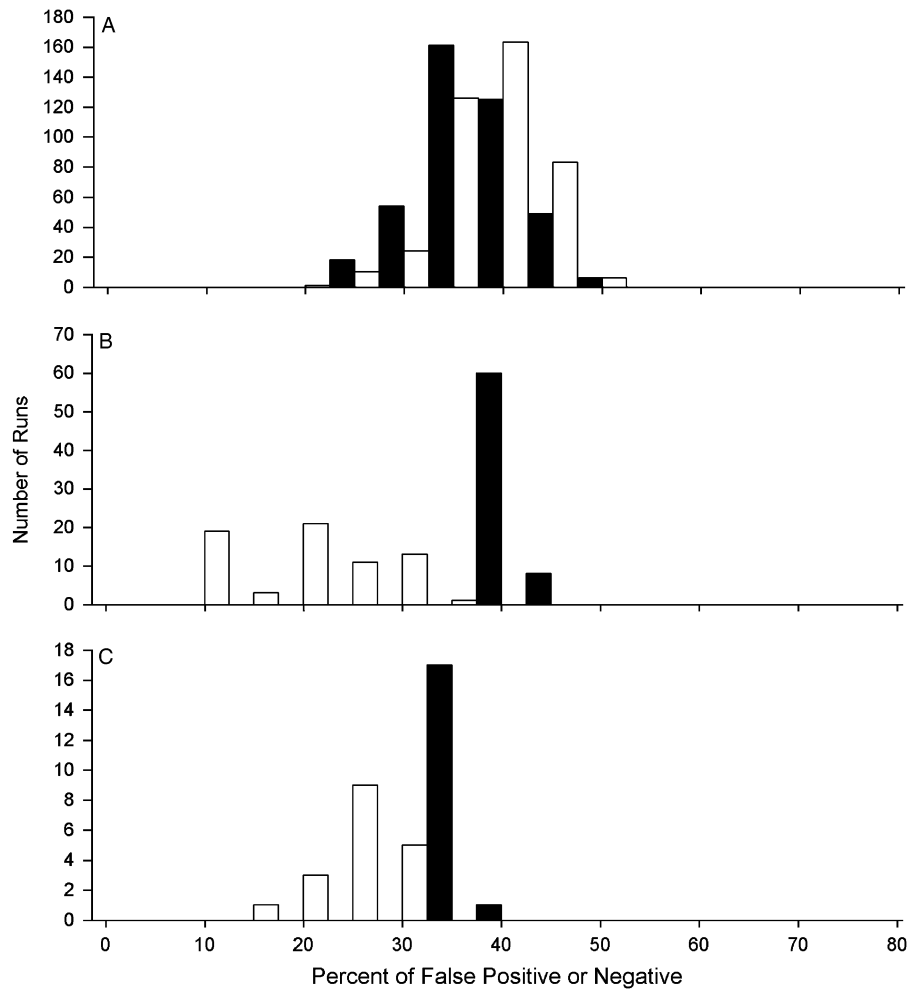
FIGURE 3. Frequency histogram for percentage of false negative (dark bars) and false positive (white bars) for (A) one-term CAI models, (B) one-term AREA models, and (C) two-term models.

isolines of rainfall and/or temperature to differentiate between the humid to sub-humid east and the sub-humid to dry west may reveal even more salient differences in fragment and habitat characteristics between a functional 'east' and 'west' for *L. chrysomelas*.

In relation to information given on habitat, shade-cocoa was the most common descriptor used by interviewees to describe the type of habitat where *L. chrysomelas* were most commonly found. Golden-headed lion tamarins have been documented using shade-cocoa in other studies (Alvez 1990, Raboy *et al.* 2004) as have many other southern Bahian animals (Faria *et al.* 2007, Cassano *et al.* 2009). 'Good' forest was the second most common descriptor. Though subjective, it connotes forest that is not likely to be extremely degraded. In our playbacks however, we did find *L. chrysomelas* in exceedingly degraded habitats. In relation to information given on forest vs. non-forest use, we had minimal evidence of *L. chrysomelas* using non-forest matrix. From a total of 246 interviewees who were specifically asked about this, only one individual reported having seen *L. chrysomelas* crossing pasture, indicating the infrequency with which they cross unsuitable terrain.

We had lower success rate in discovering *L. chrysomelas* in comparison to surveys performed 10–12 years earlier, in which 72 percent ($N = 181$) of interviews and 85 percent ($N = 27$) of forest censuses (playbacks) were positive (Pinto & Rylands 1997). These figures contrast our own results in which 42 percent of HFK interviews and 25 percent of the playback locations were positive. The difference between studies indicates a decline in metapopulation size for *L. chrysomelas*.

MODEL PREDICTABILITY.—CAI was the variable with the greatest significant predictive ability in our logistic regression randomization iterations, although in absolute terms its predictive ability (mean concordance = 72.8%) was not very strong. Nonetheless, lower CAI levels can be useful in indicating areas of the landscape at risk for not supporting *L. chrysomelas* populations. Patches with lower CAI values were characterized as narrower, having jagged edges and peninsular extensions of forest, and/or containing interior areas of non-forest in comparison with similar sized areas with higher CAI values. Figure 1B highlights patches in the MCP area

from lowest (darkest) to highest (lightest) CAI, with lower values indicating patches less likely to have *L. chrysomelas* present. Higher CAI levels may also be used as a guide to hypothesize about presence throughout their range, but the risk of false positives is greater on average.

In our study, lower CAI values often indicated a greater exposure to the interface between forest and agriculture or forest and urban areas and may present suboptimal conditions for *L. chrysomelas* due to associated edge effects and lack of sufficient interior resources. While *L. chrysomelas* use edge habitats, they also require resources that are typically more abundant in mature forests (Raboy *et al.* 2004). Ranta *et al.* (1998) demonstrated that irregularity in the shape of fragments in another region of the Atlantic forest lead to low percentages of interior forest relative to total area, even when using relatively small definition of edge width. Changes in resource availability and the physical structure of forests are potential costs to primates resulting from the severe fragmentation of the Atlantic Forest (Chiarello 2003). Increased threats of fire (Gascon *et al.* 2000, Cochrane & Laurance 2002) and mesopredators (Crooks & Soule 1999) are also probable. In addition, risks from the spread of disease (Daszak *et al.* 2000), hunting (Peres 2001), and predation from domestic dogs (Chiarello 2003) are more prevalent for tropical forest dwellers in fragmented environments due to close proximity to livestock and/or humans.

The term AREA showed up as a potentially important variable in predicting lion tamarin presence although our limited sample size failed to support its significance as a predictor in our Monte Carlo randomization experiment. Smaller patches may indeed be at risk of local extinctions. Lower carrying capacities lead to smaller populations that are less resilient to stochastic processes (demographic, environmental, and genetic) and natural catastrophes (Lacy 2000). Important resources may be limited. In a study of the Atlantic forest fragmentation in São Paulo State, Tabarelli *et al.* (1999) documented that smaller fragments had fewer species from key frugivore plant families and greater representation of ruderal ('weedy') species than larger fragments. In our survey, we did find *L. chrysomelas* present in some very small fragments. Although present, the populations may not be viable in the long term, and are likely slated for local extinction (Tilman *et al.* 1994). Genetic erosion may already be occurring in these populations, as has been documented for other recently fragmented tropical small mammal populations (Srikwan & Woodruff 2000).

Other independent variables in our model had no influence on our ability to predict presence or absence. Neither altitude nor habitat composition showed up as significant predictors despite indications from the literature that they play a prominent role in *L. chrysomelas* ecology. *Leontopithecus chrysomelas* were found both in lower montane and extremely degraded habitats during our survey. Other species of lion tamarins have also been sighted at higher altitudes (Kierulff & Rylands 2003). Such sightings alone do not indicate that these areas support lion tamarin reproduction or that the areas contain adequate resources. *Leontopithecus chrysomelas* may be transient (traveling through without using resources) in any location in which they were observed. Studies of relative density, longitudinal demographic surveys, or radio tracking may elucidate permanence versus transience in any given location. We would have expected isolation to exacerbate the risks associated with small patch size; however, the degree of patch isolation did not have an effect on predicting presence or absence. The fact that they were not found in the upper northeast corner of the MCP area may contribute to the lack of significance of this metric. This region, a previous known lacuna for the species (Rylands *et al.* 2002), was in close proximity to other fragments that did support *L. chrysomelas* (Fig. 1). Moreover, the western populations found in small and isolated fragments served as an additional confounding factor.

LIMITATIONS AND CONSIDERATIONS.—Some limitations to our analyses likely precluded obtaining more definitive results for predicting presence or absence in forest patches. Undocumented forest loss in the decade prior to our analysis may have led to some fragments being smaller than indicated by our landscape maps and potentially biasing model accuracy. Sample size and unit was another limiting factor. Larger patches may not have been adequately represented by one transect location. However, our analyses indicated that AREA was a stronger predictor of *L. chrysomelas* presence than absence suggesting a relatively low risk of missing lion tamarins with increasing area. Nonetheless, the potential confounding factor could have weakened the model results for this term, which although close, never reached significance in our Monte Carlo randomization experiment. The percent of total patch area accounted for by the broadcast range may serve as a useful covariate in future analyses. Another issue was that of recolonization. The complex extinction and recolonization processes may not be adequately assessed through a snapshot view of the landscape (static presence/absence). A patch's capacity to retain populations over time may serve as a more useful dependent variable to ascertain the state of a species metapopulation. Including additional phenology or resource availability metrics to characterize a patches' vegetative structure may also help discern stronger trends in presence or absence. Patches with richer or more diverse complex of lion tamarin resources or those with stable resources throughout the year may be more likely to contain *L. chrysomelas*. Longitudinal studies and more detailed transect work would address these latter issues, but take significant time to conduct.

CONSERVATION IMPLICATIONS.—Overall, our analysis of the landscape, survey results, and logistic regression modeling indicated that the metapopulation is facing substantial threat of local extinctions. In the west, there was less forest relative to total area, a greater percent of each patch was degraded, and forest patches were more isolated. In particular, we rarely observed *L. chrysomelas* toward the western edges of their former known range (Fig. 1A), indicating range reduction in the last few decades. Note that the patches in the highest risk categories (darker) according to Fig. 1B are small and mostly located in the west. If anthropogenic pressure steadily encroaches from the western edges towards center and local extinctions continue as a result, the western edge of the shade-cocoa region (currently midrange) may eventually become the western limit of the species range.

Given the current disquieting state of the landscape, understanding the degree of difficulty that lion tamarins have in

traversing between isolated forest fragments is critical. While not explicitly studied, researchers have suggested lion tamarins are not likely to move across non-forest matrix (Valladares-Padua *et al.* 2002). Movement has been shown to be limited due to habitat fragmentation for some small mammal species (Debinski and Holt, 2000). Our own evidence from interviewees also supports the infrequency with which lion tamarins will go into non-forest matrix. This is a concern for the metapopulation's long-term health and survival and needs to be assessed. Grativol *et al.* (2001) found marked genetic divergence in a study of four isolated populations of golden lion tamarins, likely a result of their limited dispersal capabilities in very fragmented environments. The limited vagility of lion tamarins in nonforest matrix may lead to increasingly smaller and inbred populations subject to significant population impact from aforementioned threats to small populations. Such trends are already evident for other Atlantic forest mammals. For example, the degree of matrix tolerance best accounted for the variation seen in small mammal extinction vulnerabilities from among six independent variables tested for 12 mammal species living in one or more of nine neighboring Atlantic forest fragments (Viveiros de Castro & Fernandez 2004). The negative impacts of edge effects are also a concern. Local extinction is imminent in many forest patches in the *L. chrysomelas* range. Gascon *et al.* (2000) point to the extreme danger facing the Atlantic Forest as a result of its numerous extremely small-sized fragments that are not likely to sustain themselves in the long term. The authors state that tropical fragment sizes under < 5000 ha are likely to suffer a 'receding edge phenomenon', whereby forest edges continuously recede due to a combination of dynamic edge effects occurring over time (Gascon *et al.* 2000). In the case of *L. chrysomelas*, this represents almost all of the forest fragments identified as falling within its range. In a study assessing fragments of different ages, Brooks *et al.* (1999) showed that bird extinctions occurred at alarming rates in the first few decades after fragmentation of tropical forests in Kenya, yet continued to occur thereafter. Similarly, in Southern Bahia, we can expect to see impacts on *L. chrysomelas* both from current fragmentation and also manifesting after some lag-time from previous fragmentation events.

ACKNOWLEDGMENTS

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *UTM locations of L. chrysomelas sightings from playback survey (South American 69, UTM Zone 24 South).*

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

LITERATURE CITED

ALGER, K., AND M. CALDAS. 1994. The declining cocoa economy and the Atlantic forest of Southern Bahia, Brazil: Conservation attitudes of cocoa planters. Environmentalist 14: 107–119.

ALVEZ, M. C. 1990. The role of cacao plantations in the conservation of the Atlantic forest of Southern Bahia, Brazil. PhD Dissertation. University of Florida, Florida.

BEYER, H. L. 2004. Hawth's Analysis Tools for ArcGIS. Available at http://www.spatialecology.com/htools.

BROOKS, T. M., S. L. PIMM, AND J. O. OYUGI. 1999. Time lag between deforestation and bird extinction in tropical forest fragments. Conserv. Biol. 13: 1140–1150.

CASSANO, C., G. SCHROTH, D. FARIA, J. DELABIE, AND L. BEDE. 2009. Landscape and farm scale management to enhance biodiversity conservation in the cocoa producing region of southern Bahia, Brazil. Biodiv. Conserv. 18: 577–603.

CHIARELLO, A. G. 2003. Primates of the Brazilian Atlantic forest: The influence of forest fragmentation on survival. *In* L. K. Marsh (Ed.). Primates in fragments: Ecology and conservation, pp. 99–121. Kluwer Academic/Plenum Publishers, New York, New York.

CHOMITZ, K. M., K. ALGER, T. S. THOMAS, H. ORLANDO, AND P. V. NOVA. 2005. Opportunity costs of conservation in a biodiversity hotspot: The case of southern Bahia. Environ. Dev. Econ. 10: 293–312.

COCHRANE, M. A., AND W. F. LAURANCE. 2002. Fire as a large-scale edge effect in Amazonian forests. J. Trop. Ecol. 18: 311–325.

CROOKS, K. R., AND M. E. SOULE. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400: 563–566.

DASZAK, P., A. A. CUNNINGHAM, AND A. D. HYATT. 2000. Emerging infectious diseases of wildlife– threats to biodiversity and human health. Science 287: 443–449.

DEBINSKI, D. M., AND R. D. HOLT. 2000. Review: A survey and overview of habitat fragmentation experiments. Conserv. Biol. 14: 342–355.

FAHRIG, L. 2003. Effects of habitat fragmentation on biodiversity. Ann. Rev. Ecol. Evol. Syst. 34: 487–515.

FARIA, D., M. PACIENCIA, M. DIXO, R. LAPS, AND J. BAUMGARTEN. 2007. Ferns, frogs, lizards, birds and bats in forest fragments and shade cacao plantations in two contrasting landscapes in the Atlantic forest, Brazil. Biodiv. Conserv. 16: 2335–2357.

GALINDO-LEAL, C., AND I. G. CAMARA. 2003. The Atlantic Forest of South America: Biodiversity status, threats, and outlook. Island Press, Washington, DC.

GASCON, C., T. E. LOVEJOY, R. O. JR. BIERREGAARD, J. R. MALCOLM, P. C. STOUFFER, H. L. VASCONCELOS, W. F. LAURANCE, B. ZIMMERMAN, M.

Tocher, and S. Borges. 1999. Matrix habitat and species richness in tropical forest remnants. Biol. Conserv. 91: 223–229.

Gascon, C., G. B. Williamson, and G. A. B. da Fonseca. 2000. Receding forest edges and vanishing reserves. Science 288: 1356–1358.

Goosem, M. 1997. Internal fragmentation: The effects of roads, highways, and powerline clearings on movements and mortality of rainforest vertebrates. In W. F. Laurance and R. O. Bierregaard (Eds.). Tropical forest remnants: Ecology, management, and conservation of fragmented communities, pp. 241–255. University of Chicago Press, Chicago, Illinois.

Grativol, A. D., J. D. Ballou, and R. C. Fleischer. 2001. Microsatellite variation within and among recently fragmented populations of the golden lion tamarin (Leontopithecus rosalia). Conserv. Gen. 2: 1–9.

Hosmer, D. W, and S. Lemeshow. 2000. Applied logistic regression. John Wiley & Sons, New York, New York.

IUCN. 2008. 2008 IUCN Red List of Threatened Species. ⟨www.iucnredlist. org⟩. Downloaded 26 March 2009.

Kierulff, M. C. M., and A. B. Rylands. 2003. Census and distribution of the golden lion tamarin (Leontopithecus rosalia). Am. J. Primatol. 59: 29–44.

Lacy, R. C. 2000. Considering threats to the viability of small populations using individual-based models. Ecol. Bull. 48: 39–51.

Landau, E. C., A. Hirsch, and J. Musinsky. 2003a. Cobertura vegetal e uso do solo, escala 1:100.000, data dos dados: 1996–97 (mapa em formato digital). In P. I. Prado, E. C. Landau, R. T. Moura, L. P. S. Pinto, G. A. B. Fonseca, and K. Alger (Eds.). Corredores de Biodiversidade na Mata Atlântica do Sul da Bahia. IESB/CI/CABS/UFMG/ UNICAMP.

Landau, E. C., N. A. T. Resende, and F. S. Miranda. 2003b. Rede viária do sudeste da bahia, Brasil (mapa em formato digital, modificado a partir de IBGE, 1967; SUDENE, 1976; 1977 e DERBA, 2000), escala 1:100.000. In P. I. Prado, E. C. Landau, R. T. Moura, L. P. S. Pinto, G. A. B. Fonseca, and K. Alger (Eds.). Corredores de Biodiversidade na Mata Atlântica do Sul da Bahia. IESB/CI/CABS/UFMG/UNICAMP.

Manly, B. F. J. 1991. Randomization, bootstrap and Monte Carlo methods in biology. Chapman and Hall, London, UK.

Marsh, L. K. 2003. The nature of fragmentation. In L. K. Marsh (Ed.). Primates in fragments: Ecology and conservation, pp. 1–10. Kluwer Academic/Plenum Publishers, New York, New York.

McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene. 2002. FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following website: www.umass.edu/ landeco/research/fragstats/fragstats.html.

Mills, L. S., and P. E. Smouse. 1994. Demographic consequences of inbreeding in remnant populations. Am. Nat. 144: 412–431.

Morellato, L. P. C., and C. F. B. Haddad. 2000. Introduction: The Brazilian Atlantic forest. Biotropica 32: 786–792.

Mori, S. A., B. M. Boom, A. M. de Carvalho, and T. S. dos Santos. 1983. Southern Bahian moist forests. Bot. Rev. 49: 155–232.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853–858.

Olson, D. M., and E. Dinerstein. 1998. The Global 200: A representation approach to conserving the earth's most biologically valuable ecoregions. Conserv. Biol. 12: 502–515.

Oxley, D. J., M. B. Fenton, and G. R. Carmody. 1974. The effects of roads on populations of small mammals. J. Appl. Ecol. 11: 51–59.

Peres, C. A. 2001. Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian Forest vertebrates. Conserv. Biol. 15: 1490–1505.

Pinto, L. P. S., and A. B. Rylands. 1997. Geographic distribution of the golden-headed lion tamarin, Leontopithecus chrysomelas: Implications for its management and conservation. Folia Primatol. 68: 167–180.

Prado, P. I., E. C. Landau, R. T. Moura, L. P. S. Pinto, G. A. B. Fonseca, and K. N. Alger. 2003a. Corredor de Biodiversidade da Mata Atlantica do sul da Bahia. Publication in CD-ROM. IESB/CI/CABS/UFMG/UNI CAMP, Ilheus, Brazil.

Prado, P. I., R. T. Moura, and L. P. S. Pinto. 2003b. Inventário mamíferosespécies do sudeste da Bahia, Brasil (mapa em formato digital). In P. I. Prado, E. C. Landau, R. T. Moura, L. P. S. Pinto, G. A. B. Fonseca, and K. Alger (Eds.). Corredores de Biodiversidade na Mata Atlântica do Sul da Bahia. IESB/CI/CABS/UFMG/UNICAMP.

Raboy, B. E., M. C. Christman, and J. M. Dietz. 2004. The use of degraded and shade cocoa forests by endangered golden-headed lion tamarins Leontopithecus chrysomelas. Oryx 38: 75–83.

Raboy, B. E., and J. M. Dietz. 2004. Diet, foraging, and use of space in wild golden-headed lion tamarins. Am. J. Primatol. 63: 1–15.

Ranta, P., T. Blom, J. Niemelä, E. Joensuu, and M. Siitonen. 1998. The fragmented Atlantic rain forest of Brazil: Size, shape and distribution of forest fragments. Biodiv. Conserv. 7: 385–403.

Ruiz-Miranda, C. R., and D. G. Kleiman. 2002. Conspicuousness and complexity: Themes in lion tamarin communication. In D. G. Kleiman and A. Rylands (Eds.). Lion tamarins biology and conservation, pp. 233–254. Smithsonian Institution Press, Washington, DC.

Rylands, A., M. C. M. Kierulff, and L. P. S. Pinto. 2002. Distribution and status of lion tamarins. In D. G. Kleiman and A. B. Rylands (Eds.). Lion tamarins biology and conservation, pp. 42–70. Smithsonian Institution Press, Washington, DC.

Rylands, A. B. 1989. Sympatric Brazilian callitrichids: The black tufted-ear marmoset, Callithrix kuhli, and the golden-headed lion tamarin, Leontopithecus chrysomelas. J. Hum. Evol. 18: 679–695.

Rylands, A. B., I. B. Santos, and R. A. Mittermeier. 1991-1992. Distribution and status of the golden-headed lion tamarin, Leontopithecus chrysomelas, in the Atlantic forest of Southern Bahia, Brazil. Primate Conservation 12–13: 15–23.

Saatchi, S., D. Agosti, K. Alger, J. Delabie, and J. Musinsky. 2001. Examining fragmentation and loss of primary forest in the Southern Bahian Atlantic Forest of Brazil with radar imagery. Conserv. Biol. 15: 867–875.

Srikwan, S., and D. S. Woodruff. 2000. Genetic erosion in isolated small-mammal populations following rainforest fragmentation. In A. Young and G. Clarke (Eds.). Genetics, demography and viability of fragmented populations, pp. 149–172. Cambridge University Press, Cambridge, UK.

Tabarelli, M., W. Montovani, and C. A. Peres. 1999. Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. Biol. Conserv. 91: 199–127.

Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. Nature 371: 65–66.

Valladares-Padua, C., J. D. Ballou, C. S. Martins, and L. Cullen. 2002. Metapopulation management for the conservation of black lion tamarins. In D. G. Kleiman and A. B. Rylands (Eds.). Lion tamarins biology and conservation, pp. 301–314. Smithsonian Institution, Washington, DC.

Viveiros de Castro, E. B., and F. A. S. Fernandez. 2004. Determinants of differential extinction vulnerabilities of small mammals in Atlantic Forest fragments in Brazil. Biol. Conserv. 119: 73–80.