

ABSTRACT

Title of Document: FOREST LOSS AND FRAGMENTATION IN SOUTHERN BAHIA, BRAZIL: IMPLICATIONS FOR THE EXTINCTION RISK OF GOLDEN-HEADED LION TAMARINS (*Leontopithecus chrysomelas*)

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Golden-headed lion tamarins (GHLTs; *Leontopithecus chrysomelas*) are Endangered arboreal primates endemic to the Atlantic Forest of Brazil, where continuing loss of forest and its connectivity are major threats. The objectives of my research were to assess the vulnerability of GHLTs to habitat loss, fragmentation, and threats related to small population size in the context of past, current, and future trends in range-wide forest cover in Brazil's Atlantic Forest. I did this by conducting a supervised classification of Landsat 5TM remotely-sensed imagery to define past and current forest cover in the region, analyzing connectivity patterns in a graph theoretical framework, projecting recent deforestation patterns into the future using a multi-layer perceptron neural network, and modeling GHLT metapopulation viability using

population viability analysis. I found that forest cover has declined throughout the range of the species by 13% over the last 20 years, and only one habitat patch is large enough on its own to support a genetically viable GHLT population able to recover from extrinsic threats such as fire and disease. Functional landscape connectivity, which is important for population persistence, acquisition of resources, and maintenance of genetic diversity, is low at the distance and movement cost thresholds likely associated with this arboreal species that is rarely seen in non-forest matrix. The majority of remaining forest cover throughout the species' range is found in patches that are either (1) too small to support even a single group of GHLTs or (2) found at low elevations, in areas of high human population density, or in close proximity to previously cleared areas—conditions that are associated with past deforestation patterns and that make current habitat vulnerable to loss. Finally, I found that many of the known GHLT populations have a moderate to high risk of local extinction even over short time scales and assuming no further forest loss, and their presence may represent extinction debt. Continued deforestation will accelerate population declines and local extinction events. The results of my dissertation research suggest that GHLTs and their habitat face significant threats and low viability in the future because of both ultimate and proximate drivers of extinction.

FOREST LOSS AND FRAGMENTATION IN SOUTHERN BAHIA, BRAZIL:
IMPLICATIONS FOR THE EXTINCTION RISK OF GOLDEN-HEADED LION
TAMARINS (*Leontopithecus chrysomelas*)

By

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Preface

This dissertation includes an introductory chapter, three chapters describing the dissertation research, and a conclusion chapter. All chapters were written for publication in peer-reviewed journals and, as a result, may contain some repetitive information. A single reference section is located at the end for literature cited throughout all chapters of the dissertation.

Dedication

To my parents, Richard and Patricia Zeigler: Everything that I do, including this dissertation, has not only been possible, but better, because of their bottomless love and support.

And

To Dr. Philip Nyhus: The greatest teacher in 22 years of great teachers, who—with patience, enthusiasm, and boundless knowledge--instilled in me a passion for conservation.

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I thank my team of advisors--Ruth DeFries, Ralph Dubayah, and Bill Fagan--for their support throughout my dissertation work: Ruth, for keeping me on as her student as she moved on to new opportunities at Columbia University; Ralph, for stepping in and adopting me into his lab; and Bill, for being a constant source of guidance for this lost geography student. Ruth is not listed as a co-chair because of paperwork issues just prior to my defense; however, she served in that capacity throughout my dissertation work. Chris Justice and Maile Neel, as committee members, provided critical feedback and stimulating discussions that immeasurably improved my dissertation. I also owe Maile a great deal of gratitude for providing me with the financial, intellectual, and emotional support needed to finish this degree. Although she will not get credit for being my advisor, I have felt like one of her students from day one. Becky Raboy also served in the capacity of a committee member until the week of my defense, when her inability to attend the defense made it necessary to remove her from my committee at that time. However, she was a consistent source of guidance for my research, written dissertation, and publication drafts.

Becky, Leo Oliveira, and Jim Dietz were crucial to my dissertation work. Collecting field data on the demography and behavior of golden-headed lion tamarins in Brazil is financially expensive, physically difficult, and often complicated by bureaucratic/governmental regulations. Becky, Leo and Jim generously shared their hard work and knowledge of the species so that I could parameterize my models. I believe our collaborations will make a difference for the survival of this endangered species. Leo was also an incredible host while visiting Brazil. He truly made me fall in love with his beautiful country.

I have learned a great deal from the brilliant members of the DeFries, Fagan, and Neel labs at the University of Maryland. I especially thank Christina Kennedy, Thomas Mueller, Mike Lloyd and Doug Morton for helping me with some of the technical aspects of my work.

Finally, and most importantly, I thank my parents, grandmother, brothers, Ryan, and Bart for their love and support. I could not have finished this dissertation without them.

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Chapter 1: Introduction

Habitat loss, fragmentation, and degradation are indisputably the major drivers of global biodiversity loss and species extinctions (Sala et al. 2000; Schipper et al. 2008; Wilcove et al. 1998). For species experiencing declines as a result of these threats, space, resources, metapopulation dynamics, and gene flow are diminished or disrupted as once continuous habitat is divided into small, isolated patches. The result is a decrease in survival and reproduction, ultimately reducing population abundance, distribution, and genetic diversity (reviewed in Fahrig 2003) and leaving the species vulnerable to extinction through demographic and environmental stochasticity, genetic drift, inbreeding depression, and Alleé effects (Ellstrand & Elam 1993; Oostermeijer et al. 2003). In addition, the natural recovery of populations becomes unlikely even when threats driving declines are removed as isolation reduces demographic (Brown & Kodric-Brown 1977) and genetic (Richards 2000) rescue through dispersal and immigration.

Brazil's Atlantic Forest provides a prime example of how habitat loss and fragmentation can threaten native species. It is one of the world's most endangered biomes while providing habitat for a disproportionate number of species, many of which are endemic (Myers et al. 2000; Shi et al. 2005). Only 11.73% of the original vegetation remains in the Atlantic Forest, the majority of which is found in small fragments (< 50 ha) and within potentially degraded forest edges (Ribeiro et al. 2009). Deforestation has been attributed primarily to clear cutting for timber harvest, charcoal production, cattle ranching, and monoculture plantations (Morellato &

Haddad 2000; Pinto & Wey de Brito 2003) and has been linked to widespread extinctions and population declines for a variety of species (Chiarello 1999; Pardini et al. 2005; Uezu et al. 2005).

One species impacted by the loss and fragmentation of the Atlantic Forest is the Endangered (IUCN 2010) golden-headed lion tamarin (GHLT; *Leontopithecus chrysomelas*), an arboreal primate endemic to a small region of southern Bahia, Brazil (Figure 1). In this region, GHLTs preferentially

use lowland primary forest, secondary/regenerating forest, and cocoa agroforest (Oliveira 2010; Pinto & Rylands 1997; Raboy & Dietz 2004). A survey conducted between 1991 and 1993 provides the most recent published population estimate at 6,000-15,500 individuals spanning a geographic range of 19,462 km² (3,550 km² of which was forested;

Pinto & Rylands 1997). However, recent surveys suggest a population decline and 15% range

reduction over the last 13 years (Raboy et al. 2010; Raboy unpublished data). This species is listed as Endangered due to its limited distribution, severely fragmented habitat, continuing decline in extent of occurrence, and small population size (IUCN 2010).

GHLTs are considered the least threatened of the four lion tamarin species endemic to the Atlantic Forest in the genus *Leontopithecus*. The golden lion tamarin



Figure 1. Geographic range of the golden-head lion tamarin in Bahia, Brazil.

(*L. rosalia*) was recently upgraded to Endangered status after over 30 years of intensive conservation effort, and today only an estimated 1,000 individuals remain in 104.5 km² of forest. Because of extensive deforestation throughout the species' range, very little opportunity exists for population expansion, and the population would remain below the minimum viable size even if all currently available habitat becomes occupied (Kierulff et al. 2008a). The black lion tamarin (*L. chrysopygus*) is listed as Endangered with an estimated 1,000 individuals surviving in 11 isolated populations, 10 of which are not considered viable in the mid- to long-term (Kierulff et al. 2008c). Finally, the black-faced lion tamarin (*L. caissara*) has an estimated 260 individuals in 3 populations and is listed as Critically Endangered (Kierulff et al. 2008b). The history and current status of the GHLT's three congeners provide a cautionary lesson for what can be expected if habitat and populations are not immediately protected.

The Bahia biogeographical sub-region, of which the GHLT geographic range is a part, is considered the most well-preserved sub-region in the Atlantic Forest (Ribeiro et al. 2009; Silva & Casteleti 2003). The slower rate of deforestation, and thus the less severe GHLT population decline compared to other lion tamarins, has been attributed to the fact that cocoa production is a major economic activity in this region. In southern Bahia, cocoa is produced through an agroforestry system known as 'cabruca' that cultivates cacao trees planted in the understory of a tall native tree canopy. Because a native tree canopy persists, cabruca is of high biodiversity value (Alves 1990; Faria et al. 2006) and is considered important habitat for GHLTs (Oliveira 2010; Raboy et al. 2004). These agroforests covered 18% of the species'

range in 1995 (Landau et al. 2003) and are estimated to support a large portion of the remaining wild GHLT population (Rylands & Pinto 1991).

Persistence of cabruca agroforests and native forest cover throughout the GHLT range, however, is uncertain. Since the early 1990's, the price of cocoa has fallen dramatically while fungal epidemics threaten to destroy entire plantations, and it is becoming increasingly more profitable for farmers to clear cut their land for timber sale (Alger & Caldas 1994) or for conversion to cattle pasture or other agricultural systems of low biodiversity value (Schroth & Harvey 2007).

Given the uncertain future of remaining habitat for GHLTs, understanding which habitat patches are particularly valuable for continuing GHLT persistence or vulnerable to future deforestation is of conservation priority. Such knowledge is especially critical for the proactive protection of existing habitat and populations, preventing the severe population declines and limited opportunities for recovery associated with the three other lion tamarin species.

Research Objectives

The objectives of my dissertation research were to assess the vulnerability of GHLTs to habitat loss, fragmentation, and threats related to small population size given past, current, and likely future trends in range-wide forest cover in Brazil's Atlantic Forest.

Specifically:

1. How did forest cover throughout the GHLT range change between 1987 and 2007?
2. How much forest remains currently as habitat for GHLTs?

3. How vulnerable is current forest cover to future deforestation?
4. How many forest patches currently exist throughout the species' range that are large enough to support a minimum viable population of GHLTs under varying levels of risk?
5. What is the current level of functional connectivity between habitat patches for GHLTs?
6. Could conspecific or heterospecific attraction alter measurements of functional connectivity patterns for this social species?
7. How viable are GHLT metapopulations on small, relatively isolated habitat patches?

The information acquired by answering these questions is critical to channeling limited conservation resources and research efforts to priority areas and to informing conservation decisions for the species. In addition, lion tamarins are a flagship and umbrella species in Brazil, and conservation efforts directed towards GHLTs will likely result in the protection of numerous other species and their habitats (Dietz et al. 1994c).

Mechanisms of Extinction

To best protect endangered species such as the GHLT, one must first understand the complex mechanisms driving a species towards extinction. In most examples of historical species extinctions, a deterministic agent of decline is the ultimate cause of extinction (Simberloff 1986) that first forces a contraction in range size, number of populations, and number of individuals, as described in Caughley's (1994) declining

population paradigm. Agents of decline are typically one (or more) of Diamond's (1989) 'evil quartet': overkill, habitat destruction and fragmentation, invasive species, or chains of extinctions. After the ultimate cause of extinction works to dramatically reduce the number and size of populations, stochastic proximate causes of extinction (Simberloff 1986) work to eliminate the last remaining individuals in what Caughley (1994) terms the 'small population paradigm'. Once a species is restricted to a single population with few individuals, the final decline to extinction is typically the result of demographic stochasticity, genetic deterioration, catastrophic extrinsic forces, or social dysfunction (Simberloff 1986). Finally, cascading effects caused by synergies between and among ultimate and proximate drivers of extinction can radically accelerate population declines and increase extinction risk (the extinction vortex; Brook et al. 2008; Fagan & Holmes 2006; Gilpin & Soulé 1986). These mechanisms of extinction can be applied both to the extinction of the entire species or to the local extinction of isolated populations.

For GHLTs, forest loss and fragmentation are the ultimate agents of decline that could make the resulting small, isolated populations vulnerable to local extinction through stochastic processes. Given enough local population extinctions, the risk of extinction for the entire species in a single catastrophic event becomes more probable (Reed 2004). The broad goal of my dissertation research is to understand how both ultimate and proximate drivers of extinction impact the survival of GHLT populations throughout the species' range.

Ecology of Golden-Headed Lion Tamarins

GHLTs are small, arboreal primates endemic to a 19,462 km² area of the Atlantic Forest in southern Bahia, Brazil (Pinto & Rylands 1997). Range is limited by the Rio de Contas to the north, Atlantic Ocean to the east, Rio Jequitinhonha to the south, and increasing elevation with associated changes in forest physiognomy to the west (Rylands et al. 1994). Forest cover in this region is characterized by fragmented seasonal semi-deciduous tropical rainforest in the west and a mixture of cabruca agroforest and contiguous coastal evergreen tropical rainforest in the east (Pinto & Rylands 1997).

GHLTs are territorial, cooperatively breeding animals and form groups usually composed of a reproductive female, one to three adult males, and their offspring (Dietz et al. 1994b). Groups typically have 4 to 7 individuals (average 5) but can range from 2 to 12 individuals (Raboy 2002; Raboy unpublished data). Territory sizes for lion tamarins are large for New World primates in general and larger than expected based on the species' body mass (Dietz et al. 1997). At the time of analysis for my dissertation research, observed GHLT territory sizes ranged from 36 ha to 200 ha (Dietz et al. 1996b; Raboy & Dietz 2004; Rylands 1989) with densities ranging from 0.1 to 0.053 GHLTs per ha (Raboy unpublished data; Holst et al. 2006). More recently, Oliveira (2010) observed GHLT territories as low as 22 ha and densities as high as 0.17 GHLTs per ha in cabruca agroforest.

Within their territories, GHLTs use primary and secondary regenerating forest as well as cabruca agroforest (Raboy et al. 2004; Raboy & Dietz 2002) below 500 m elevation (Pinto & Rylands 1997). These forests provide critical resources such as

sleeping holes (Raboy et al. 2004) and a diet rich in fruits, flowers, nectar, insects, small vertebrates, and gums (Raboy & Dietz 2004).

Modeling Framework: A Note on Methods

I used various modeling approaches to characterize current forest cover amount, connectivity, future vulnerability to deforestation, and local population extinction risk. To characterize current forest cover, I conducted a supervised classification of remotely-sensed imagery using a maximum likelihood algorithm. This traditional methodology is frequently used in remote sensing classification (Mather 2004) and has previously provided robust classifications of semi-deciduous Atlantic Forest (de Carvalho et al. 2004).

I used a combination of approaches in circuit and graph theory to determine patterns of functional habitat connectivity for GHLTs. Ecological circuit theory employs the principles behind electrical circuit theory, which models how electrical currents move between resistors. In ecological circuit theory, the flow of current becomes the movement of individuals, resistors become habitat patches, and resistance translates into the opposition of a given habitat type to the movement of individuals. An overall measure of effective resistance (also resistance distance) can be calculated as a measure of isolation between pairs of habitat patches (McRae et al. 2008). Circuit theory is ideal for estimating the probability of dispersal between habitat patches because it considers characteristics of the matrix separating habitat patches, multiple pathways between habitat patches, and the width of those pathways (McRae 2006; McRae & Beier 2007; McRae et al. 2008).

I then used measures of effective resistance as the probability of movement between pairs of habitat patches in a graph theory framework to determine the overall level of functional habitat connectivity in the GHLT landscape. Like circuit theory, graph theory has recently been applied to connectivity studies in ecology (Bunn et al. 2000; Minor & Urban 2007; Rothley & Rae 2005; Urban & Keitt 2001) and may provide the best measurement of

connectivity when considering the tradeoff between information content and data requirements (Calabrese & Fagan 2004). In this approach, habitat patches are ‘nodes’ and the links between those

patches are ‘edges’ on a graph (Figure 2). A graph (i.e. landscape) is considered connected when an edge exists between every pair of

nodes (Urban & Keitt 2001). A graph theory approach is particularly useful in prioritizing nodes (i.e. patches) based on graph position and associated importance to maintaining connectivity between other nodes (Calabrese & Fagan 2004; Urban & Keitt 2001).

I used predictive landcover change modeling in a multi-layer perceptron (MLP) neural network to assess the vulnerability of forest to future deforestation. In general, the network projects historical patterns of deforestation to ‘predict’ future

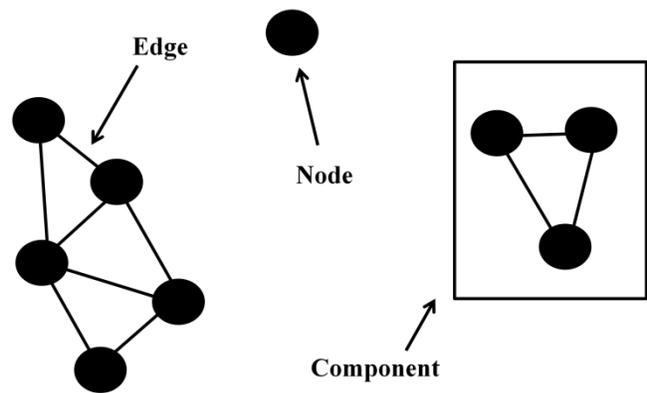


Figure 2. Graph theory terminology. A graph is defined by nodes representing habitat patches and edges representing potential species-specific dispersal links between patches. A series of connected nodes is a component while nodes not linked by an edge to another node represent isolated patches.

forest patterns. The MLP chooses a random sample of cells that transitioned from forest to non-forest as well a sample of cells that persisted as forest from maps input by the user spanning two dates. The network uses half of these samples as training data to develop a multivariate function that predicts each cell's potential for change from forest to non-forest based on a given location's landscape characteristics (e.g. elevation, distance from roads, etc) while reserving the second half of the samples for validation. The MLP assigns weights corresponding to each landscape characteristic's importance (i.e. its association with cells that transitioned from forest to non-forest) and adjusts those weights following progressive iterations as the model 'learns' by minimizing error between the training and validation samples. The resulting output is a transition potential matrix for every cell in the landscape that can be translated into the relative vulnerability of forest to deforestation in the future (Atkinson & Tatnall 1997; Richards & Jia 1997). The MLP neural network has been advocated as a tool for landcover classification and modeling because it has demonstrated the ability to perform rapidly and accurately, to incorporate *a priori* knowledge and realistic physical constraints, and to incorporate different types of data (reviewed in Atkinson & Tatnall 1997).

Finally, I used population viability analysis (PVA), which considers both anthropogenic ultimate and stochastic proximate drivers of extinction, to model local extinction risk for small GHLT populations. Defined broadly, PVA is the use of quantitative methods to forecast the future status of a population (Morris & Doak 2002) and has become one of the most rigorous planning tools available in endangered species conservation (Frankham et al. 2002; Hedrick et al. 1996).

Through computer simulations, PVA provides a simplified representation of a real biological system that extracts demographic trends from complex processes to make predictions regarding extinction risk under a range of management and environmental scenarios (Lacy & Miller 2002; Miller & Lacy 1993). This tool can clarify assumptions, integrate knowledge from multiple sources, force biologists to be more explicit in their reasoning, identify which model structures and parameters are important, and guide future data collection (Burgman & Possingham 2000; Walsh et al. 1995). Additionally, applying sensitivity analysis to PVA models can highlight life history stages that are particularly important to the stability and growth of a population, with important implications for conservation, biological control and sustainable extraction (Benton & Grant 1999).

Although PVA has been strongly advocated by some conservationists (e.g. Morris et al. 2002; Schemske et al. 1994), it has also been criticized because uncertainty inherent in the modeling process may make this tool more appropriate for assessing relative risks and comparing effects of management actions than for assessing absolute extinction risks and prescribing population sizes (Beissinger & Westphal 1998; Menges 2000; Reed et al. 2002; Shaffer et al. 2002; Taylor et al. 2002). PVA is also often not robust when demographic data are limited (Ruckelshaus et al. 1997), and lack of data is of particular concern for endangered species (Schemske et al. 1994). Still, conservation biology is a crisis discipline (Soulé 1985) that requires quick decisions despite incomplete data. PVA has value even when uncertainty exists (Brook et al. 2000) and still provides one of the strongest

management tools available for incorporating science into conservation decision-making (Brook et al. 2002).

Dissertation Outline

My dissertation research is organized in three parts and is described here in Chapters 2 through 4. In Chapter 2, I analyzed current forest distribution and recent trends in deforestation throughout the species' range by conducting a supervised classification of Landsat 5TM remotely-sensed imagery from 1987 and 2007. From these classified images, I created binary forest/non-forest habitat maps clipped to the GHLT range boundary and compared the overall amount and distribution of forest habitat between the two time periods. In this chapter, I also identified the habitat patch size that could support a hypothetical minimum viable population (MVP) of GHLTs under a range of risk scenarios using population viability analysis and located patches meeting those size requirements on the 2007 forest map. Landscape and demographic data generated in this chapter provided the foundation for subsequent analyses in Chapters 3 and 4.

In Chapter 3, I assessed functional landscape connectivity, according to the 2007 forest cover map, for GHLTs using a combination of circuit and graph theoretical approaches. This has important implications for metapopulation dynamics, patch colonization/extinction rates, and gene flow for the species.

In this chapter, I was also interested in exploring how the social behavior of this cooperatively breeding species could theoretically impact measurements of landscape connectivity. Measurements of functional connectivity traditionally focus

on structural landscape attributes (e.g. distance and matrix type between habitat patches) and on how species interact with those structural attributes. However, I suggest that social behaviors (specifically conspecific and heterospecific attraction) also impact connectivity by changing how dispersers move with respect to occupied patches. I again analyzed functional connectivity using circuit and graph theoretical approaches but altered dispersal rules in two additional scenarios (for a total of three scenarios). In the second scenario, I increased the cost threshold for occupied patches, allowing dispersers to move over more costly matrix to reach an occupied patch (simulating that attraction could increase landscape connectivity). I also explored a third scenario where dispersers were only motivated to move to occupied patches (simulating that attraction could decrease landscape connectivity). These scenarios were compared to the estimate of functional connectivity in the first scenario that did not consider conspecific/heterospecific attraction.

I explored the future viability of GHLT habitat and populations in Chapter 4. I used IDRISI's Land Change Modeler to explore landscape characteristics (e.g. elevation, distance from roads, etc) that were associated with recent deforestation patterns and to highlight forested areas that are vulnerable to future deforestation given these patterns. I also used population viability analysis to explore the extinction risk of known GHLT metapopulations. This chapter provides a broad discussion of GHLT extinction risk based on both ultimate and proximate threats.

Finally, in Chapter 5, I conclude my dissertation by summarizing key findings and making recommendations for future research. I also synthesize the results of Chapters 2, 3, and 4 to highlight priority habitat patches. I suggest that forest patches

that are (1) large enough to support a minimum viable population, (2) large enough to support a genetically viable population, (3) important for the maintenance of functional landscape connectivity, and/or (4) known to support populations of GHLTs are of disproportionate value for GHLT conservation. Forest patches that meet one or more of these criteria should be prioritized for research, surveys, protection, and reintroduction.

Through my dissertation research, I highlight that, despite the fact that the GHLT has been relatively secure as compared to other lion tamarin species, populations and habitat are at risk. Protective measures will be of critical importance, and I identify priority habitat areas for future research and protection while providing information for scientifically-informed conservation planning.

Chapter 2: Identifying Important Forest Patches for the Long-Term Persistence of the Endangered Golden-Headed Lion Tamarin (*Leontopithecus chrysomelas*)

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Introduction

The Atlantic Forest is one of the world's hotspots for biodiversity, providing habitat for a disproportionately high number of species and facing severe deforestation at 88.27% loss of the region's original forest cover (Myers et al. 2000; Ribeiro et al. 2009; Shi et al. 2005). Deforestation has been attributed to economic activities; 80% of Brazil's gross domestic product is generated in the Atlantic Forest through intensive timber harvest, charcoal production, cattle ranching, and monoculture plantations (Morellato & Haddad 2000; Pinto & Wey de Brito 2003). Because of the highly fragmented nature of forest patches within the Atlantic Forest, the few remaining large forest patches may be especially important for the persistence and genetic stability of a variety of forest species (Brito & Fernandez 2002; Brito & Grelle 2006; Chiarello 1999; Chiarello & de Melo 2001; Metzger et al. 2009; Vieira et al. 2009). Large patches are more likely to have enough resources to maintain self-sustaining source populations that do not rely on immigrants for population persistence (Pulliam 1988) whose individuals may then contribute to an entire regional population through dispersal and metapopulation dynamics (Hanski 1991; Radford & Bennett 2004). Such paired source-sink systems contribute positively to

metapopulation size and persistence (Howe et al. 1991), and the larger patches, sometimes termed ‘key patches’ (Verboom et al. 2001), are thus critical to landscape planning. Locating large patches within the range of a species can help to prioritize locations for surveys, research, and habitat conservation.

Golden-headed lion tamarins (GHLTs; *Leontopithecus chrysomelas*) are one of many endemic and threatened species of the Atlantic Forest. Large forest patches are especially important for this Endangered (IUCN 2010) arboreal primate that maintains large home ranges at relatively low population densities. In this chapter, my objectives were to determine (1) a range of area requirements for a self-sustaining, minimum viable population of GHLTs under various risk scenarios and (2) the location of actual patches meeting these area requirements throughout the species’ range in Brazil. A number of other landscape characteristics such as functional connectivity between habitat patches (Anzures-Dadda & Manson 2007; Fagan et al. 2002; Fahrig & Merriam 1985; Groom 1998; Root 1998), amount of edge (Lopes et al. 2009), past land-use (Metzger et al. 2009), and habitat quality within patches (Holmes & Sherry 2001) are also important for species persistence. However, incorporating these landscape characteristics is beyond the scope of this chapter but will serve as the focus of Chapter 3. Here, I propose a selective process by which key geographic areas can be quickly identified and used to direct species conservation and research efforts.

Methods

Study Species

The last published estimate of GHLT population size, based on a 1991-1993 survey, was 6,000-15,500 individuals spanning a range of 19,462 km² (Pinto & Rylands 1997). However, a more recent survey suggests the possibility of considerable reductions in population size and range since that time (Raboy unpublished data; Raboy et al. 2010). Forest cover in this region is characterized by highly fragmented seasonal semi-deciduous tropical rainforest in the west and more contiguous coastal evergreen tropical rainforest in the east. GHLTs use primary and secondary/regenerating forest as well as cabruca agroforest (Raboy & Dietz 2004; Figure 3) below 500 m elevation (Pinto & Rylands 1997). Based on a study in Una Biological Reserve, GHLTs form groups averaging five individuals (Raboy 2002). Territory size ranges between 36 ha (Rylands 1989) and 200 ha (Dietz et al. 1996a; Raboy & Dietz 2004; Raboy et al. 2004).



Figure 3. (a) A juvenile golden-headed lion tamarin (GHLT). Habitat for GHLTs includes (b) primary, (c) secondary, and (d) cabruca agroforests. (photos taken by S. Zeigler, 2006).

Determining Minimum Area Requirements

To calculate the area requirements for a minimum viable population (MVP) of GHLTs, I began by determining the MVP size in the population viability analysis (PVA) program Vortex ver9.72 (Appendix I; Lacy 2000). I define the MVP size as the smallest size at which the population is self-sustaining with a reproductive rate that exceeds mortality despite the potential effects of natural catastrophes and demographic, environmental, and genetic stochasticity, resulting in a persistent population that does not rely on immigration (Shaffer 1981).

Baseline demographic parameters for the PVA model were calculated from field observations and from published literature on GHLTs (Table 1). Field observations of the number of deaths, emigrations, immigrations, and births each year for GHLTs were made by B. E. Raboy as part of a long-term monitoring project in Una Biological Reserve. Demographic rates used in this study were based on six habituated GHLT groups observed between 1995 and 2007 as part of this monitoring project. Two of the groups were followed for 12 years, 1 group was followed for 9 years, 1 group was followed for 7 years, and 2 groups were followed for 5 years. Average mortality rate was calculated for each sex and five age classes (0-1 years, 1-2 years, 2-3 years, 3-4 years, and adults). I did not differentiate mortality rates by sex for the 0-1 age class because the sex of infants was often unknown. The fate of some individuals was unknown through the course study, and, given the high rate of mortality for individuals unable to successfully emigrate into a new group, I assumed that 75% of all disappearances were deaths except in the case of infants in the 0-1

Table 1. Parameters used in Vortex ver9.72 to model the minimum viable population size for golden-headed lion tamarins.

Parameter	Definition	Baseline Value	
Species Description			
Inbreeding Depression ¹	Considers reduction in first-year survival for inbred individuals	yes	
Number of Lethal Equivalents ¹	Average impact of inbreeding on first-year survival	4.07	
Dispersal			
		No dispersal, hypothetical single population	
Reproductive System and Rates			
Reproductive System ²	Indicates whether species is monogamous or polygynous	Monogamous	
Age First Offspring (female) ²	Age at which females begin breeding	4 years	
Age First Offspring (male) ²	Age at which males begin breeding	4 years	
Max Age Reproduction ²	Age at which individuals cease producing offspring	16 years	
Max # Progeny ³	Largest number of offspring a single female can produce in a given year	4 offspring	
1 offspring		33.3%	
2 offspring		45.5%	
3 offspring		4.5%	
4 offspring		16.7%	
Sex Ratio at Birth ²	Average percentage of newborn males born	50% males	
% Adult Females Breeding ³	Mean percentage of females that breed in a given year	82.9%	
% Males in Breeding Pool ²	Mean percentage of males that breed in a given year	100%	
Mortality			
Mortality Rates ³ (environmental variation)	Mean mortality rate for each age class in a given year	Males (EV ⁴)	Females (EV ⁴)
0-1 year old (infant)		35.0% (0%)	35.0% (0%)
1-2 years old		13.9 (0)	14.8 (13.0)
2-3 years old		4.0 (3.0)	26.5 (0)
3-4 years old		5.4 (0)	28.1 (12.1)
> 4 years old (adult)		16.2 (1.6)	13.3 (0)

¹J. Ballou personal communication, Ralls et al. 1988

²Holst et al. 2006

³B. Raboy unpublished data. Data based on observations of 6 GHLT groups (+/- 12 years). See Methods for how these rates were calculated from raw demographic data.

⁴Value of 0 indicates that all variation observed could be accounted for by demographic variance, which is automatically incorporated in Vortex.

year age class. All disappearances for infants were assumed to be deaths as individuals in this age class have never been seen emigrating alone. Mortality for the other age classes was calculated as:

$$\text{Average mortality} = (N_{\text{deaths}} + 0.75 * N_{\text{disappearances}}) / N_{\text{total}}$$

I calculated the percentage of females breeding as:

$$\text{Percentage females breeding} = N_{\text{females that had offspring}} / N_{\text{total females}}$$

Finally, females are known to produce a total of one to four offspring per reproductive year based on one to two breeding cycles in a single year. Thus, I calculated the frequency of litter sizes of one, two, three, or four offspring per female per reproductive year as:

$$\text{Frequency of litter size } i = N_{\text{litters of size } i} / N_{\text{total litters of all sizes}}$$

Here ‘litter’ is used in the language of the program used to conduct PVA modeling and reflects the number of offspring produced per female per reproductive year, not the number of offspring produced in a single reproductive event. Lion tamarins give birth to singletons or twins one or two times a year.

Total variance in mortality, frequency of females breeding, and frequency of each litter size was calculated according to Kendall (1998) while demographic and

environmental variances were calculated according to Akcakaya (2002). These values were used to incorporate demographic and environmental stochasticity separately in PVA modeling.

To determine the MVP size, I kept all baseline parameters (Table 1) the same with the exception of initial population size (N_0) and carrying capacity (K). I assumed that N_0 was at K and systematically increased these two parameters from a starting population size of five until the population had a 98% probability of persistence for 100 years (Threshold 1). I was also interested in how large a population would need to be to retain 98% of its genetic diversity, what I define as a ‘genetically viable’ population. Thus, I further increased population size until the population had both a 98% probability of persistence and maintained 98% of its genetic diversity for 100 years (Threshold 2). These thresholds have been used in previous modeling studies as the acceptable levels of risk for the species (Holst et al. 2006). For both thresholds, population size was increased in multiples of five individuals to correspond to the average GHLT group size. As social animals, a stable and self-sustaining population of GHLTs is likely composed of several groups and would be a multiple of five assuming an average group size of five. My models assumed that habitat quality and quantity did not change through time. I ultimately modeled the required size necessary for a single hypothetical population to persist with no immigration or emigration.

Simulations for four scenarios under each threshold were conducted to determine the population size necessary for recovery from catastrophes under a number of different acceptable risk levels: (1) baseline with no catastrophes; (2)

disease, 2% frequency with a 25% decrease in survival; (3) fire catastrophe, 2% frequency with a 50% reduction in survival; and (4) combination of both the fire and disease catastrophes. Fire and disease, as individual and combined threats, were modeled as catastrophes within Vortex where survival was reduced for both sexes across all age classes as specified during random catastrophe years. Reproduction remained unaffected. Because this model follows a single hypothetical population and is not spatially-explicit, catastrophes could impact any individual within the population. These particular catastrophes and the frequency and severity in which they affected the population were chosen because they have been cited in previous modeling studies as realistic for the species (Ballou et al. 1998; Holst et al. 2006; Seal et al. 1990).

For each MVP size determined in the four PVA scenarios at the two thresholds (a total of eight MVP sizes), I multiplied the population size by published density estimates for GHLTs to determine a corresponding minimum area requirement. GHLTs have been observed at high (0.1 GHLT/ha), medium (0.067 GHLT/ha) and low (0.053 GHLT/ha) densities (Holst et al. 2006), likely reflecting differences in habitat type/quality (eg. primary forest versus regenerating forest). The eight MVP sizes were multiplied by all three density estimates to determine a range of minimum area requirements due to uncertainty in density.

Analysis of the Landscape

To determine the location of patches meeting minimum area requirements, I conducted a supervised classification using the maximum likelihood algorithm (de Carvalho et al. 2004) in ENVI ver4.3 on 30x30 m resolution Landsat 5TM remotely-

sensed imagery. I performed the classification on two sets of the four overlapping Landsat scenes covering the GHLT range. In the first set, hence forth referred to as the '1987 mosaic', Landsat 5TM images were captured in September 1986, August 1988, and June 1987. The second set, the '2007 mosaic', consisted of Landsat 5TM images captured in June 2004, July 2007, August 2007, and August 2008. The four images from each time period were orthorectified to Landsat 7ETM+ imagery and mosaicked to form a single image. Pixels were classified as (1) forest, (2) non-forest, (3) clouds, (4) cloud shadows, and (5) water. GPS points for forest collected between 2005 and 2009 (Oliveira unpublished data; Raboy unpublished data) were used as training (2,146 points) and validation (2,144 points) data. A previous landscape classification by Laudau et al. (2003) provided training (701 points) and validation (701 points) data for non-forest areas. I calculated accuracy of the supervised classification with a confusion matrix (Foody 2002) and found an accuracy of 92.30% (kappa coefficient 0.80) for the 1987 mosaic and an accuracy of 93.50% (kappa coefficient 0.83) for the 2007 mosaic.

In ArcGIS ver9.3 (ESRI), areas of cloud cover were filled in using Landsat 5TM imagery from May 1994 and June 1986 for the 1987 mosaic and from June 2004, January 2005, September 2006, and April 2007 for the 2007 mosaic. The 1987 and 2007 mosaics were then processed through the majority filter to remove noise, clipped based on the boundary of the GHLT range, and grouped into patches. The range boundary to the west is based on a minimum convex polygon created from all historical past published registries of the species (Prado et al. 2003) while the Atlantic Ocean serves as the principal range boundary to the east. The Rio de Contas and Rio

Jequitinhonha rivers marked the northern and southern limits, respectively, of the species' range (Pinto & Rylands 1997). The portions of forest patches that fell outside of these boundaries were not considered in my analysis.

Cloud cover and the presence of monoculture plantations, typically not used as habitat by GHLTs, within the area of study presented two potential problems that could not be removed for subsequent analysis. Monoculture plantations were not distinguished from the forest category in my classification because of the difficulties in reliably separating these classes in this region of Brazil (Lawrence et al. 1995). However, according to a previous landscape classification, monoculture plantations represented less than 1% of the total landcover within the GHLT range in 1995 (Landau et al. 2003) and should not greatly impact my analysis. Areas covered by clouds and their shadows were removed as much as possible with the alternate imagery described above; however, some areas were covered by clouds or shadows in both sets of images. Such areas, which covered 1.68% and 1.22% of the 1987 and 2007 mosaics, respectively, were not included in my analysis.

Using these processed 1987 and 2007 mosaics, I then identified forest patches meeting the minimum area requirement for each modeling scenario and GHLT density estimate. Because GHLTs are unlikely to use forest above 500 m elevation, I also removed portions of forest patches that were above 500 m in ArcGIS using elevation data from the Shuttle Radar Topography Mission (Farr et al. 2007). I then repeated the identification of patches meeting the minimum area requirements for each modeling scenario and GHLT density estimate.

I concluded my analysis by comparing patches where I would expect to find GHLTs based on the modeling work presented here with the patches that are actually occupied by GHLTs. I overlaid 90 positive survey locations collected between 2005-2008 by the Conexão Mico Leão survey project (Neves 2008; Raboy et al. 2010) over the 2007 mosaic. ‘Positive survey locations’ included confirmed sightings of and vocalizations from GHLTs by field teams in playback studies as well as recent sightings by local residents with high forest knowledge (Raboy et al. 2010). Some survey locations did not directly align with a forest patch on my forest map (37 points), and I assigned these points to the nearest patch. In the three instances where it was not clear which patch was closest, the survey location was not included in analysis. Survey points were matched to patches on the landscape in order to determine the range of patch sizes occupied.

Results

Demographic Analysis

According to stochastic PVA analysis, at least 70 GHLTs are needed for a self-sustaining population with a 98% probability of persistence over 100 years if no catastrophes are considered. MVP sizes of 90, 170, and 250 GHLTs are needed for a population that can persist despite disease, fire, or fire with disease catastrophes, respectively (Table 2). Based on these values, habitat patches as small as 700 ha (assuming baseline scenario and high population density) and as large as 4,717 ha (assuming fire with disease scenario and low population density) would be needed to

Table 2. Minimum viable population (MVP) size and corresponding minimum area requirement for golden-headed lion tamarins (GHLT) under low (0.053 GHLT/ha), medium (0.067 GHLT/ha), and high (0.1 GHLT/ha) densities.

Scenario	MVP size (# of GHLTs)	Minimum Area Requirement (ha)			$N_{t=100}$	r (sd)	Probability of Survival (%)	Genetic Diversity (%)
		Low Density	Medium Density	High Density				
<i>Threshold 1: 98% Probability of Survival</i>								
Baseline	70	1,321	1,045	700	58	0.013 (0.085)	98.0	79.2
Disease	90	1,698	1,343	900	72	0.024 (0.091)	98.0	82.2
Fire	170	3,208	2,537	1,700	137	0.020 (0.107)	98.2	89.0
Disease with Fire	250	4,717	3,731	2,500	193	0.018 (0.114)	98.2	91.6
<i>Threshold 2: 98% Probability of Survival and Maintenance of Genetic Diversity</i>								
Baseline	780	14,717	11,642	7,800	779	0.051 (0.032)	100.0	98.0
Disease	810	15,283	12,090	8,100	785	0.043 (0.057)	100.0	98.0
Fire	920	17,358	13,731	9,200	834	0.038 (0.095)	100.0	98.0
Disease with Fire	960	18,113	14,328	9,600	837	0.026 (0.122)	100.0	98.0

support a self-sustaining GHLT population depending on the acceptable level of risk conservationists are willing to consider (Table 2).

Substantially higher population sizes are necessary to ensure that 98% of genetic heterozygosity is maintained over 100 years when various possible catastrophes are considered: 780 GHLTs (baseline), 810 GHLTs (disease), 920 GHLTs (fire), and 960 GHLTs (fire with disease; Table 2). These MVP sizes translate to habitat patches that are at least 7,800 ha (assuming baseline scenario and high population density) to 18,113 ha (assuming fire with disease scenario and low population density; Table 2).

Landscape Analysis

Between 1987 and 2007, forested area, the number of forest patches, and the average size of forest patches within the GHLT range decreased (Figure 4; Table 3). In 1987, forest covered 1,111,657 ha of the GHLT range in 17,132 patches with a mean patch size of 71 ha. The amount of forest decreased by 2007 to 965,861 ha in 15,713 patches with a mean patch size of 61 ha (Table 3). The net forest loss was 13% between 1987 and 2007. Only 5% of the 15,713 forest patches within the GHLT range in 2007 were larger than the smallest published GHLT territory size (Table 3). Thus, only a fraction of the total available forest patches are likely large enough to support even a single GHLT group.

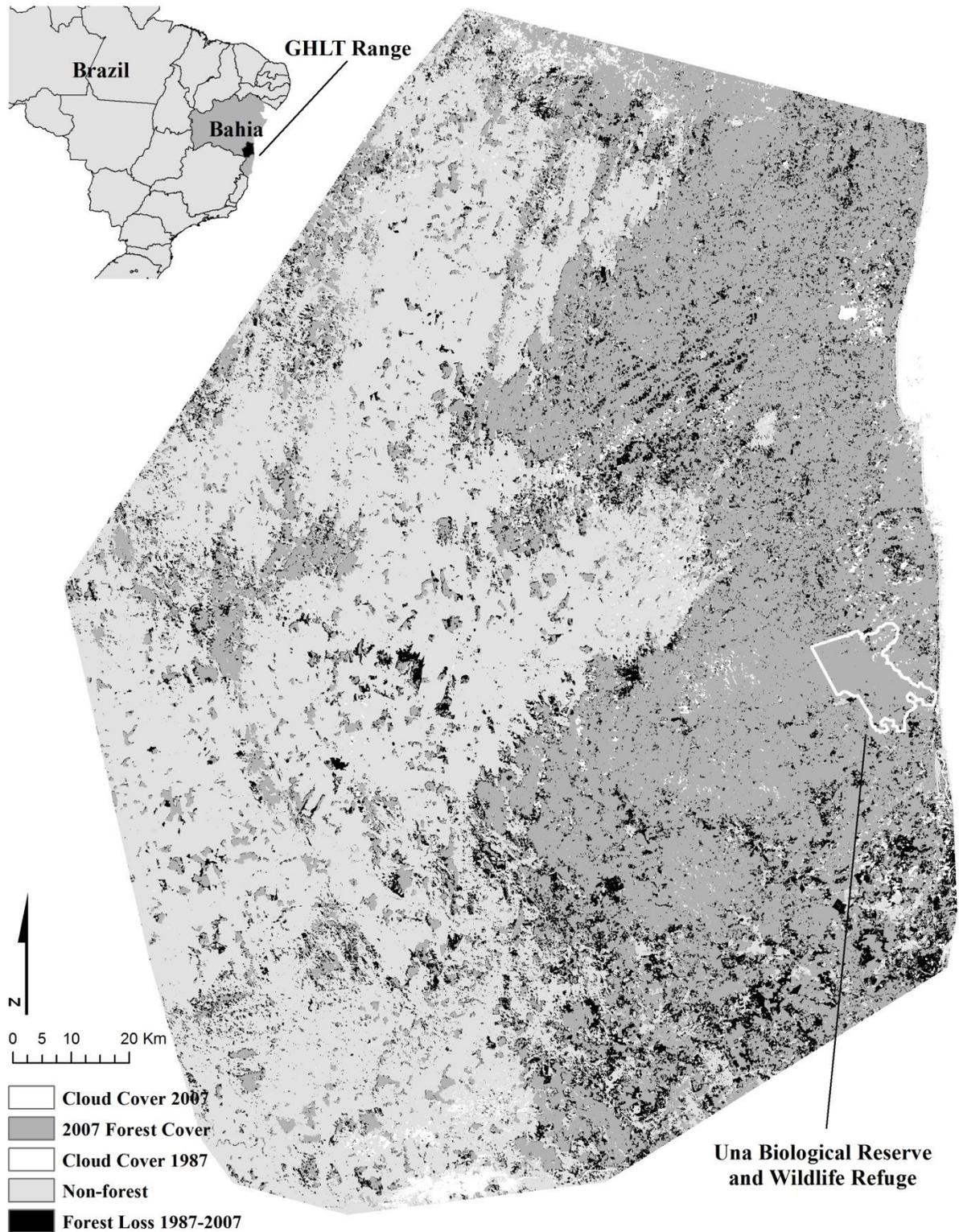


Figure 4. Deforestation between 1987 and 2007 throughout the range of the golden-headed lion tamarin in Bahia, Brazil.

Table 3. Forest cover and number of forest patches meeting area requirements for a minimum viable population under four catastrophe scenarios for the golden-headed lion tamarin (GHLT) assuming a medium density of 0.067 GHLT/ha. Numbers of patches are shown for 1987 and 2007 as well as for 2007 after all high elevation (> 500 m) forest was excluded from analysis.

Scenario	Minimum Area Requirement (ha)	Number of Patches		
		1987	2007	2007 (no high elevation forest)
Total Forested Area	-----	1,111,657 ha	965,861 ha	880,179 ha
Total Number of Patches	-----	17,132	15,713	15,502
Mean Patch Size	-----	71 ha	61 ha	-----
Number of Patches Equal to or Larger than Smallest Published Territory Size	36	810	778	742
<i>Threshold 1: 98% Probability of Survival</i>				
Baseline	1,045	27	22	18
Disease	1,343	20	20	14
Fire	2,537	7	9	5
Fire with Disease	3,731	5	6	4
<i>Threshold 2: 98% Probability of Survival and Maintenance of Genetic Diversity</i>				
Baseline	11,642	2	2	2
Disease	12,090	2	2	2
Fire	13,731	1	2	1
Fire with Disease	14,328	1	1	1

According to PVA modeling, forest patches exist within the GHLT range that could support a population of GHLTs with a 98% probability of persisting over 100 years. In 1987, assuming medium GHLT density, 27 patches (baseline), 20 patches (disease), 7 patches (fire), and 5 patches (fire with disease) were large enough to support populations under the various risk scenarios (Table 3). Due to habitat loss and fragmentation over the subsequent 20 years, the number of patches able to support the same population sizes in 2007 were 22 (baseline), 20 (disease), 9 (fire), and 6 (fire with disease; Table 3; Figure 5a).

Although the largest patch in 1987 (872,502 ha) decreased in size by 2007 (741,973 ha), it still remained the largest patch in the GHLT range. However, the identity and location of many of the other large forest patches changed throughout the 20 year span of my landscape analysis. Of the top 10 largest patches in 1987, 4 were fragmented into patches that were smaller than the 1,045 ha needed to support a self-sustaining population at baseline conditions in 2007. Two of the 10 largest patches in 1987 remained within the 10 largest patches in 2007, although these patches decreased in size between 1987 and 2007. Four of the 10 largest patches in 2007 had previously been connected to the largest patch in 1987.

Fewer patches were able to support a population that could also retain 98% of its genetic heterozygosity. In 1987, two patches were large enough to support a genetically viable population of GHLTs assuming medium GHLT density for the baseline and disease catastrophe scenarios while only one patch could support such a population under the fire and fire with disease catastrophe scenarios. These patches were very large (872,502 ha and 13,575 ha) and were located only in the eastern

portion of the species' range. In 2007, there were two patches large enough to sustain a viable GHLT population and its genetic heterozygosity assuming medium density under the baseline, disease, and fire catastrophe scenarios and one patch under the fire with disease scenario. The largest patch able to sustain a genetically viable population in 1987 (872,502 ha) was the same patch in 2007 (741,973 ha). However, the second patch able to sustain a genetically viable population in 1987 fragmented into smaller patches below the minimum area requirement while the second patch able to sustain a genetically viable population in 2007 (13,735 ha) had been part of the largest patch in 1987.

High elevation areas may limit the amount of area within a given forest patch that GHLTs can utilize. Previous studies cite that the elevation limit for the species is 500 m (Pinto & Rylands 1997). After removing forest cover above 500 m from my forest map, I found fewer patches with enough low elevation forest to sustain populations of GHLTs with a 98% probability of persistence: 18 patches (baseline), 14 (disease), 5 (fire), and 4 (fire with disease; Table 3; Figure 5b). Two patches were able to support populations with 98% probability of survival and 98% genetic heterozygosity under the baseline and disease scenarios while one patch could support such a population under the fire and fire with disease scenarios (Table 3; Figure 5b).

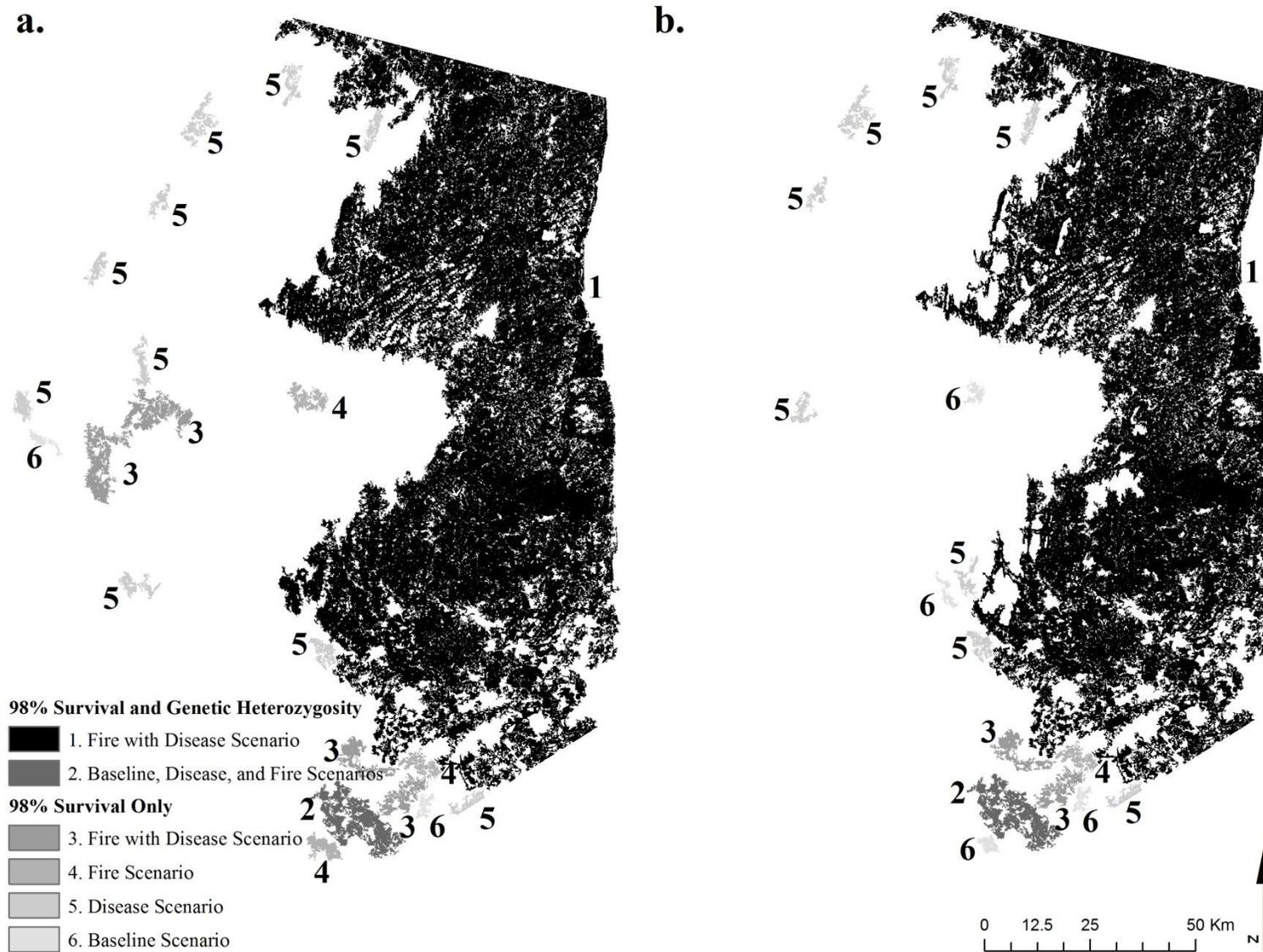


Figure 5. Forest patches meeting the minimum area requirements. Patches could support a population of golden-headed lion tamarins at medium density with a 98% probability of survival (1-6) and 98% of its original genetic heterozygosity (1, 2) for 100 years at baseline with no catastrophes (2, 6) and with a risk of disease (2, 5), fire (2, 4), and fire with disease (1, 3). (a) depicts patches considering all forest cover within the patch while (b) depicts patches after all forest above 500 m elevation was removed from the patch.

Discussion

Patch Size and Occupancy

Positive survey locations for GHLTs indicated that patch occupancy was not limited to patches meeting the minimum area requirements determined here. For the 21 occupied patches in the 2007 mosaic, 4 patches were larger than the baseline minimum area requirement of 1,045 ha, 11 patches were between 36 ha (the smallest published GHLT territory size) and 1,045 ha, and 6 patches were less than 36 ha. Small patches could have been occupied during these years for several reasons. In most of the surveys, patches were sampled one or two times, and occupancy is thus a snapshot of GHLT occupancy and movement at that time. An individual GHLT may have been in a given location temporarily as it moved between or in and out of larger forest patches in search of additional resources. Patches may have been occupied by declining populations, and positive survey locations in smaller patches may represent extinction debt (Tilman et al. 1994) or time-lags between past land use and current species dynamics (Metzger et al. 2009). Finally, smaller patches may be functionally connected, allowing GHLTs to move among patches in search of resources, and the functional size of patches may be larger than the structural size. Connectivity can be a particularly important attribute of a landscape for species survival (Arroyo-Rodriguez & Mandujano 2009), and assessing the implication of varying levels of inter-patch connectivity for GHLTs represents my next step in identifying geographic regions of the GHLT's landscape for targeted conservation action.

Deforestation and Conservation Implications

As with other studies identifying important forest patches for species survival in the Atlantic Forest (Brito & Fernandez 2002), I found only one to two forest patches (depending on risk scenario considered) that are theoretically large enough to support a genetically viable, self-sustaining population of GHLTs over 100 years. However, this should not imply that the species is secure from continuing population decline or extinction. Forest cover in this region is changing quickly. My analysis indicates a net forest loss of 13% in the GHLT range between 1987 and 2007, or 0.65% loss per year if constant deforestation rate is assumed. My estimate of loss is relatively congruent with the deforestation rate in the state of Bahia as a whole. Between 2000 and 2005, 2.2% (or 0.44% per year) was lost within the state (Fundacao SOS Mata Atlantica & INPE 2008). The Bahia biogeographical sub-region (Silva & Casteleti 2003), of which the GHLT range is a part, is the second most well-preserved sub-region in the Atlantic Forest with 17.7% of the original forest cover remaining (Ribeiro et al. 2009). It is conceivable that deforestation pressure in the more well-preserved sub-regions like Bahia will increase as what little forest remains in sub-regions like Sao Francisco (4.7% remaining forest cover) and Interior Forest (7.1% remaining forest cover) is completely lost (Ribeiro et al. 2009). In addition, a large percentage of available forest cover for use by GHLTs is currently in the form of cabruca plantations, covering 18% of the total range of the species in 1995 (Landau et al. 2003). These plantations are becoming threatened as the low price of cocoa and fungal epidemics infecting cacao trees and fruit make it more profitable for land-owners to convert their cocoa agroforestry systems to cattle pastures and other

agricultural systems of low biodiversity value (Schroth & Harvey 2007). Such land conversion would drastically reduce the amount of available habitat for GHLTs.

Although one to two forest patches in the GHLT range could theoretically support a self-sustaining, genetically viable population of GHLTs despite catastrophes, there is only one federally protected reserve known to currently support GHLTs where continuing deforestation is unlikely. A previous modeling study found that this reserve, Una Biological Reserve (Figure 4), is large enough to safeguard the species *if* the park is able to hold a high or medium density of GHLTs and forest regeneration continues to increase the park's carrying capacity as projected. However, at lower densities or when carrying capacity did not increase, genetic diversity fell below the 98% threshold (Holst et al. 2006). Fire threat was also not included in the model but may be a real and present threat given the level of farming activity bordering the reserve. Given that some of the lowest densities were observed for GHLTs within the reserve in some years (Raboy & Dietz 2004), expansion of the size of the reserve is critical.

The distribution of forest patches throughout the GHLT range is also important. A genetic study of four subpopulations of a closely related species, the golden-lion tamarin (*Leontopithecus rosalia*), showed significant differences in the total number of alleles, heterozygosity, and allelic frequency among subpopulations (Grativol et al. 2001). The smallest and largest genetic differences between populations corresponded to the smallest and largest linear distances between populations (Grativol et al. 2001). Although a genetic study has yet to be completed for GHLTs, a behavioral study comparing subpopulations in the eastern and western

portions of their range found differences in the foraging ecology of the species, suggesting adaptation to local environments (Guidorizzi 2008). It is possible that GHLTs found in the western semi-deciduous tropical rainforest are genetically distinct from individuals found in coastal evergreen tropical rainforest in the east. Thus, it may be important that large populations are protected in both the eastern and western portions of the GHLT range to ensure the conservation of the species and its genetic diversity. Currently, no patches large enough to maintain a population of GHLTs with 98% genetic heterozygosity for 100 years are found in the western portion of the species' range. In addition, habitat loss and fragmentation were considerably higher in the western portion of the range between 1987 and 2007, and, again, the only federally protected area known to currently support a population of GHLTs lies in the eastern portion of the species' range. Raboy et al. (2010) confirm that many local extinctions have already occurred in the west within the last few decades and many more are imminent.

Finally, in addition to continuing deforestation threats, PETROBRAS, a Brazilian energy company, has invested in a multimillion dollar project to construct the Southeast Northeast Interconnection Gas Pipeline (GASENE). When completed, this natural gas pipeline will run 1,387 km from Rio de Janeiro to Catu along the Atlantic coast (PETROBRAS 2006; Piquet & Miranda 2009; Tubb 2006). A section of this pipeline is slated to run through the GHLT range (Figure 6), fragmenting the largest forest patch in half through the entire length of the patch. The short-term impacts of construction and the long-term impacts of the pipeline itself on GHLT metapopulation survival and movement are currently unknown. However, the

internal fragmentation caused by this development project will likely impact the species throughout the construction zone (Goosem 2003).



Figure 6. Early construction of the PETROBRAS natural gas pipeline slated to run through the range of the golden-headed lion tamarin in Bahia, Brazil. (photos taken by S. Zeigler, 2006)

In conclusion, two large forest patches exist that could theoretically support a genetically viable, self-sustaining population of GHLTs able to recover from moderate catastrophes while one patch could support such a population under more severe catastrophes. Only one federally protected reserve known to currently support a population of GHLTs exists within the range of the species while continuing deforestation, land conversion, and construction projects such as the PETROBRAS pipeline are real and major threats to the remaining GHLT habitat patches. Research into the quality and occupancy of the largest patches highlighted here as well as additional protection of habitat needs to be a high priority for the conservation of GHLTs.

Chapter 3: Conspecific and Heterospecific Attraction in Assessments of Functional Connectivity

Introduction

Functional habitat connectivity, historically defined as the “degree to which a landscape facilitates or impedes movement among resource patches” (Taylor et al. 1993) for a given species, is often critical to the survival of populations and ultimately a species itself. Connectivity allows foraging across multiple habitats (Kozakiewicz 1995), resource supplementation and complementation (Dunning et al. 1992), recolonization of extirpated patches (Henderson et al. 1985), rescue effect of declining populations through immigration (Brown & Kodric-Brown 1977), and reduction of inbreeding depression (Richards 2000). Population persistence has been correlated with high levels of habitat connectivity for many species (e.g. Anzures-Dadda & Manson 2007; Fagan et al. 2002).

Given the importance of connectivity for population and species persistence, understanding potential movement pathways (or lack thereof) between habitat patches is essential for managing populations, especially in fragmented landscapes. As the definition suggests, measurements of functional connectivity have traditionally focused on the structural attributes of landscapes and on how individuals move in response to those attributes given species-specific movement behaviors. In these measurements, important landscape features for functional connectivity have included inter-patch / nearest neighbor distance (Goodwin & Fahrig 2002; Radford & Bennett

2004) as well as the nature of the matrix between habitat patches (Anderson et al. 2007; Ricketts 2001). Finally, the degree to which patches can be considered functionally connected depends on species-specific traits such as vagility (D'Eon et al. 2002), perceptual range (Baguette & Van Dyck 2007), and degree of habitat specialization (With & Crist 1995).

I suggest that, in addition to landscape features and the behaviors of individuals in response to those features, measurements of functional connectivity patterns should also reflect social behaviors that incorporate the motivation of individuals to disperse from and settle into a different habitat patch. In this chapter, I focus specifically on the social behaviors conspecific and heterospecific attraction (Mönkkönen 1990; Stamps 1988) and on how these behaviors could impact measurements of connectivity. In conspecific or heterospecific attraction, potential dispersers use public social information (i.e. information that is available to all individuals and is extracted from interactions with or observations of other organisms; Wagner & Danchin 2010) to inform their own dispersal and settlement decisions. If the communicated information motivates dispersers to move toward that habitat patch, occupied patches could act as magnets by drawing dispersers more often and perhaps over riskier matrix habitats (Figure 7a). This would result in movement to occupied forest patches where connectivity might not otherwise be expected, thereby increasing the overall level of functional landscape connectivity (Figure 7b). For example, certain avian species are more likely to cross forest boundaries into open matrix habitat in the presence of tufted titmice, leading to more movement between patches in risky landscapes (Sieving et al. 2004).

Conversely, dispersers may not be motivated to move to vacant, although suitable, habitat patches without conspecific or heterospecific cues (Seppänen et al. 2007). This may be especially true for species where information regarding the location of a neighboring patch is available through conspecific or heterospecific cues but is not otherwise available through visual cues (e.g. the potential disperser cannot see a neighboring patch but it is aware of its existence because it can hear calls from individuals on that neighboring patch; Fletcher & Sieving 2010). If dispersers are unmotivated to move to an unoccupied patch, there may be no connectivity where movement might otherwise be expected, leading to lower overall landscape connectivity (Figure 7c). In each case, measurements of functional connectivity patterns that include the effects of occupancy and social behavior could differ from measurements that simply incorporate landscape features.

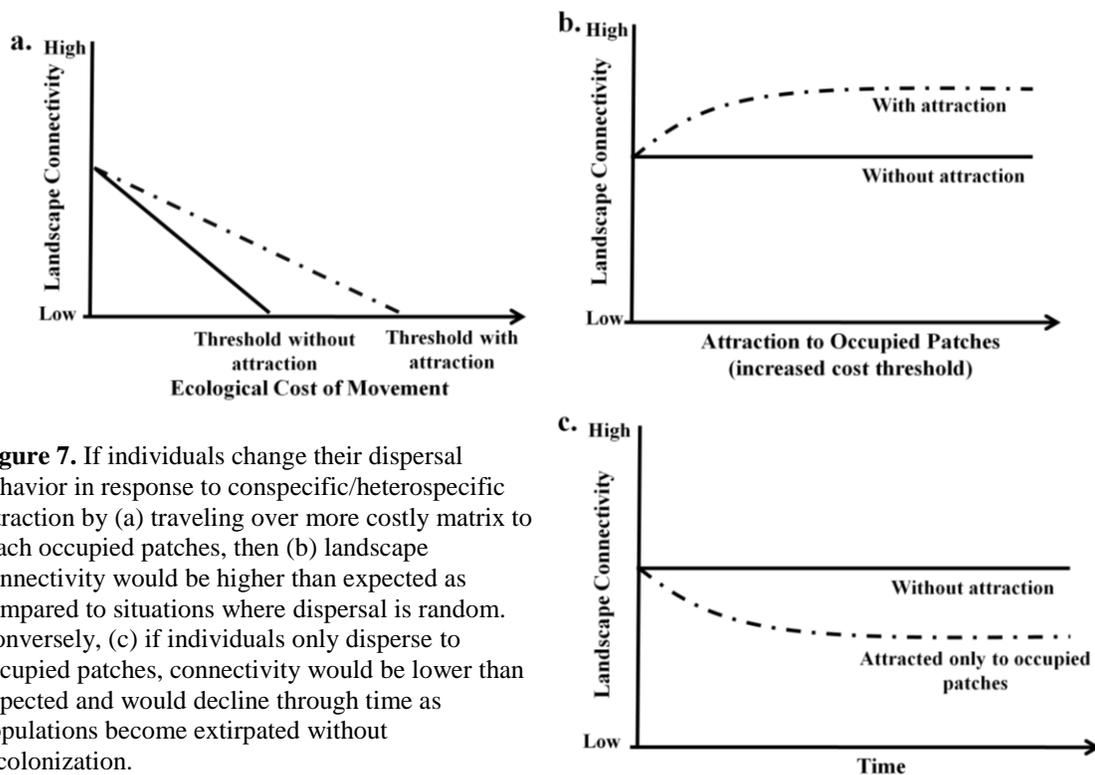


Figure 7. If individuals change their dispersal behavior in response to conspecific/heterospecific attraction by (a) traveling over more costly matrix to reach occupied patches, then (b) landscape connectivity would be higher than expected as compared to situations where dispersal is random. Conversely, (c) if individuals only disperse to occupied patches, connectivity would be lower than expected and would decline through time as populations become extirpated without recolonization.

The importance of conspecific attraction has been discussed briefly in relation to metapopulation colonization/extinction dynamics (Ray et al. 1991; Smith & Peacock 1990), but the importance of heterospecific attraction and the role of conspecific/heterospecific attraction in measurements of functional connectivity has not been examined in depth (but see Fletcher & Sieving 2010). Here I assess functional connectivity patterns, with and without conspecific/heterospecific attraction, among forested habitat patches for the Endangered (IUCN 2010) golden-headed lion tamarin (GHLT; *Leontopithecus chrysomelas*) throughout the species' range in Bahia, Brazil (Figure 8). My objectives were (1) to analyze range-wide functional connectivity for the species using traditional methodology and (2) to explore how including conspecific and heterospecific attraction could alter measurements of functional connectivity. With this chapter, it is my intention to conceptually discuss the role of social behaviors in connectivity analysis, and scenarios described here are not intended to explain the current distribution of this species.

Conspecific and Heterospecific Attraction

Many species preferentially immigrate and settle into habitat patches that are already occupied by their own species (e.g. Danchin et al. 1998; Stamps 1988). In other cases, rates of settlement and colonization appear to be enhanced by the actions or presence of heterospecifics, in particular by individuals belonging to ecologically-similar species (e.g. Mönkkönen & Forsman 2002; Parejo et al. 2004). Although the reasons for such attraction are often unclear, evidence suggests that individuals settle near conspecifics or ecologically-related heterospecifics because (1) the presence of

others acts as an indicator of habitat quality (Valone 1989) or (2) individuals benefit in some way (e.g. increased mating opportunities, foraging success, predator protection) by settling near neighbors (Alleé et al. 1949).

When dispersers use public information to assess habitat suitability, they spend less time in search of suitable habitat and thereby reduce search-related movement costs (Stamps et al. 2005). Theoretical models suggest that informed individuals should have higher fitness than individuals that disperse and settle at random (Boulinier & Danchin 1997; Fletcher 2006). Similarly, individual dispersers of species adapted to living in social groups should also benefit from moving directly into an occupied habitat patch provided they can successfully assimilate into a new group. Species form conspecific groups for benefits that include increased foraging efficiency (Terborgh 1983) or increased protection from predators (Chapman & Chapman 2000). Some species also form heterospecific (or polyspecific) associations for similar reasons. Heterospecific associations are prevalent for primates, especially between species within the family Callitrichidae which includes marmosets and tamarins (e.g. Buchanan-Smith 1990; Terborgh 1983). Such associations increase foraging efficiency as species guide each other to food sources (Terborgh 1983) and flush out insects to individuals waiting lower in the canopy (Peres 1992). Increased protection afforded by membership in heterospecific groups allows profitable foraging in otherwise less-used, riskier habitats (Bshary & Noë 1997) across a larger foraging range (Terborgh & Janson 1986). Heterospecific associations also allow for increased protection from predators through better predator detection/vigilance (Gautier-Hion et al. 1983), dilution (Hamilton 1971), and communal defense and

mobbing (Altmann 1956). Moreover, it may be more advantageous for small conspecific groups to initiate heterospecific associations as opposed to increasing conspecific group size in order to minimize intraspecific competition for mates and food (Noë & Bshary 1997; Seppänen et al. 2007). Overall, dispersers drawn to patches already occupied by resident groups of the same species or an ecologically-similar species may have a higher chance of integrating into a new social group and benefiting from the increased protection or foraging efficiency provided by that group, ultimately resulting in higher fitness for dispersers who preferentially settle in occupied patches.

Study System: Golden-Headed Lion Tamarin (GHLT)

GHLTs are arboreal primates endemic to a 19,462 km² range of the Atlantic Forest in southern Bahia, Brazil (Pinto & Rylands 1997; Figure 8). Forest cover in this region is characterized by highly fragmented seasonal semi-deciduous tropical rainforest in the west and more contiguous coastal evergreen tropical rainforest in the east.

GHLTs preferentially use primary and secondary/regenerating forest as well as cabruca agroforests (Raboy & Dietz 2004) below 500 m elevation (Pinto & Rylands 1997).

GHLTs are cooperatively breeding primates that live in conspecific groups typically consisting of a single reproductive female, one to three adult males, and their juvenile offspring (Dietz et al. 1994a). GHLTs have also been observed associating with groups of Wied's marmosets (*Callithrix kuhlii*; Oliveira 2010) more often and longer than expected by chance (Raboy 2002). In one instance, a dispersing male GHLT joined a group of Wied's marmosets where it lived for over four months

(Oliveira unpublished data). Like GHLTs, the Wied's marmosets are cooperatively breeding with groups averaging 4.3 individuals per group (Raboy 2008). Both species subsist on a diet of ripe fruits, insects, and small vertebrates (Rylands 1989). Oliveira (2010) speculates that associations between the species occur for enhanced predator protection; associations were significantly more common in habitat types with higher GHLT-predator encounters, in the first half of the day when more GHLT-predator encounters occurred, and within the first three months of a reproductive event when groups are more vulnerable predator attacks.

In cooperatively breeding species such as GHLTs, where typically only a single male and female breed per group, the need to find mating opportunities may drive an individual's decision to disperse from its natal territory. This is supported by the fact that GHLTs exhibit prospecting behaviors before making permanent dispersal decisions (Oliveira unpublished data). Although group-level immigration and emigration rates are relatively low (0.61 and 0.53 individuals/group/year, respectively), most GHLTs leave their natal territories between 2 and 4 years of age (Raboy 2002). Males and females are equally likely to disperse from their natal territories, but males are more likely to successfully emigrate into new groups (Raboy 2002). Dispersing GHLTs have been documented by Raboy (2002) traveling alone (56% of time) or in same sex pairs or trios (44%).

Less is known about how far dispersing GHLTs will travel. GHLTs spend 43% of their daily activity budget on locomotion, moving on average 1,410 m to 2,175 m per day (Raboy & Dietz 2004; Rylands 1989); however, these movements were confined to the territorial ranges of those particular groups. The majority of

evidence for long-distance dispersal movements consists of a few anecdotal observations by field researchers. Individuals have been observed on two occasions traveling over 4 km (straight line distance; Raboy 2002; Oliveira unpublished data) through forest from their natal territories. A GHLT was also observed crossing an open field, which is the matrix landcover type characteristic of this system, over a distance of 175 m (Raboy unpublished data) while a pair of golden lion tamarins (*L. rosalia*) were seen dispersing through open field over a distance of 1 km (Grativol et al. 2001). However, GHLTs are rarely seen moving through open pasture (Raboy et al. 2010; Guidorizzi unpublished data) and experts estimate that consistent movements between patches more than 100 m apart are unlikely for lion tamarins (J. Mickelberg personal communication).

Methods

Analysis of Habitat

A binary map of forest / non-forest habitat within the GHLT geographic range served as the foundation of my study of functional connectivity. This map was created through a supervised classification of Landsat 5TM remotely-sensed imagery from 2004 to 2008 (see Zeigler et al. 2010 for further details on how this map was created). To overcome processing limitations and to facilitate computations in programs used to analyze connectivity patterns, I resampled the cell size of the forest map from 30 m to 200 m and divided the GHLT range into north and south regions separated by the Rio Pardo (Figure 8). Large rivers such as the Rio de Contas and Rio Jequitinhonha

(Figure 8), which mark the northern and southern boundaries of the species' range, as well as the Rio Pardo, which roughly cuts through the center of the GHLT range, likely serve as barriers to GHLT movement (Rylands 1989). Therefore, it is unlikely that dividing the GHLT range at the Rio Pardo affected the results of the range-wide connectivity analysis. These two regions were processed separately for all subsequent analysis in my study.

From these processed maps of forest cover in the northern and southern regions of the GHLT range, I selected patches 36 ha or larger in area to serve as source patches in assessments of functional connectivity. This is the smallest recorded GHLT home range size (Rylands 1989) and represents the smallest patch size that a group of GHLTs will likely inhabit with any permanence.

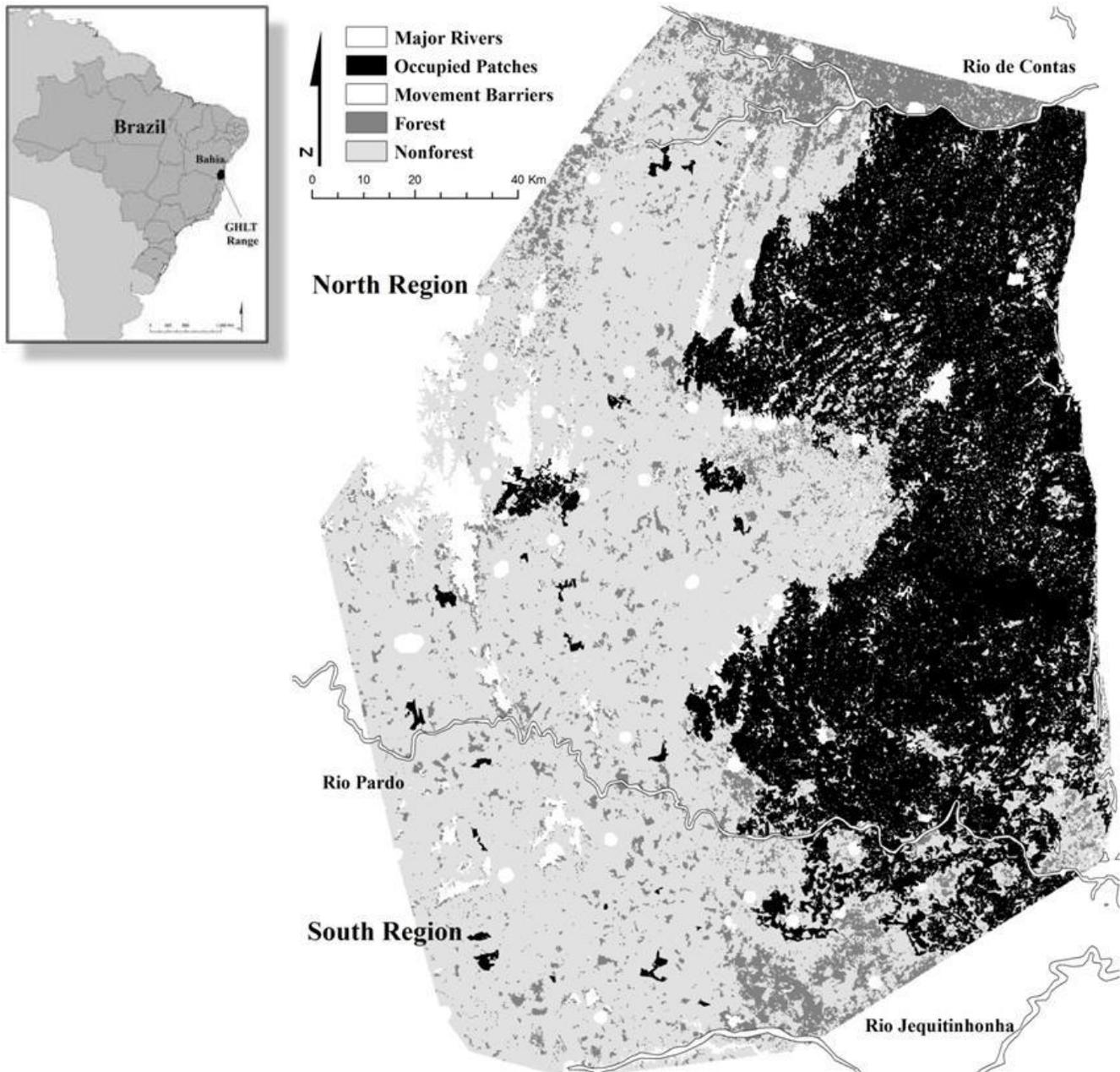


Figure 8. Resistance (ecological cost) map used in Circuitscape ver3.5 to predict the movement of GHLTs between habitat patches. Forest (dark gray) had the lowest movement resistance and non-forest (light gray) had the highest movement resistance. Areas above 500 m elevation, large rivers, and urban areas acted as barriers to movement (white). Patches displayed in black were occupied by GHLTs or Wied’s marmosets according to a 2005-2008 survey by Neves (2008) and Raboy et al. (2010).

Assessment of Movement Patterns

I examined pathways of potential GHLT movement among forest patches using Circuitscape ver3.5 (McRae 2006). Circuitscape employs the principles of circuit theory to model animal movement and considers matrix landscape features separating patches, multiple pathways between patches, and the width of those pathways to inform the likelihood that an animal will move between any two habitat patches (McRae 2006; McRae et al. 2008).

Inputs into Circuitscape were a patch identification file and a raster landscape resistance map, both of which were ASCII files exported from raster maps in ArcGIS ver9.3 (ESRI). The patch identification file contained the location and unique identification code for the 769 individual habitat patches 36 ha or larger in the landscape. In the landscape resistance map, each cell was given a resistance value associated with how easily an animal could move through that cell/landscape type with values equaling 1 (low resistance) for forest cells, 50 (high resistance) for non-forest cells, and no data (barrier to movement) for urban areas with a 1 km buffer, areas of elevation greater than 500 m, and rivers (Figure 8). Absolute resistance values were chosen arbitrarily but reflect the reduced movement (and increased resistance) for individuals in non-forest matrix. Observations and expert opinion suggest that predation levels are higher and that GHLTs, as arboreal primates, are much less likely to move through the open pasture that dominates the matrix in this landscape as compared to forest (Raboy et al. 2010; Guidorizzi unpublished data; Raboy personal communication). Studies assessing the sensitivity of least-cost routes of animal movement found that such models are most sensitive to the relative values

of landcover types in the matrix and not the values distinguishing habitat and inhospitable matrix types (Rayfield et al. 2010). Similarly, Lee-Yaw et al. (2009) found that models of connectivity for wood frogs were most sensitive to absolute dispersal barriers, not the resistance values given to landscape variables. Because I incorporated movement barriers and only a single matrix type, I do not believe that absolute resistance values arbitrarily chosen here will greatly impact connectivity results.

The final output of my analysis in Circuitscape was a unitless ‘resistance distance’ between every pair of patches. The resistance distance is a composite of Euclidean distance, number of possible pathways, width of those pathways, and ecological cost of traveling between a given pair of forest patches (McRae 2006). Thus, patches with low resistance distance values (values approaching 0) are close together, have multiple wide movement pathways, and have little hostile matrix between them. Resistance distance values were used as inputs in all three connectivity modeling scenarios (see below).

I also examined movement pathways in terms of Euclidean distance between patches in Circuitscape for one of the scenarios (see below). Methods previously described in Circuitscape were repeated, but the analysis of movement pathways was capped at distance thresholds of 50 m, 100 m, 500 m, 1 km, and 5 km while the cost of those pathways was ignored (e.g. at a distance threshold of 50 m, movement between patches occurred only between pairs of patches separated by an edge-to-edge distance of 50 m or less). The resulting output from Circuitscape indicated whether any pair of patches was connected by movement at each distance threshold,

irrespective of cost but limited by movement barriers (urban areas, rivers, and high elevation).

Assessment of Functional Connectivity

To assess functional connectivity, I used a graph theoretical approach (Urban & Keitt 2001) in the program Conefor Sensinode ver2.2 (Saura & Torne 2009). Input files for Conefor Sensinode were a patch identification file from Circuitscape and a file containing the distance between pairs of habitat patches. Depending on the scenario, either the resistance distance matrices or Euclidean distance matrices created in Circuitscape were used as the ‘distances’ between pairs of habitat patches.

I determined eight metrics of landscape connectivity within Conefor Sensinode: number of links among patches, number of components, area of the largest component, average area of all components, number/percentage of patches in the largest component, number/percentage of isolated patches, and the integral index of connectivity (IIC; Table 4). IIC (Pascual-Hortal & Saura 2006) was calculated as:

$$IIC = \frac{\left(\sum_{i=1}^n \sum_{j=1}^n (a_i * a_j) / (1 + nl_{ij}) \right)}{A_L^2}$$

where n is the total number of patches in the landscape, a_i and a_j are the areas of patch i and patch j respectively, nl_{ij} is the number of links in the shortest path between patches i and j , and A_L is the total size of the landscape. This metric is based on the habitat availability concept where the patch itself is a space within which connectivity occurs, integrating both inter- and intra-patch connectivity in the measure of total landscape connectivity.

Table 4. Metrics used to measure functional landscape connectivity for golden-headed lion tamarins in Bahia, Brazil.

Metric	Value if No Connectivity		Value if Total Connectivity		Behavior with Increasing Connectivity:
	North	South	North	South	
Number of Links	0	0	∞	∞	Increases
Number of Components	540	229	1	1	Decreases
Size of Largest Component	654,256 ha	44,204 ha	812,816 ha	116,988 ha	Increases
Average Component Size	235 ha	87 ha	812,816 ha	116,988 ha	Increases
Number (Percentage) of Patches in Largest Component	1 (0.1%)	1 (0.4%)	540 (100%)	229 (100%)	Increases (Increases)
Number (Percentage) of Isolated Patches	540 (100%)	229 (100%)	0 (0%)	0 (0%)	Decreases (Decreases)
Integral Index of Connectivity (IIC)	0	0	1	1	Increases

Connectivity Modeling Scenarios

I modeled functional landscape connectivity under three scenarios:

1. *Scenario One: General Functional Landscape Connectivity.* Functional landscape connectivity was based only on landscape features, and conspecific/heterospecific attraction was not considered. Dispersal could occur between any pair of patches falling within given resistance distance and Euclidean distance thresholds. It is unknown how costly is too costly when it comes to dispersal decisions across matrix for GHLTs, and some dispersers

may be more willing to cross hostile matrix than others. Such dispersers may travel farther across open pasture, allowing connections between patches with high resistance distance values. Other dispersers may only travel between patches where forested stepping stones reduce movement costs, allowing connections only between patches with low resistance distance values. There is also uncertainty surrounding how far GHLTs will disperse across open matrix between habitat patches. Thus, I examined connectivity patterns at multiple resistance distance and Euclidean distance thresholds to explore the consequences of varying opportunities for dispersal between patches and expect connectivity to increase with increasing thresholds.

2. *Scenario Two: Dispersers Increase Resistance Distance Threshold in Response to Attraction.* I assumed that a disperser, responding to conspecific/heterospecific attraction, would risk higher movement costs to reach an occupied patch. Thus, the resistance distance threshold would increase due to conspecific/heterospecific attraction. I modeled this possible scenario by first assuming a baseline resistance distance threshold of one (i.e. any pair of patches, irrespective of occupancy, was considered connected if it was separated by a resistance distance value of one or less). I then assumed that occupied patches would draw dispersers across higher resistance distance thresholds. For example, in the simulation where the threshold for occupied patches was increased to five, a pair of patches could be considered connected if it met one of two criteria: (1) the pair was separated by a resistance distance value of one or less OR (2) the pair was separated by a resistance distance

value of five or less and one of those patches was occupied. Simulations were repeated such that the resistance distance threshold for occupied patches was increased to 10, 20, 30, or 40.

3. *Scenario Three: Dispersers Only Move Between Occupied Patches.* I assumed that dispersers would only move to occupied patches in response to conspecific/heterospecific attraction. Thus, connectivity could only occur for pairs of patches that fell within the maximum resistance distance threshold AND where one of those patches was occupied.

Scenarios two and three explored possible ways in which conspecific/heterospecific attraction could impact connectivity measures, and patch occupancy by GHLTs and/or Weid's marmosets was important for these two scenarios. Patches were considered occupied by GHLTs and/or Wied's marmosets based on positive survey results between 2005 and 2008 by Neves (2008) and Raboy et al. (2010; Figure 8). I did not differentiate between patch occupancy by GHLTs versus Wied's marmosets because the relative strength of conspecific versus heterospecific attraction is unknown and because the overall known level of occupancy throughout the landscape is low. Because my analysis employs a graph theoretical framework and is not a simulation of metapopulation dynamics, occupancy does not change through time to reflect colonization and local extinction of patches.

Results

Scenario One: General Functional Landscape Connectivity

Functional landscape connectivity for the GHLT was extremely low according to the IIC metric (all distance thresholds) and at small resistance distance and Euclidean distance thresholds for all other metrics (Figure 9) in both the north (Table 5) and south (Table 6) regions. The number of components and the number/percentage of isolated patches decreased while the number of links, average component size, largest component size, and number/percentage of patches connected to the largest component increased dramatically with increasing resistance and Euclidean distance thresholds (Table 5; Table 6; Figure 9). According to IIC, connectivity also increased with increasing resistance distance and Euclidean distance thresholds, although less substantially (Table 5; Table 6). Critical distances, where connectivity did not increase appreciably with further increases in distance, were at a resistance distance of 30 and at a Euclidean distance above 5 km (Figure 9).

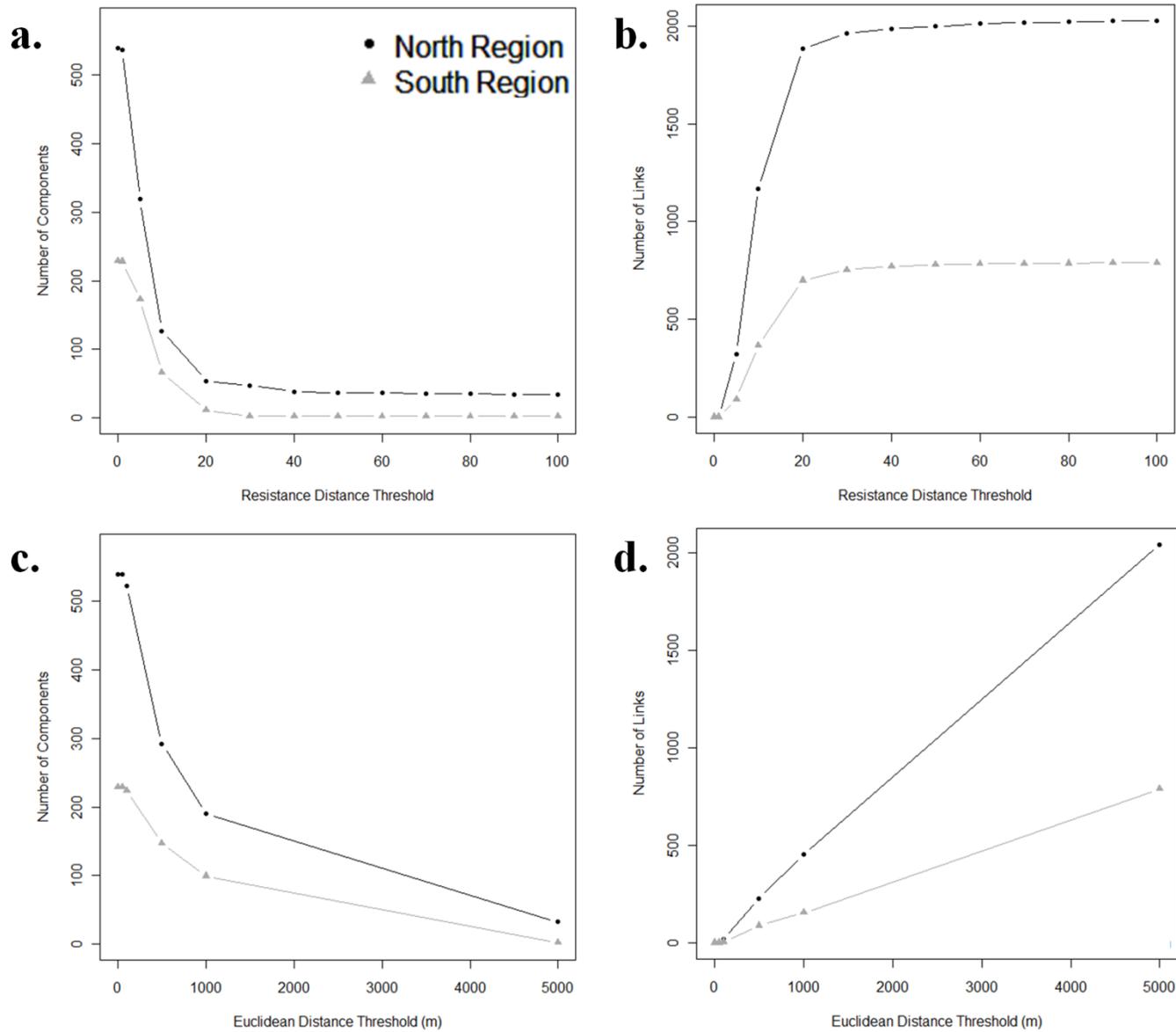


Figure 9. Range-wide functional connectivity, as measured by (a, c) the number of components and (b, d) the number of links among habitat patches for golden-headed lion tamarins in the north (circles) and south (triangles) regions of the species' range at varying (a, b) resistance distance and (c, d) Euclidean distance thresholds.

Table 5. Metrics describing functional habitat connectivity for golden-headed lion tamarins in the region north of the Rio Pardo in Bahia, Brazil at varying resistance distance and Euclidean distance thresholds.

Distance	IIC	Size of Largest Component (ha)	Average Component Size (ha)		Patches in Largest Component		Isolated Patches (no links)	
			With Largest Component	Without Largest Component ¹	Number	%	Number	%
<i>Resistance Distance (unitless)</i>								
0	0.131	654,256	540	249	1	< 1	540	100
1	0.135	674812	1,468	212	1	< 1	536	99
5	0.138	694,336	2,471	295	118	22	270	50
10	0.142	731,016	6,206	454	328	61	95	18
20	0.145	772,364	14,596	299	470	87	48	9
30	0.145	772,912	16,771	333	475	88	41	8
40	0.145	776,388	20,743	320	486	90	33	6
50	0.145	776,760	21,895	327	491	91	33	6
60	0.145	776,760	21,895	327	491	91	33	6
70	0.145	776,824	22,521	335	492	91	32	6
80	0.145	776,824	22,521	335	492	91	32	6
90	0.145	776,888	23,183	343	493	91	31	6
100	0.145	776,888	23,183	343	493	91	31	6
200	0.145	776,980	23,885	351	494	91	30	6
300	0.145	777,044	24,632	361	495	92	29	5
<i>Distance (m)</i>								
0	0.131	654,256	1,462	249	1	< 1	540	100
50	0.131	654,256	1,462	249	1	< 1	538	99.6
100	0.131	654,860	1,507	255	6	1	511	95
500	0.137	688,420	2,699	243	102	19	225	42
1000	0.138	695,416	4,147	490	144	27	124	23
5000	0.145	772,240	24,632	515	495	92	29	5

¹Because the area of the largest component was so much larger than the next largest component (due to the substantial area of the largest patch in the landscape), I calculated the average component area with and without the largest component to eliminate the effect of that component on average area.

Table 6. Metrics describing functional habitat connectivity for golden-headed lion tamarins in the region south of the Rio Pardo in Bahia, Brazil at varying resistance distance and Euclidean distance thresholds.

Distance	IIC	Size of Largest Component (ha)	Average Component Size (ha)		Patches in Largest Component		Isolated Patches (no links)	
			<i>With Largest Component</i>	<i>Without Largest Component²</i>	<i>Number</i>	<i>%</i>	<i>Number</i>	<i>%</i>
<i>Resistance Distance (unitless)</i>								
0	0.008	44,204	469	277	1	< 1	229	100
1	0.009	50,944	471	248	1	< 1	227	99
5	0.014	80,648	620	154	43	19	159	69
10	0.014	83,832	1,626	361	77	34	43	19
20	0.016	105,608	9,754	168	212	93	7	3
30 ¹	0.016	107,248	53,646	44	228	99.6	1	< 1
<i>Distance (m)</i>								
0	0.008	44,204	469	277	1	< 1	229	100
50	0.008	44,204	469	277	1	< 1	229	100
100	0.008	44,848	479	280	3	1	220	96
500	0.013	78,252	730	199	41	18	115	50
1000	0.014	81,132	1,084	267	51	22	61	27
5000	0.016	107,248	53,646	44	228	99.6	1	< 1

¹Results same for all resistance distances between 30 and 300.

²Because the area of the largest component was so much larger than the next largest component (due to the substantial area of the largest patch in the landscape), I calculated the average component area with and without the largest component to eliminate the effect of that component on average area.

Scenario Two: Dispersers Increase Resistance Distance Threshold in Response to Attraction

Functional connectivity increased for both the north and south regions as resistance distance threshold was increased for occupied patches (Figure 10). In this scenario where dispersers crossed more hostile matrix to reach an occupied patch in response to conspecific/heterospecific attraction, connectivity measurements were substantially higher compared to measurements not including attraction.

Scenario Three: Dispersers Only Move to Occupied Patches

Connectivity decreased for both the north and south regions as dispersal was limited to occupied patches (as compared to connectivity when dispersal could occur between any pair of patches within the resistance distance threshold; Figure 11). In this scenario, where dispersers limited dispersal decisions in response to conspecific/heterospecific attraction, connectivity measurements were dramatically lower than expected as compared to measurements not including attraction.

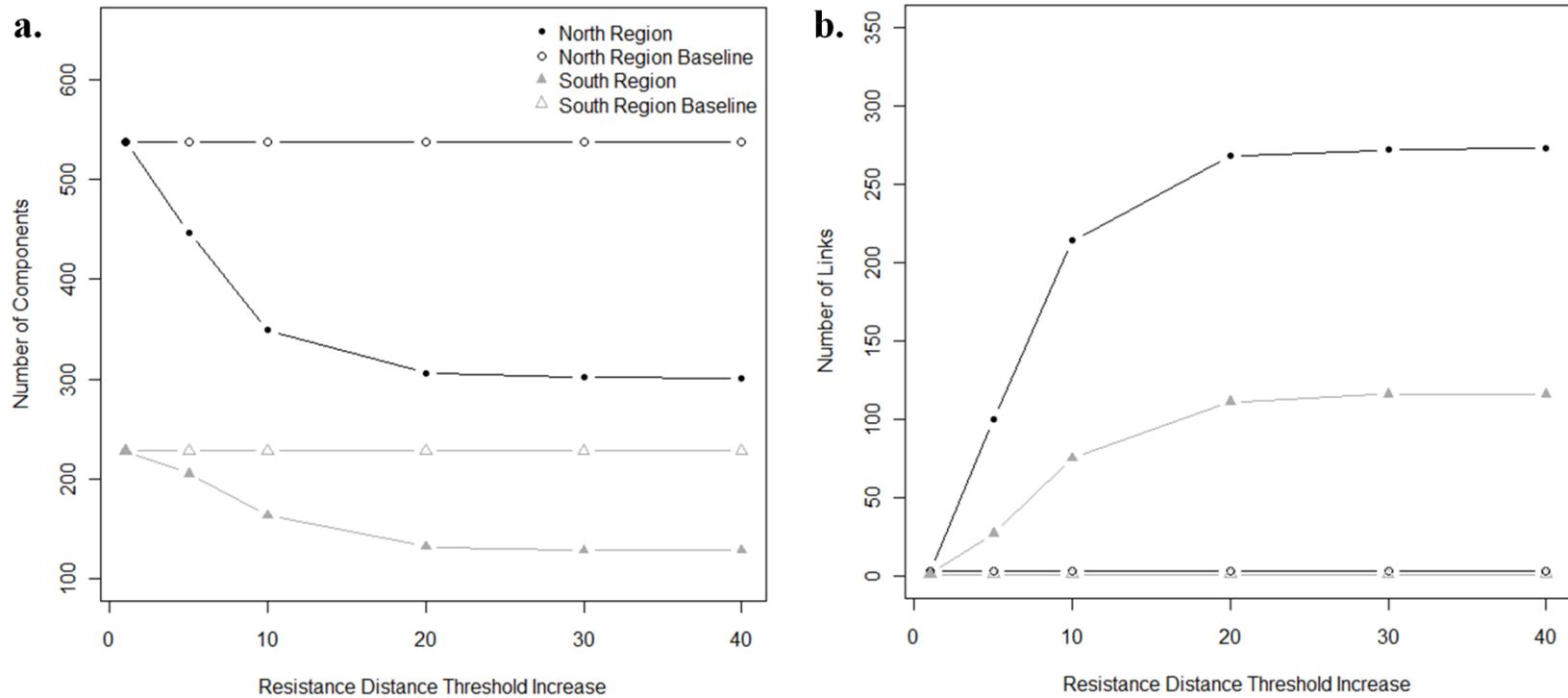


Figure 10. Functional connectivity, as measured by (a) the number of components and (b) the number of links among habitat patches in the north (circles) and south (triangles) regions of the species' range, for golden-headed lion tamarins. Connectivity models assumed that dispersers are willing to move across more costly matrix to reach occupied patches in response to conspecific/heterospecific attraction (scenario two; closed symbols) as compared to the baseline scenario of random dispersal at a constant cost threshold of one (open symbols).

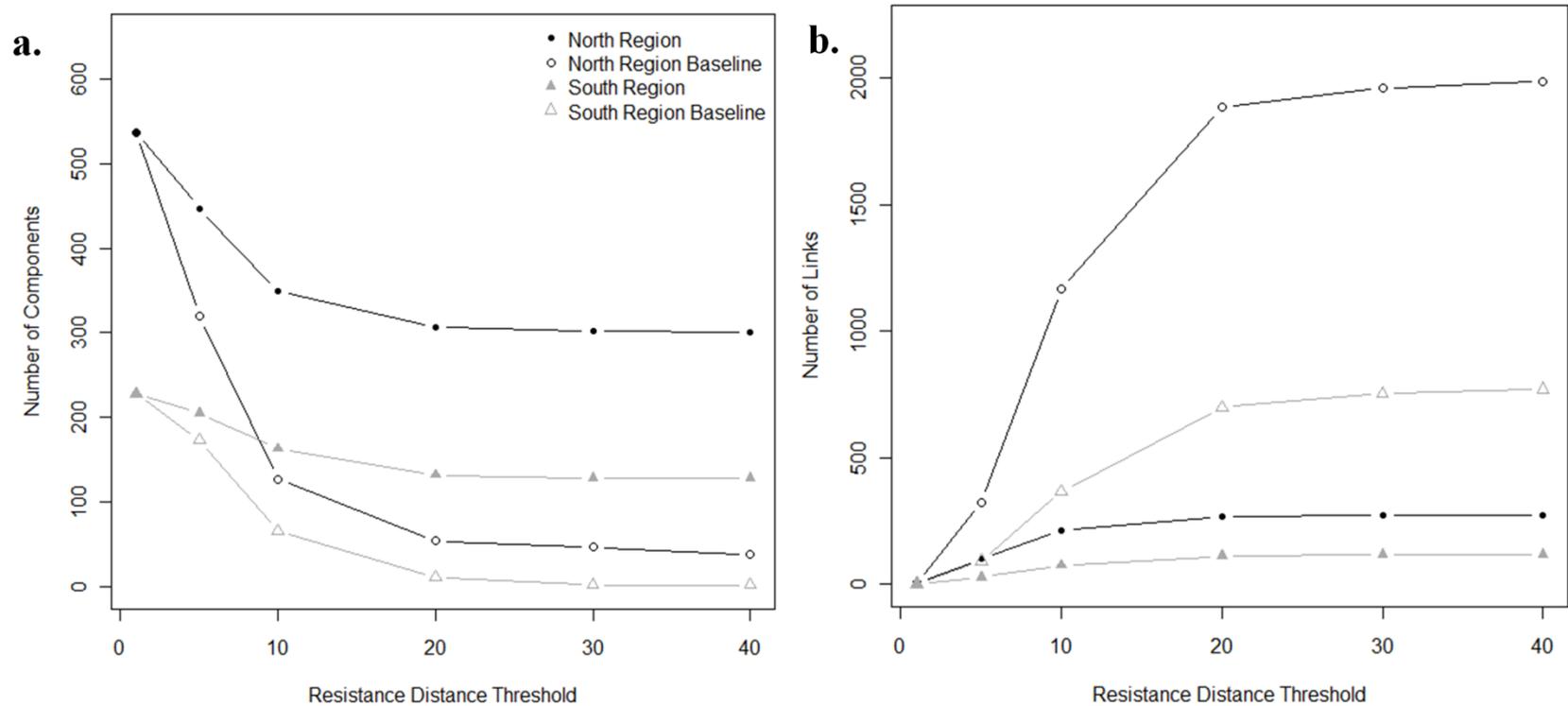


Figure 11. Functional connectivity, as measured by (a) the number of components and (b) the number of links among habitat patches in the north (circles) and south (triangles) regions of the species' range, for golden-headed lion tamarins. Connectivity models assumed that dispersers would only move to occupied patches in response to conspecific/heterospecific attraction (scenario three; closed symbols) as compared to the baseline scenario of random dispersal at equivalent distance thresholds (open symbols).

Discussion

General Functional Landscape Connectivity

Realistic distance thresholds for GHLTs are most likely between 1 and 5 (resistance distance) and between 100 m and 1 km (Euclidean distance). At these thresholds, range-wide functional landscape connectivity for GHLTs is low. Average component sizes (excluding the area of the component that contained the very large eastern patch) ranged from 154 ha to 295 ha with 50% to 99% of patches isolated at resistance distances between 1 and 5. For Euclidean distances between 100 m and 1 km, average component size (not including the largest component) ranged from 255 ha to 490 ha with 23% to 95% of patches isolated. This low level of connectivity, and associated low level of consistent inter-patch movement, may have important implications for the survival of the GHLT metapopulation by not allowing access to multiple habitats and resources (Dunning et al. 1992; Kozakiewicz 1995), the rescue of declining populations through immigration and increased genetic heterozygosity (Brown & Kodric-Brown 1977; Richards 2000), and recolonization of extirpated patches (Henderson et al. 1985). Local extinctions are expected to occur, ultimately resulting in a range contraction as populations along the edge of the geographic range are lost without recolonization (Channell & Lomolino 2000a, b; Lomolino & Channell 1995). A contraction at the southwestern portion of the species' range, where habitat loss and fragmentation have been especially high, was observed in recent years (Raboy et al. 2010; Raboy unpublished data), and loss of connectivity may be responsible for this pattern. Studies that examine how connectivity has

changed in that area of range reduction represent possible future directions for research.

In addition, Zeigler et al. (2010) found that only a small percentage of forest patches (22 out of 15,713; 0.14%) in the GHLT range are large enough on their own to support a viable population that is not reliant on the influx of new immigrants. An even smaller percentage of forest patches (2 out of 15,713; 0.01%) can support genetically viable populations of GHLTs. Even at a Euclidean distance threshold of 1 km, an optimistic distance for how far a GHLT will travel through non-forest matrix, the average component size (excluding the largest component) is 490 ha and 267 ha north and south of the Rio Pardo, respectively. Thus, even allowing for resource acquisition by movement between patches, the combined component area available for most populations of GHLTs is likely much lower than the 1,045 ha required to support a viable population of GHLTs. Relatively isolated populations restricted to small patches or components of patches, without the influx of new immigrants or additional space to allow for population expansion, will quickly become vulnerable to extinction through demographic and environmental stochasticity, genetic drift, inbreeding depression, and Alleé effects (Ellstrand & Elam 1993; Oostermeijer et al. 2003). Because little opportunity may exist for consistent inter-patch movement over areas large enough to support a viable population, large habitat patches are of critical importance for the conservation of the species (Zeigler et al. 2010).

Social Behavior in Measures of Connectivity

Predicted connectivity patterns changed as I incorporated conspecific/heterospecific attraction into my analysis. If, as in scenario two, dispersers change their behavior by

traveling across more hostile matrix to reach occupied patches, functional landscape connectivity would increase relative to scenario one where social behavior was not considered. Conversely, if dispersers only move between occupied patches (scenario three), functional connectivity would be lower than expected, especially in landscapes where only a small percentage of all patches are occupied. Neighboring patches separated by short distances and mildly hostile matrix, a situation where some connectivity may be expected, may have no exchange of individuals if one of those patches is unoccupied. Over longer time frames, as individuals preferentially choose to settle in occupied habitat patches, metapopulation extinction/colonization dynamics will be strikingly different as well (Smith & Peacock 1990). For example, new individuals dispersing into already occupied patches may provide a rescue effect for those populations while vacant patches with otherwise suitable habitat remain vacant. Populations would quickly become aggregated in response to conspecific/heterospecific attraction (Seppänen et al. 2007), resulting in the distributional patterns that have been observed for the Columbian ground squirrel (Weddell 1991), bobolink, and savanna sparrow (Nocera et al. 2006). Ultimately, extinction rates for existing populations and colonization rates in vacant habitat patches will be lower than expected with random dispersal (Ray et al. 1991; Smith & Peacock 1990). Such changes in metapopulation dynamics and distributional patterns may have severe consequences for the extinction risk of GHLTs and other organisms where conspecific/heterospecific attraction influences movement decisions. As fragmentation and the distance between habitat patches in the landscape increases, the distance between patches may become too large, and

potential dispersers may not be able to perceive the social stimuli that indicates a neighboring patch is occupied, thereby further depressing dispersal and colonization rates (Ray et al. 1991). Over time, individuals would eventually be found in a few populations and habitat patches, increasing the probability of simultaneous extinction due to stochasticity (Gilpin 1990).

Study Limitations: Perceptual Range

One important consideration not explicitly incorporated into my analysis of functional connectivity is the perceptual range of the species. A species' perceptual range defines the "fraction of the landscape that is both detectable and accessible via movement, and therefore defines the spatial scale at which an individual interacts with the landscape" (Olden et al. 2004). Most studies of perceptual range focus on a species' ability to visually perceive landscape elements (e.g. Mech & Zollner 2002); however, in the case of conspecific/heterospecific attraction, perceptual range would refer to a disperser's ability to see, hear or smell other individuals in the landscape. Long-range communication among callitrichid primates occurs through vocal signals called 'long-calls'. Long-calls are used to defend territories against other groups, to maintain group cohesion, and to attract mates (reviewed in Snowdon et al. 1986). In addition, a number of studies have found that different callitrichid species share vocal signals (Epple 1969) and respond to each other's vocalizations as often as they respond to conspecific vocalizations (e.g. Porter 2001), facilitating coordination between heterospecific groups.

In my study system, auditory stimuli would most likely influence long-distance attraction of dispersers to other GHLTs or marmosets (and occupied habitat

patches). Attraction will only occur, and can only impact connectivity patterns, within the auditory perceptual range of the species. However, it is not clear how close a dispersing GHLT would need to be to an occupied habitat patch to hear other monkeys and to perceive that the patch is in fact occupied. This uncertainty limits my ability to understand the degree to which conspecific or heterospecific attraction impacts movement decisions and overall connectivity patterns in this landscape.

Perceptual range is also context-dependent (Zollner & Lima 1997). For example, the olfactory-based perceptual range of cactus bugs (*Chelinidea vittiger*) was dependent on the size of the target habitat patch, matrix structure, and the direction of the habitat patch relative to prevailing winds because of how scent travels in the system (Schooley & Wiens 2003). In the case of GHLTs, conspecific or heterospecific vocalizations may travel farther in open pasture than they would in dense forest canopy, and the perceptual range of the species may change depending on surrounding landcover type.

Conclusions

Traditional measurements of functional connectivity considering only patch size, location, and surrounding matrix do not capture the movement dynamics and distributional patterns seen in real systems (Winfree et al. 2005). Like Fletcher and Sieving (2010), I suggest that social behaviors and the transfer of information between conspecifics and/or heterospecifics interact with structural connectivity to influence functional connectivity for certain species. In cases where dispersers cross more hostile matrix to reach occupied patches or travel only to occupied patches,

measurements of functional connectivity would be different than expected in cases of random dispersal, as explored with GHLTs in this chapter. I recommend that conspecific/heterospecific attraction be further researched in the context of connectivity in future field studies and that attraction be explored in measurements of connectivity for social species and species that utilize public information.

Chapter 4: Assessing Range-Wide Deforestation Vulnerability and Extinction Risk of Small Golden-Headed Lion Tamarin (*Leontopithecus chrysomelas*) Metapopulations

Introduction

Population declines and species extinctions are often the result of complex combinations of ultimate and proximate forces. In most examples of species extinctions, an ultimate deterministic agent of decline first forces a contraction in range size, number of populations, and number of individuals (Simberloff 1986). Agents of decline are typically one (or more) of Diamond's (1989) 'evil quartet' of overkill, habitat destruction and fragmentation, invasive species, or chains of extinctions. After the ultimate drivers dramatically reduce the number and size of populations, proximate drivers of extinction (Simberloff 1986) eliminate the last remaining individuals through demographic stochasticity, genetic deterioration, catastrophic extrinsic forces, or social dysfunction (Caughley 1994; Simberloff 1986). In addition, cascading effects caused by synergies among ultimate and proximate drivers of extinction can radically accelerate population declines and time to extinction (i.e. the extinction vortex; Brook et al. 2008; Fagan & Holmes 2006; Gilpin & Soulé 1986).

For the Endangered (IUCN 2010) golden-headed lion tamarin (GHLT; *Leontopithecus chrysomelas*), the ultimate cause of population decline has been the loss and fragmentation of habitat. This species is endemic to a small area of Brazil's Atlantic Forest (Figure 12), a threatened biome that currently retains only 11.73% of

its original forest cover in primarily small (< 50 ha) and often degraded fragments (Ribeiro et al. 2009). Within the GHLT geographic range, Zeigler et al. (2010) found that the region experienced a net forest loss of 13% as well as a decrease in the number and mean size of forest patches between 1987 and 2007. Today, functional connectivity among remaining forest patches is low (Chapter 3) and few of these patches are large enough to support a viable population of GHLTs with high genetic diversity (Zeigler et al. 2010). Deforestation throughout Brazil's Atlantic Forest has been attributed primarily to clear cutting for economic activities like timber harvest, charcoal production, cattle ranching, and monoculture plantations (Morellato & Haddad 2000; Pinto & Wey de Brito 2003) and has been linked to widespread extinctions and population declines for a variety of other species (Chiarello 1999; Pardini et al. 2005; Uezu et al. 2005).

Despite intense threats to GHLT survival, this species is considered the least threatened of the four lion tamarin species of the genus *Leontopithecus* endemic to the Atlantic Forest; GHLTs have an estimated population size of 6,000-15,500 individuals spanning a range of 14,962 km² according to a 1991-1993 survey (Pinto & Rylands 1997). The GHLT's three congeners have been driven precariously close to extinction by habitat loss and fragmentation. The golden lion tamarin (*L. rosalia*) was recently upgraded to Endangered status after over 30 years of intensive conservation effort, and today only an estimated 1,000 individuals remain in 104.5 km² of forest. Because of extensive deforestation throughout the species' range, very little opportunity exists for population expansion, and the population would remain below the minimum viable size even if all currently available habitat becomes

occupied (Kierulff et al. 2008a). The black lion tamarin (*L. chrysopygus*) is listed as Endangered with an estimated 1,000 individuals surviving in 11 isolated populations, 10 of which are not considered viable in the mid- to long-term (Kierulff et al. 2008c). Finally, the black-faced lion tamarin (*L. caissara*) has an estimated 260 individuals in 3 populations and is listed as Critically Endangered (Kierulff et al. 2008b). The history and current status of the GHLT's three congeners provide a cautionary lesson for what can be expected if habitat and populations are not immediately protected.

The Bahia biogeographical sub-region, of which the GHLT range is a part, is considered the most well-preserved sub-region in the Atlantic Forest (Ribeiro et al. 2009; Silva & Casteleti 2003). The slower rate of deforestation, and ultimately the higher abundance of GHLTs compared to other lion tamarins, has been attributed to the fact that cocoa production is a major economic activity in this region. In southern Bahia, cocoa is produced through an agroforestry system known as 'cabruca' that maintains a tall native tree canopy to shade cacao trees planted in the understory. Because a native tree canopy persists, cabruca is of high biodiversity value (Alves 1990; Faria et al. 2006) and is considered important habitat for GHLTs (Oliveira 2010; Raboy et al. 2004). Cabruca agroforests covered 18% of the species' range in 1995 (Landau et al. 2003) and are estimated to support a large portion of the remaining wild GHLT population (Rylands & Pinto 1991).

Despite the former relative security of the species compared to other lion tamarins, persistence of cabruca agroforest and remaining native forest cover in southern Bahia is uncertain, as is the fate of GHLTs reliant on this forest. Because the price of cocoa has fallen dramatically and the fungal epidemic witch's broom,

which can only be controlled through costly manual trimming and burning, is destroying healthy cacao trees, it is becoming increasingly more profitable for farmers to clear cut their land for timber sale (Alger & Caldas 1994) or for conversion to cattle pasture or other agricultural systems of low biodiversity value (Schroth & Harvey 2007).

Given the uncertain future of remaining habitat for GHLTs, understanding which currently forested areas are particularly vulnerable to future deforestation is of conservation priority. In addition, while the ramifications of habitat loss and fragmentation as ultimate agents of decline are fairly clear, vulnerability of GHLT populations due to proximate threats related to small population size are not. Understanding risk as a result of both ultimate and proximate drivers of extinction and to the synergistic interplay of these forces is especially important to proactively protect existing habitat and populations, preventing GHLTs from succumbing to the same fate as the three other lion tamarin species. The objectives of this chapter are to (1) understand landscape characteristics associated with recent deforestation patterns throughout the GHLT range; (2) identify forested areas that are vulnerable to deforestation in the future; and (3) determine the local extinction risk for small, otherwise isolated metapopulations of GHLTs.

Methods

Vulnerability to Future Deforestation

I used IDRISI's Land Change Modeler (LCM; Clark Labs) extension for ArcGIS ver9.3 (ESRI) to understand patterns of forest cover and to predict vulnerability of

current cover to future deforestation. The extension integrates historical landcover change patterns between two user-specified time periods and landscape characteristics associated with those patterns to project future patterns of (and vulnerability to) change (see Appendix III for a detailed description of LCM).

I analyzed historical deforestation patterns between 1987 and 2007 using binary forest/non-forest landcover maps created through a supervised classification of Landsat 5TM remotely-sensed imagery from 1986-1988 ('1987 forest map') and from 2004-2008 ('2007 forest map'; see Zeigler et al. 2010 for further details on how maps were created). These maps served as base landcover maps for analysis in LCM.

In LCM, I investigated the explanatory power of landscape characteristics for elevation (0 - 1,171 m; Farr et al. 2007), human population density (0 - 449 people per square km; CIESIN et al. 2005), distance from cities (0 - 24,809 m; Prado et al. 2003), distance from major roads (0 - 10,859 m; Prado et al. 2003), and distance from previously cleared areas (0 - 2,603 m; according to the 1987 forest cover map) on past deforestation trends using the Cramer's V statistic. This statistic indicates the degree to which each landscape characteristic is associated with the distribution of forest. Only elevation, human population density, and distance from previously cleared areas had Cramer's V values greater than the threshold of 0.15 recommended by Clark Labs (Clark Labs 2007) and were used in my subsequent model of vulnerability to deforestation. These layers acted as the 'potential drivers of change' in LCM.

I then calculated a transition potential matrix using a multi-layer perceptron (MLP) neural network (Atkinson & Tatnall 1997) in LCM. The MLP chose a

random sample of cells that transitioned from forest to non-forest as well as a sample of cells that persisted as forest between the 1987 and 2007 forest maps. It used half of these samples as training data to develop a multivariate function that predicted each forest cell's potential for change to non-forest based on that cell's values for associated landcover characteristics (distance from previously cleared areas, elevation, and human population density) while reserving the second half of the samples for validation. The MLP assigned weights to each landcover characteristic (representing the strength of that characteristic's association with the distribution of forest) and adjusted those weights following each iteration as the model 'learned' by minimizing error between the training and validation samples. I used a sample size of 10,000 cells, a learning rate of 0.001, and a momentum factor of 0.5 in the MLP model. The resulting multivariate function, following 10,000 iterations, had an accuracy of 75% and was then applied to the remaining cells to produce a transition potential matrix for every forest cell in the 2007 forest map.

Finally, I used the transition potential matrix in LCM to create a map depicting the relative vulnerability of forest cells in 2007 to conversion to non-forest in the future. In this map, each 30 m cell that was classified as forest in 2007 was given a relative vulnerability index value ranging from 0 (no vulnerability to deforestation) to 100 (highest vulnerability to deforestation) based on underlying landcover characteristics (elevation, human population density, distance from previously cleared areas) at that location. I further processed this map such that cells with a vulnerability index ranging from 0 – 33 had low relative deforestation vulnerability, cells with an index ranging from 34 – 66 had medium relative

deforestation vulnerability, and cells with an index ranging from 67 – 100 had high relative deforestation vulnerability.

GHLT Population Viability

Because I was interested in the vulnerability of GHLTs to both ultimate and proximate threats, I also examined the viability of metapopulations on small, relatively isolated habitat patches. I modeled the viability of GHLT metapopulations inhabiting a subset of forest patches known to be occupied according to prior surveys and landscape analyses. According to Zeigler et al. (2010), 21 forest patches in the 2007 forest map were occupied based on the most recent GHLT surveys by Raboy et al. (2010) and Neves (2008; Figure 12). One of these patches was the largest forest patch in the GHLT range at 741,973 ha, which is large enough to support a genetically viable population of GHLTs over 100 years (Zeigler et al. 2010). An additional ten occupied patches were functionally connected to this extremely large habitat patch within a Euclidean distance threshold of 1 km (Chapter 3), and GHLT populations on these occupied patches will likely persist with continuing immigration from stable source populations inhabiting the large patch. The remaining ten occupied patches were relatively isolated and small, characteristic of the majority of forest patches in the GHLT range (Zeigler et al. 2010; Chapter 3), and I focused population modeling in this chapter on populations inhabiting those forest patches (Figure 13).

To delineate areas for population modeling, I calculated the Euclidean distance between every pair of forest patches on the 2007 forest map in ArcGIS and used the graph theory program Conefor Sensinode ver2.2 (Saura & Torne 2009) to

identify components of patches functionally connected within 1 km. Components containing 1 of the 10 occupied patches of interest were subset from the main landcover map in ArcGIS for spatially-explicit population modeling (Figure 13; Table 7).

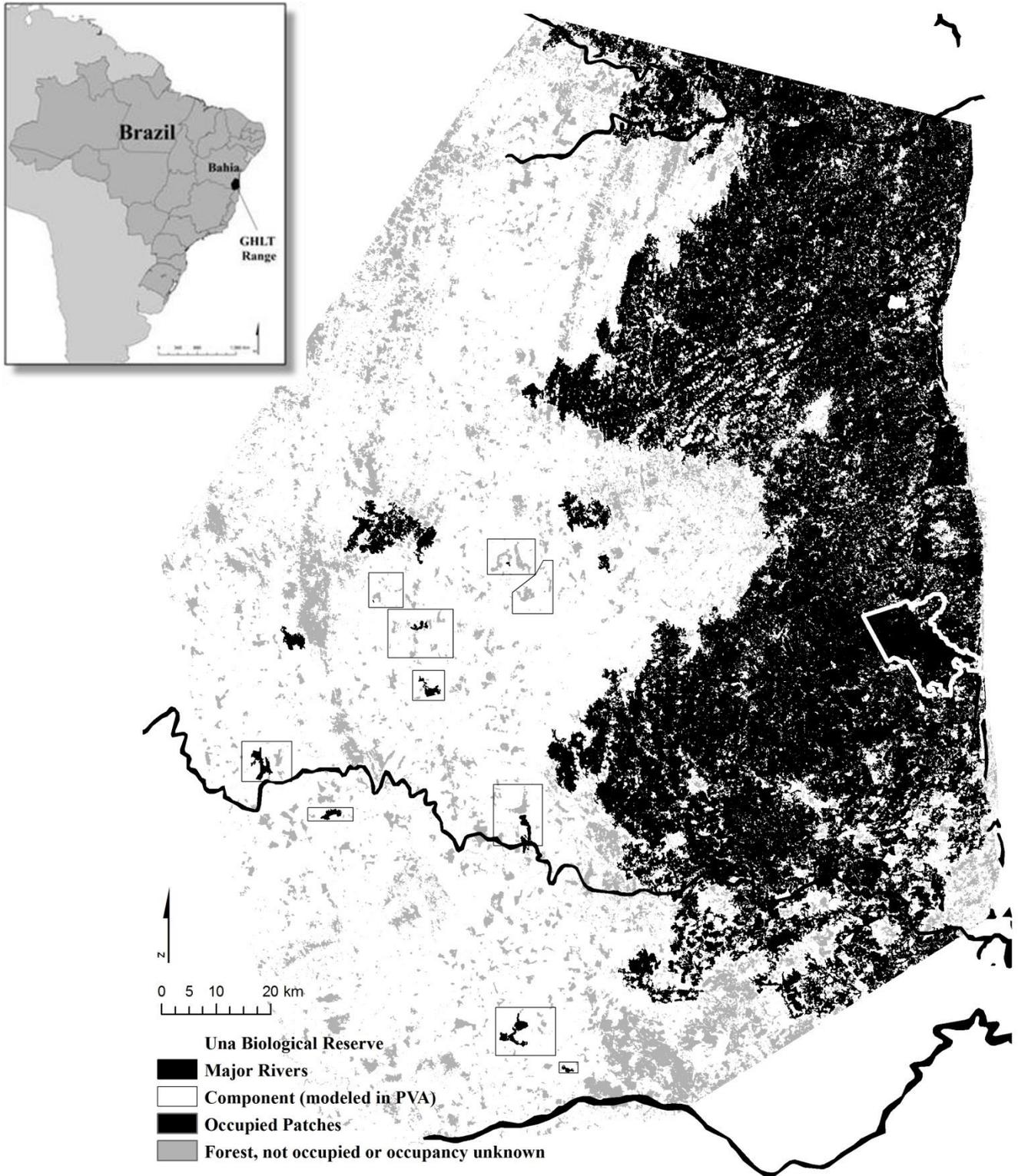


Figure 12. Forest patches occupied by golden-headed lion tamarins (GHLT; shown in black) according to surveys between 2005-2008 by Raboy et al. (2010) and Neves (2008). I modeled the viability of small metapopulations (circled in black) not connected to populations on the large eastern patch. Populations on occupied patches not circled in black are functionally connected to the large eastern patch and are likely to persist with continued immigration from source populations on that large patch.

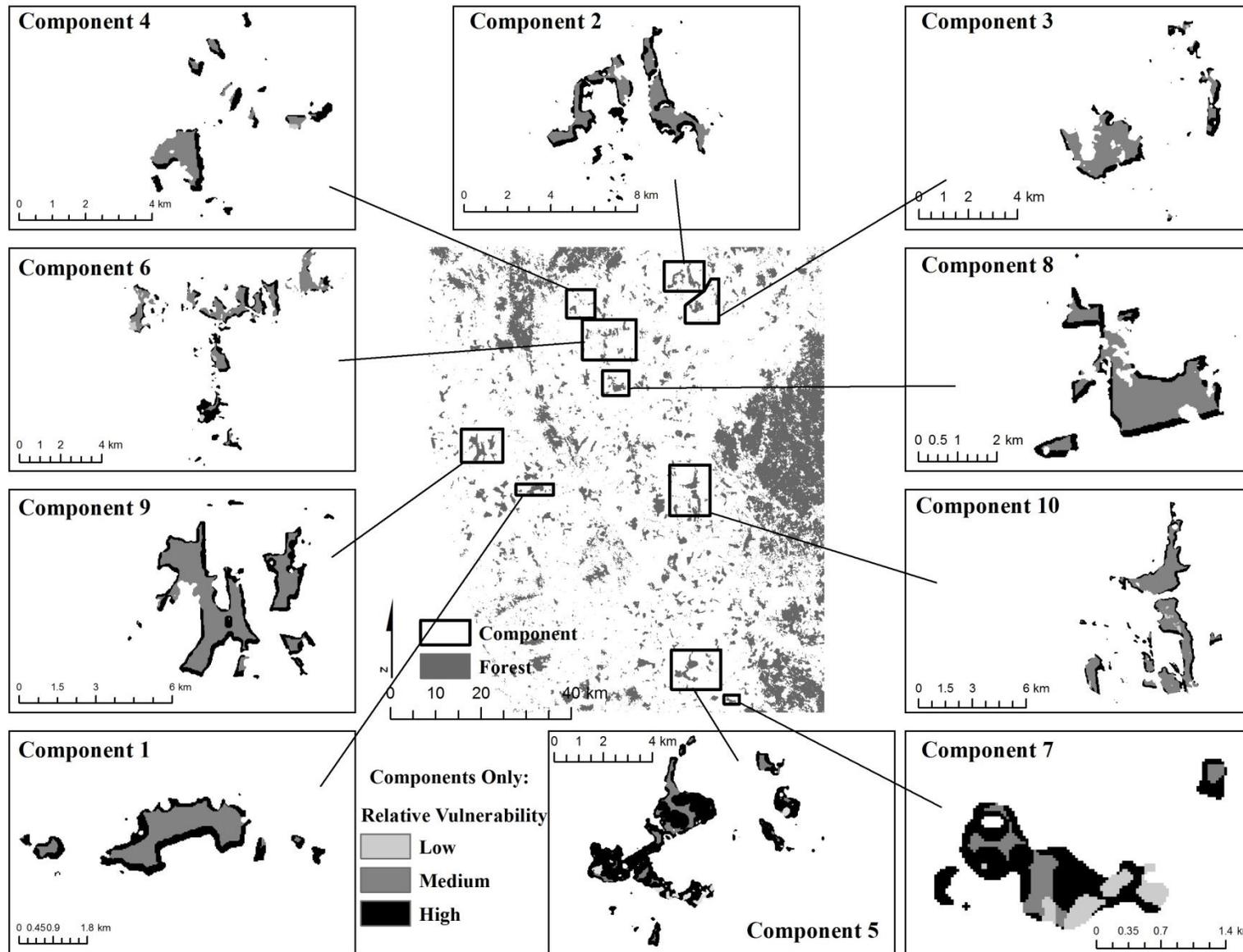


Figure 13. Habitat components used in this study to delineate and model metapopulations of golden-headed lion tamarins in Vortex ver9.98. Components consist of (1) select forest patches known to be occupied according to 2005-2008 surveys by Raboy et al. (2010) and Neves (2008) and (2) neighboring forest patches that are functionally connected within 1 km according to graph theory.

Table 7. Physical characteristics of components used to define and to model metapopulations of golden-headed lion tamarins in RAMAS GIS ver5.0 and Vortex ver9.98.

Component	Total Forest (ha)	Number of Patches	Number of Patches > 36 ha ¹	Area of Largest Patch (ha)	Number of Populations	Carrying Capacity (# of GHLTs)
1	471	10	1	394	4	45
2	1007	34	3	423	6	98
3	610	18	2	440	4	60
4	293	20	1	159	6	26
5	1211	21	4	924	7	118
6	991	52	7	244	10	85
7	153	4	1	134	2	14
8	564	13	2	478	4	56
9	1307	15	3	896	5	128
10	1424	28	4	579	7	134

¹36 ha is the smallest recorded GHLT territory size (Rylands 1989) and the smallest patch size likely to support a population of GHLTs for any length of time.

I then conducted population viability analysis (PVA) modeling for each metapopulation on the components of interest using a combination of the programs RAMAS GIS ver5.0 (Akcakaya & Root 2005) and Vortex ver9.98 (Figure 14; Miller & Lacy 2005). RAMAS GIS is a spatially-explicit PVA program designed to link GIS-generated spatial data to demographic metapopulation models for extinction risk assessment and operates through interactions between five sub-programs (Akcakaya 2005). Vortex is an individual-based PVA program that simulates effects of both deterministic forces and demographic, environmental, and genetic stochastic events to assess extinction risk (Miller & Lacy 2005). Both programs have been used to model a wide variety of species and validated for predictive accuracy (Brook et al. 2000).

**RAMAS GIS ver5.0
Spatial Sub-Program**

- ↓
- Calculates Spatial Structure:**
- Aggregation of patches
 - Assignment of populations
 - Carrying capacity
 - Distance between patches
 - Distance-dependent dispersal rates

Vortex ver9.98

- ↑
- Increases Population Size:**
- Reproduction / births
 - Immigration
-
- Reduces Population Size or Rate of Population Growth:**
- Stage-specific mortality
 - Mortality in dispersal
 - Emigration
 - Alleé effects
 - Density dependence
 - Inbreeding depression

- Deforestation Models (reduces K):**
- No future deforestation
 - 0.65% forest loss per year
 - 1.3% forest loss per year

- Results:**
- Final population size
 - Risk of extinction
 - Genetic diversity

Figure 14. Schematic of methodology used to model the extinction risk of small metapopulations of golden-headed lion tamarins in RAMAS GIS ver5.0 and Vortex ver9.98.

In RAMAS GIS, I used the spatial sub-program to calculate spatially-explicit parameters that I then used in Vortex to structure populations. Parameters calculated in RAMAS GIS included the number of populations (or size of metapopulation) a component could support, carrying capacity of individual patches, distance between patches within a component, and distance-dependent probability of dispersal among patches within a component. After defining GHLT breeding habitat as forest below 500 m elevation, I aggregated adjacent breeding habitat cells (8-neighbor rule) into distinct habitat patches and assigned a population to each patch with a carrying capacity of at least one individual. I assumed that the carrying capacity of each patch was based on a density of 0.1 GHLTs/ha, the highest density observed in the field and the most likely density of small, degraded patches typical of the western GHLT range (Holst et al. 2006; Rylands 1989). Finally, the edge-to-edge distance between patches was calculated in RAMAS GIS and used to determine the probability of dispersal between populations according to the negative exponential function (Wolfenbarger 1946):

$$M_{ij} = e^{-\frac{D}{b}}$$

where M_{ij} is the proportion of individuals that disperse between patches i and j , D is the distance between patches i and j , and b is the average dispersal distance GHLTs typically travel between patches. This function was used to calculate dispersal probability up to some maximum dispersal distance, D_{\max} . I assumed that GHLTs could disperse as far as 1 km between habitat patches (D_{\max}), the longest documented distance a lion tamarin has traveled over open field (Grativol et al. 2001), but that

most GHLTs only move up to 100 m between patches (*b*; J. Mickelberg personal communication).

I then combined information about the spatial structure of components and their GHLT metapopulations with demographic information in Vortex to assess population viability (see Appendix I for program algorithm and Appendix II for full model parameterization). GHLT survival and reproductive rates used in Vortex were based on field observations on the number of deaths, emigrations, immigrations, births, and reproducing females by B. Raboy as part of a long-term monitoring project in Una Biological Reserve (see Zeigler et al. 2010 for detailed demographic calculations). I assumed that density dependence acted under a ceiling model to reduce population size near carrying capacity and that Alleé effects (Alleé et al. 1949) further reduced population size at very low population sizes. In Vortex, ceiling density dependence is automatically modeled by truncating populations greater than carrying capacity at the end of each year while Alleé effects are modeled by reducing the percentage of females breeding at low population densities. I incorporated inbreeding depression, which increases the probability that inbred offspring will die within their first year. I also assumed that both demographic and environmental stochasticity act on populations. Metapopulations were initialized in a stable stage distribution and an initial population size at carrying capacity.

I used distance-dependent dispersal rates calculated in RAMAS GIS to inform dispersal in Vortex. In the five instances (metapopulations on components 2, 3, 4, 5, and 9) where the percentage of dispersers leaving a single population was greater than 25% of the total population size according to the distance-dependent dispersal

equation, I reduced emigration rates from that population to 25%. This prevented the majority of individuals in the population from emigrating, an unlikely situation in the wild. In addition, I multiplied dispersal rates by the ratio of population size to carrying capacity so that dispersal rates were highest as the population size approached carrying capacity. A higher mortality rate (50%) was imposed on dispersers, and I restricted dispersal to individuals age two years and older (Raboy 2002; Raboy unpublished data).

I modeled metapopulation dynamics for each component under three landscape scenarios in Vortex to explore the ramifications of varying levels of continued forest loss:

1. Forest cover does not change in the future.
2. Forest continues to be lost at the recent deforestation rate of 0.65% per year (Zeigler et al. 2010).
3. Forest continues to be lost at twice the recent deforestation rate per year.

Forest loss was modeled by decreasing carrying capacity by either 0.65% or 1.3% per year for every population within each metapopulation over the course of the 100 year simulation.

I modeled stochastic population dynamics for 100 years with 1,000 iterations. I noted the deterministic rate of population growth as well as the stochastic average probability of local extinction, median time to local extinction, percentage genetic heterozygosity remaining, and average final population abundance after 100 years.

Sensitivity Analysis

I conducted sensitivity analysis in Vortex to explore the importance of certain parameters on estimates of extinction risk. By identifying model parameters that have a disproportionately strong impact on population trajectories (e.g. specific life history stages), sensitivity analysis can direct management actions and research efforts (Crouse et al. 1987; Mills & Lindberg 2002). It can also highlight the impact of parameter uncertainty on estimates of extinction risk and other model results.

Uncertainty is inherently part of any predictive demographic model and can occur for a number of reasons. Model parameters may have been calculated from limited field data over short time periods with large sampling error or from field data that are not representative of long-term averages or future conditions. In addition, data necessary to calculate parameters may never have been measured at all, and modelers must use values based on expert opinion or anecdotal evidence (Miller & Lacy 2005).

Sensitivity analysis can quantify the impact of parameter uncertainty on modeling results.

To test model sensitivity, I independently varied values for the Alleé parameter, percentage of females breeding, correlation in environmental variation among populations, maximum age of reproduction, disperser survival rate, minimum disperser age, and dispersal rates within a range of values realistic for the species. These parameters were specifically chosen for sensitivity testing because of uncertainty in the values used in the baseline models. I used logistic regression to examine if changes in the values for each parameter were significantly correlated with changes in extinction risk (Cross & Beissinger 2001; McCarthy et al. 1995, 1996).

Results

Vulnerability to Deforestation

I found that elevation, human population density, and distance from previously cleared areas were strongly associated with the distribution of forest in landcover maps while distance from roads and distance from cities were not (Table 8). Distance from previously cleared areas had a substantially greater association with forest cover than all other landscape characteristics. Accordingly, forested areas in regions with low elevation, high human population density, and short distances from previously cleared areas were particularly vulnerable to deforestation in the future (Figure 13; Figure 15). The majority of forest (65% of forest area) had a medium relative deforestation vulnerability index ranging between 33 - 66, although a large percentage of forest (34% of forest area) had a high relative deforestation vulnerability index ranging between 67 - 100 (Figure 16).

Table 8. Landscape characteristics explored in Land Change Modeler (LCM; Clark Labs) as potential drivers of change. Variables with a high Cramer's V statistic (greater than 0.15 as recommended by Clark Labs (2007)) were strongly associated with the distribution of forest cover in 2007 and were subsequently used to model future deforestation vulnerability.

Variable	Cramer's V Statistic (Forest)	Included in Transition Model?
Distance from previously cleared areas	0.7248	Y
Distance from cities	0.1245	N
Distance from roads	0.0754	N
Elevation	0.3957	Y
Human population density	0.3662	Y

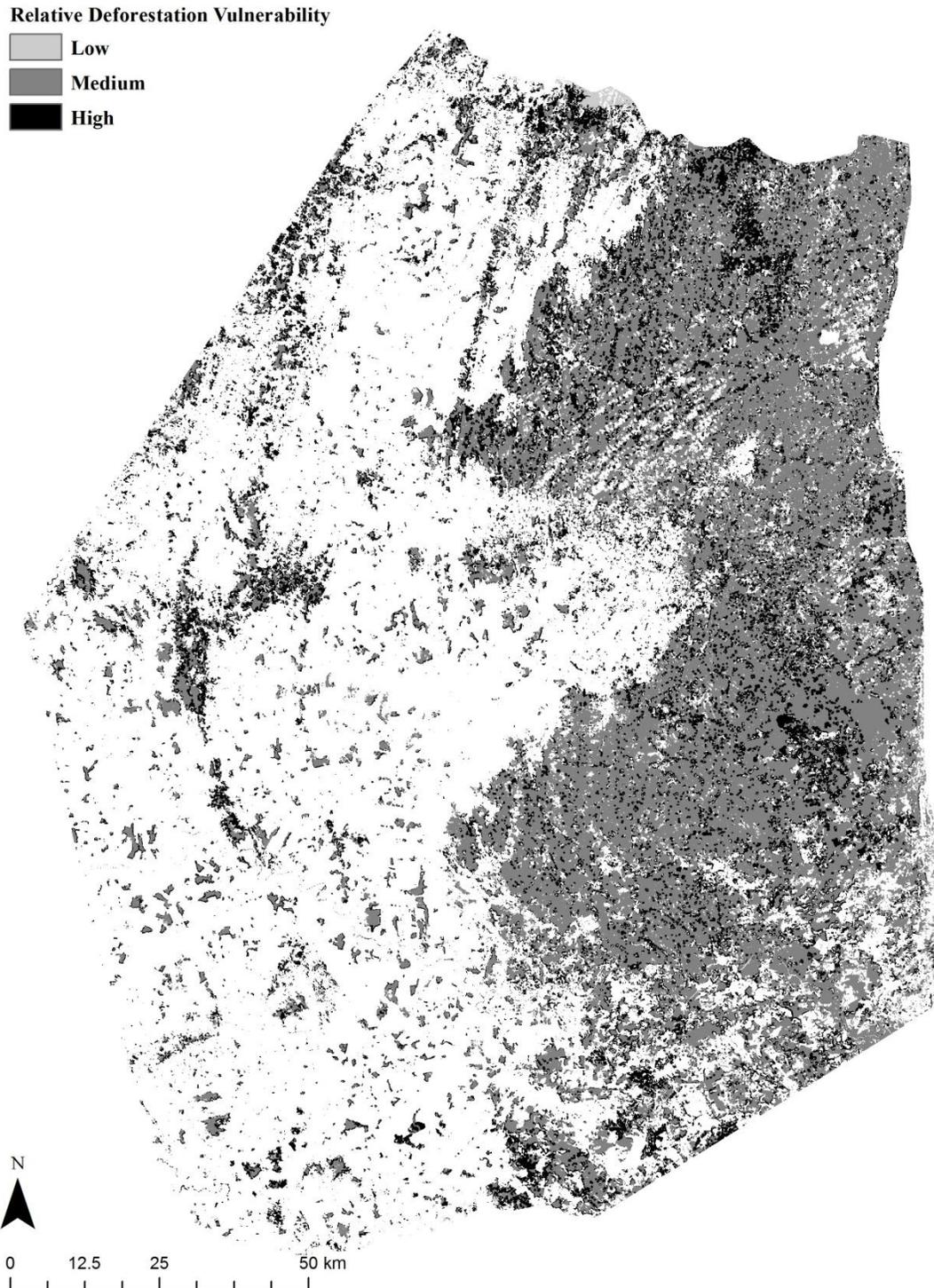


Figure 15. Index of relative vulnerability to future deforestation as determined in Land Change Modeler (LCM). According to the LCM model, forest cells in the 2007 landcover map are highly vulnerable to future deforestation (vulnerability index approaching 100; shown in black) if they are at low elevations, in areas of high human population density, or close to previously cleared areas.

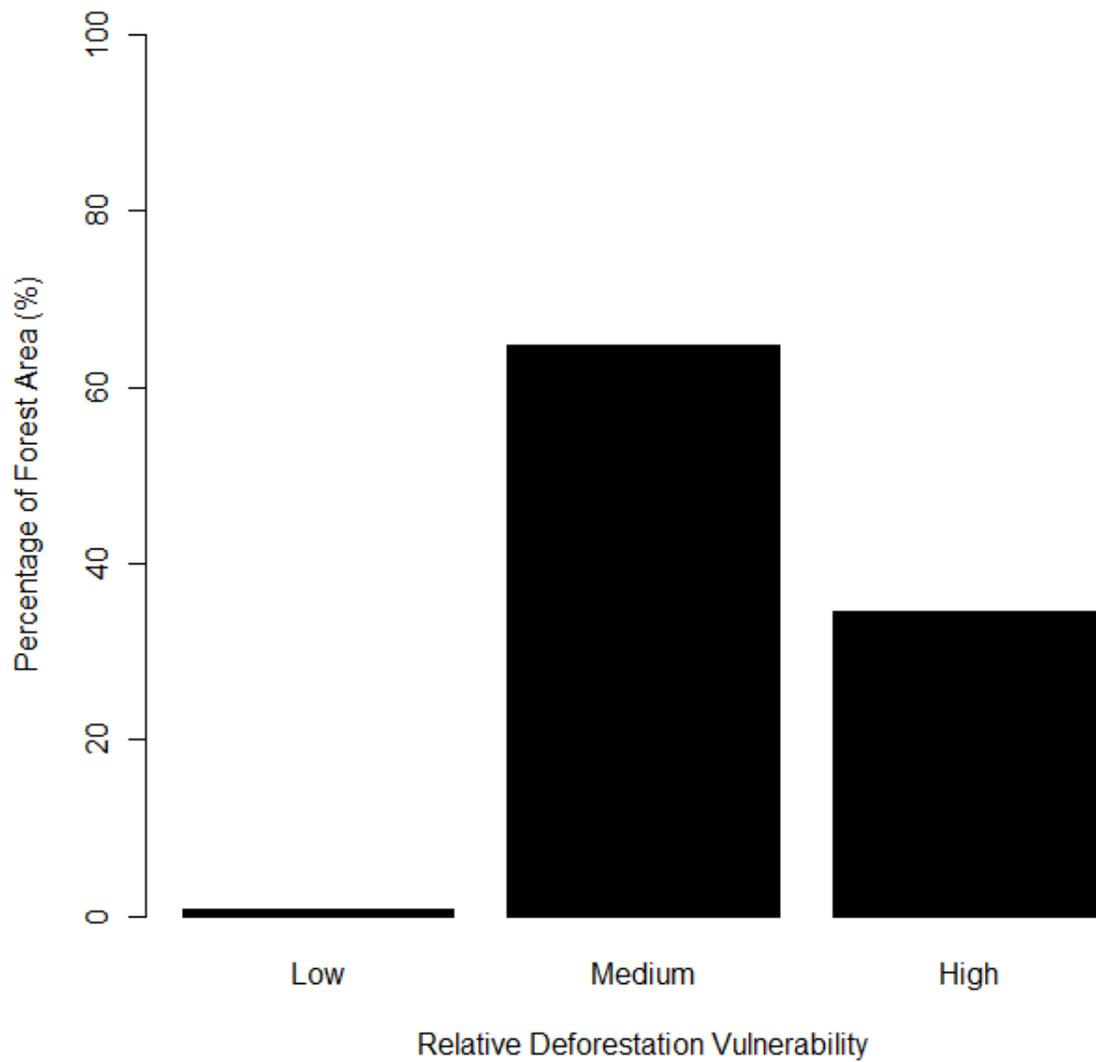


Figure 16. Relative deforestation vulnerability of current forest cover throughout the range of the golden-headed lion tamarin. Forest with high relative deforestation vulnerability was found at low elevation, high human population density, and short distances from previously cleared areas.

GHLT Population Viability on Small Habitat Patches

According to the deterministic analysis of stage-specific vital rates used in Vortex, populations modeled here should be growing slightly or remaining stable with $\lambda = 1.0467$. However, this value does not consider the impacts of processes like density dependence or environmental/demographic stochasticity, and stochastic simulations suggest that populations are in fact declining (Figures 17; Figure 18).

In the baseline stochastic model, which assumed no additional forest loss, all metapopulations had less than 30% risk of local extinction within 20 years. However, the risk of local extinction increased over longer time periods with metapopulations on 4 and 7 components having a greater than 80% probability of extinction within 50 and 100 years, respectively. Only metapopulations on components 3, 5 and 10 had less than 80% probability of local extinction within 100 years (Figure 17). No metapopulations met the population viability criterion of 2% probability of local extinction in 100 years (Holst et al. 2006; Zeigler et al. 2010). Metapopulations on all components experienced substantial declines in abundance through time with the metapopulation on component 5 having the highest abundance at 19 individuals by year 100 (Figure 18). Genetic heterozygosity also declined through time for metapopulations on all components (Figure 19), and no metapopulation maintained over 98% of its original genetic heterozygosity by year 100.

In models where continuing deforestation was incorporated by reducing carrying capacity by 0.65% or 1.3% per year, metapopulation abundance and genetic heterozygosity decreased while local extinction risk increased substantially as compared to the baseline model (Figure 17; Figure 18; Figure 19). Metapopulations

on all but two components had a risk of extinction greater than 80% in the model of current deforestation rate (0.65% per year) by year 100, and metapopulations on all components had a 100% probability of extinction by year 100 in the model of double the current deforestation rate (1.3% per year). No metapopulation had more than three individuals remaining by year 100 under the deforestation models. Finally, the highest level of genetic heterozygosity was for the metapopulation on component 5 with only 62% of its original genetic diversity remaining by year 100 under the most optimistic model of no future deforestation.

Sensitivity Analyses

Parameter sensitivity varied by metapopulation (Table 10). Models for metapopulations on all components were significantly sensitive to only one parameter, the percentage of females breeding and were never sensitive to correlation of environmental variation among populations. In addition, some models were sensitive to the Alleé parameter, maximum age of reproduction, disperser survival rate, and dispersal rate depending on the metapopulation/component.

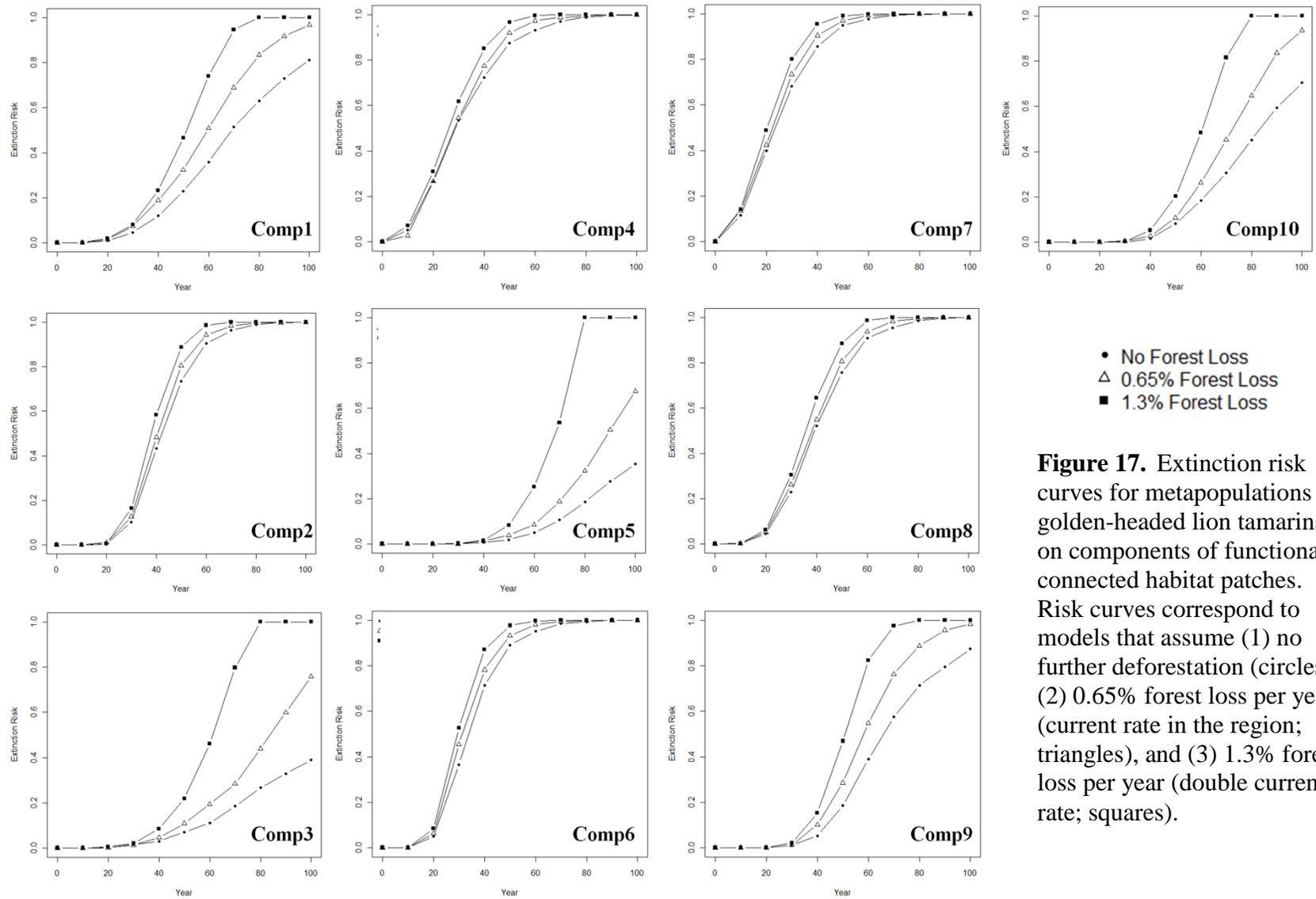


Figure 17. Extinction risk curves for metapopulations of golden-headed lion tamarins on components of functionally connected habitat patches. Risk curves correspond to models that assume (1) no further deforestation (circles), (2) 0.65% forest loss per year (current rate in the region; triangles), and (3) 1.3% forest loss per year (double current rate; squares).

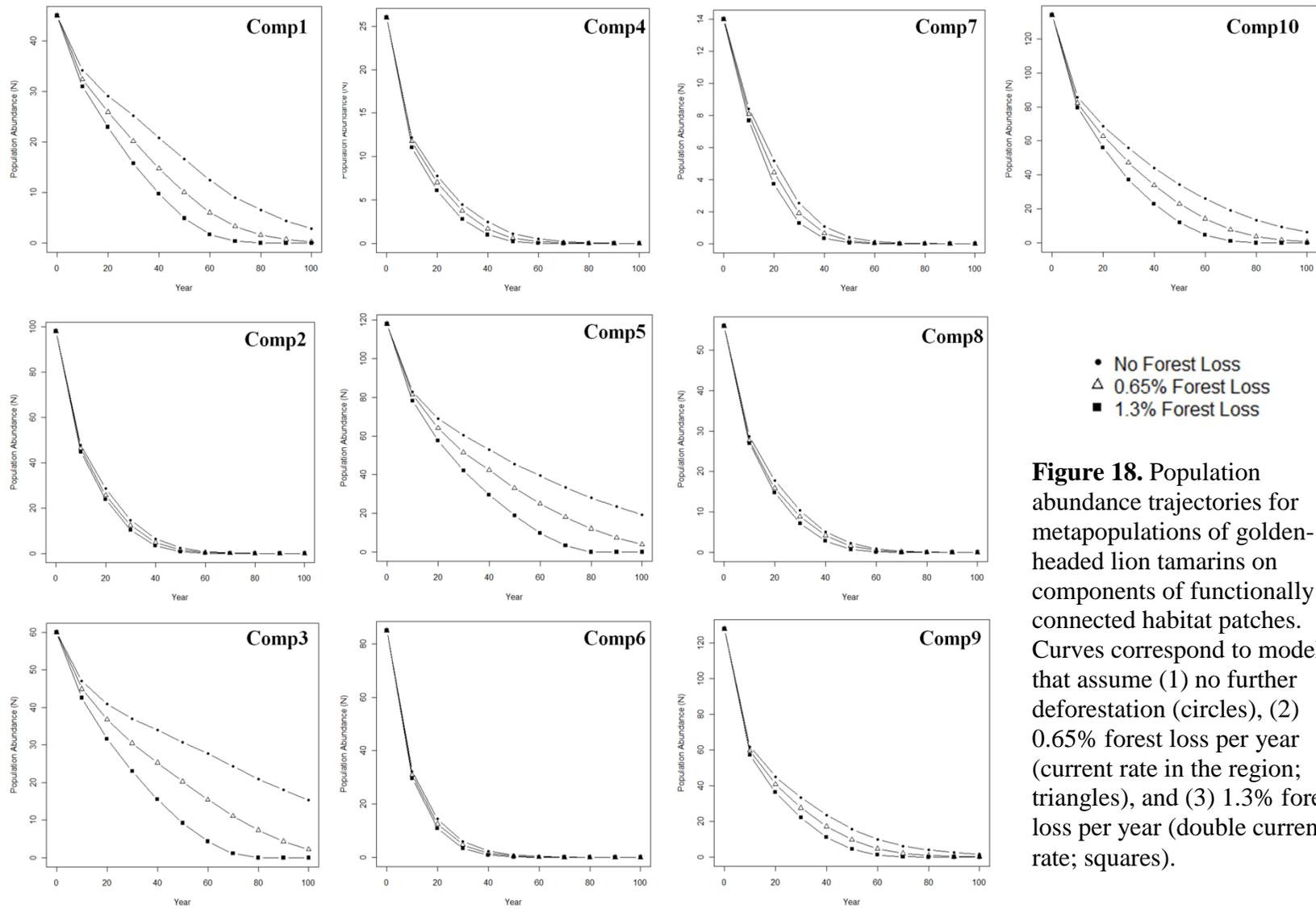


Figure 18. Population abundance trajectories for metapopulations of golden-headed lion tamarins on components of functionally connected habitat patches. Curves correspond to models that assume (1) no further deforestation (circles), (2) 0.65% forest loss per year (current rate in the region; triangles), and (3) 1.3% forest loss per year (double current rate; squares).

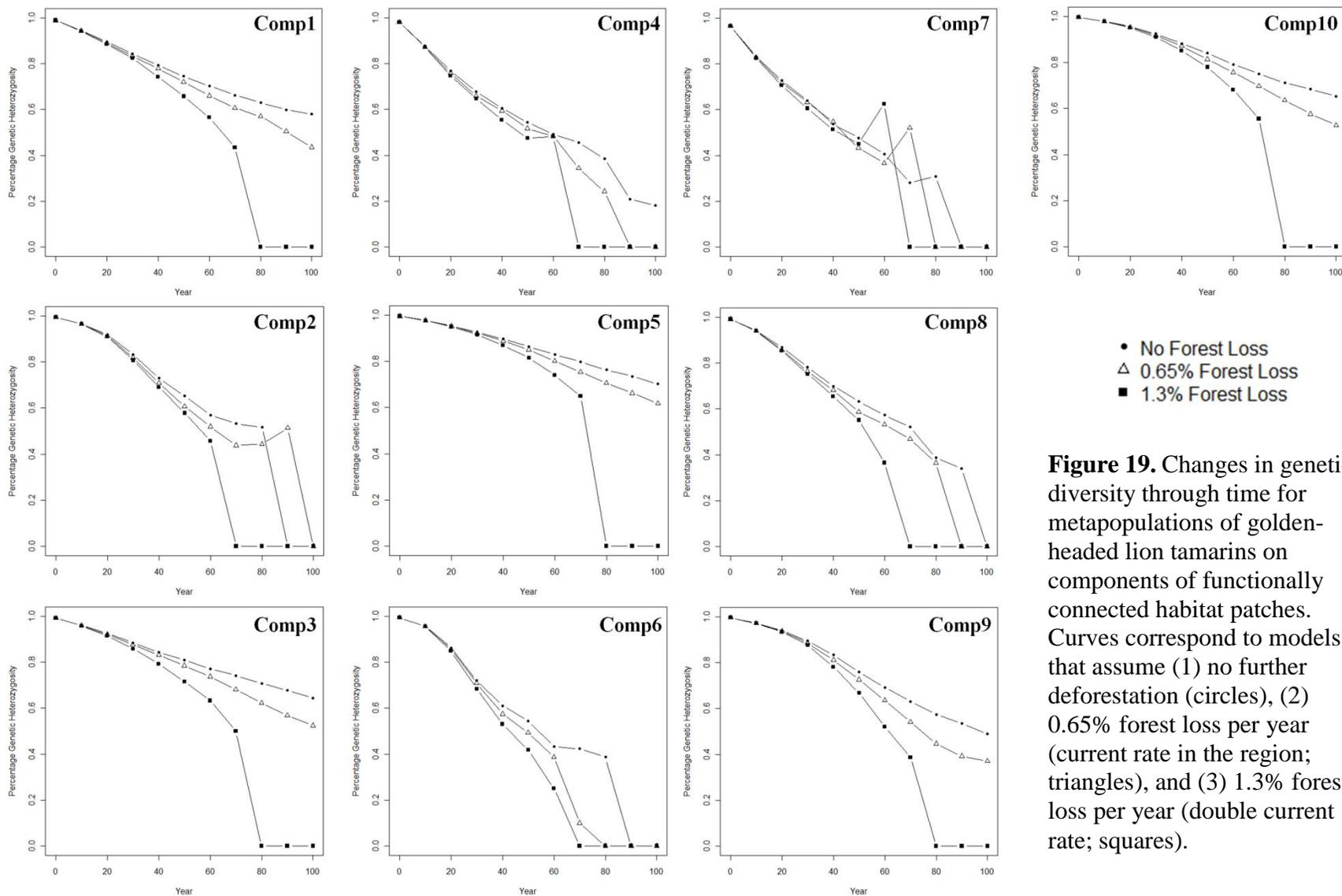


Figure 19. Changes in genetic diversity through time for metapopulations of golden-headed lion tamarins on components of functionally connected habitat patches. Curves correspond to models that assume (1) no further deforestation (circles), (2) 0.65% forest loss per year (current rate in the region; triangles), and (3) 1.3% forest loss per year (double current rate; squares).

Table 9. Model sensitivity to select parameters for metapopulations on a subset of the components modeled here according to logistic regression. Coefficients were significant at p-values < 0.001 (*).

Component	Description	Parameter	Minimum Value	Maximum Value	Standardized Coefficient
3	Moderate abundance, low dispersal rate, low extinction risk	Alleé Parameter	0	25	0.292 *
		Percentage Females Breeding	0.5(%Breeding)	1.5(%Breeding)	-8.294*
		Population Correlation	0	1	-0.022
		Max Reproductive Age	10	17	-0.493*
		Disperser Survival Rate	1%	100	-0.001
		Min Disperser Age	2	4	-0.012
		Dispersal Rate	0.5(D)	2(D)	0.049
5	High abundance, high dispersal rate, low extinction risk	Alleé Parameter	0	25	0.003
		Percentage Females Breeding	0.5(%Breeding)	1.5(%Breeding)	-11.65*
		Population Correlation	0	1	-0.101
		Max Reproductive Age	10	17	-0.565*
		Disperser Survival Rate	1%	100	-0.005*
		Min Disperser Age	2	4	-0.529*
		Dispersal Rate	0.5(D)	2(D)	3.208*
7	Low abundance, low dispersal rate, high extinction risk	Alleé Parameter	0	25	0.068
		Percentage Females Breeding	0.5(%Breeding)	1.5(%Breeding)	-7.372*
		Population Correlation	0	1	0.002
		Max Reproductive Age	10	17	-5.45E-10
		Disperser Survival Rate	1%	100	-0.013
		Min Disperser Age	2	4	-1.47E-15
		Dispersal Rate	0.5(D)	2(D)	-4.53E-9
10	High abundance, moderate dispersal rate, moderate/high extinction risk	Alleé Parameter	0	25	0.369*
		Percentage Females Breeding	0.5(%Breeding)	1.5(%Breeding)	-9.789*
		Population Correlation	0	1	-0.025
		Max Reproductive Age	10	17	-0.573*
		Disperser Survival Rate	1%	100	-0.030*
		Min Disperser Age	2	4	-0.405*
		Dispersal Rate	0.5(D)	2(D)	3.384*

Discussion

Ultimate Threats: Vulnerability from Habitat Loss

GHLTs are at risk due to both ultimate and proximate threats. Throughout the GHLT range, recent forest loss occurred in areas at low elevation, with high human population density, and at short distances from previously cleared areas. These landscape characteristics are associated with areas where much of the remaining forest cover still occurs, and the majority of habitat for GHLTs (65 – 34%) is highly threatened if recent deforestation patterns continue. In addition, metapopulation models show that, at the current rate of forest loss of 0.65% per year, 7 out of 10 metapopulations I examined have an 80% or higher probability of going extinct over 100 years. If deforestation is accelerated to double the current rate of loss (1.3% per year), all metapopulations have a 100% probability of local extinction.

The loss of forest in areas with medium or high relative vulnerability would leave the GHLT landscape as lacking in contiguous forest cover as that of the three other lion tamarin species. The GHLT's congeners are restricted to extremely small habitat patches, and little hope exists for future population expansion given current forest cover and configuration. To protect GHLTs from the same fate, forest within the GHLT range must be protected now while it still exists. Currently, there is only one federally protected reserve within the species' range. Una Biological Reserve and Wildlife Refuge (IUCN Category Ia) was created in 1980 explicitly for the protection of GHLTs and is closed to public use with the exception of scientific research and environmental education (Rylands & Brandon 2002). Despite successful efforts to enlarge the reserve over the last 30 years, previous modeling

studies suggest that it is not large enough to support a genetically viable population of GHLTs over the longterm (Holst et al. 2006). An additional three state environmental protection areas and one state park also exist in the northeast quadrant of the GHLT range (IUCN & UNEP 2009), although recent surveys have been unable to locate GHLTs in that region (Raboy et al. 2010). Continued efforts for additional federally protected areas, further expansion of Una Biological Reserve, and promotion of private reserves (RPPNs) will be critical for the protection of the species and its vulnerable habitat.

Proximate Threats: Vulnerability Inherent to Small Populations

GHLTs are also at risk due to proximate threats associated with small population size. According to deterministic analysis of the vital rates used in Vortex, GHLT populations should be increasing ($\lambda = 1.0467$). However, I found that the majority of stochastic metapopulation models simulated here had an 80% or higher probability of local extinction within the next 100 years even when no further deforestation occurred. Many taxonomic groups and species exhibit time-lags in their responses to reductions in forest area and connectivity (Tilman et al. 1994), particularly when those reductions occur quickly as seen in the Atlantic Forest (Brooks & Balmford 1996; Fahrig 2005; Metzger et al. 2009). The current presence of the GHLT metapopulations modeled here despite high probabilities of extinction may simply reflect extinction debt (Tilman et al. 1994), and continuing local population extinctions like those already observed for the species may be expected (Raboy et al. 2010).

Even when ultimate agents of decline are removed, GHLTs still have a high probability of extinction from proximate drivers like demographic and environmental stochasticity, genetic deterioration, and social dysfunction. Genetic deterioration may be of particular concern for small populations of GHLTs. Although it is unclear whether low levels of polymorphism and heterozygosity are the result of founder effects or a natural condition, lion tamarins have the lowest levels of genetic diversity reported for any primate (Forman et al. 1986). Low diversity is expected from this species even at relatively large populations because the species' propensity for twins, monogamous mating system, and social structure (small family groups with a single breeding pair) reduce the number of possible allelic combinations (Forman et al. 1986). In addition, moderate levels of inbreeding are linked to significantly higher juvenile mortality rates (Ballou 1985; Ralls & Ballou 1982a, b; Ralls et al. 1988). Thus, genetic drift and inbreeding depression may cause a reduction in already low genetic diversity for GHLTs, ultimately reducing survival of offspring and reproductive success.

In addition to genetic deterioration, small GHLT metapopulations are also vulnerable to Alleé effects (Alleé et al. 1949), which describe the reduction in per capita growth rate at low population densities. Alleé effects can occur when a species population size falls below a critical number of individuals required for anti-predator vigilance or defense, social thermoregulation, collective modification of the environment, inbreeding avoidance, mate attraction, or conspecific enhancement of reproduction (Stephens & Sutherland 1999). GHLTs and other cooperatively-breeding species are predicted to be especially vulnerable to Alleé effects because

offspring survival is dependent on the presence of helpers at a critical group size (Courchamp et al. 1999; Dobson & Lyles 1989). Thus, when the number of individuals in a patch or metapopulation falls below some critical value, GHLTs may be unable to (1) find mates or (2) successfully rear offspring, collectively reducing reproductive success. Sensitivity analysis showed that Alleé effects have a major impact on population persistence for small GHLT metapopulations (Table 10). Extinction risk significantly increased with Alleé parameter (i.e. the critical population size below which Alleé effects impact the population) for two of the four metapopulations tested and with the percentage of females breeding (which was reduced at low population sizes due to Alleé effects) for all metapopulations tested.

Metapopulation Characteristics and Probability of Extinction

Metapopulations that had the lowest probability of local extinction in 100 years were located in some of the largest components (Table 7). Component 5, with a metapopulation that had a 35% probability of extinction, was composed of 1,211 ha of forest (largest patch = 440 ha). Component 10, whose metapopulation had a 70% chance of extinction in 100 years, was composed of 1,424 ha of forest (largest patch = 579 ha). Both of these components had enough forest cover to support a minimum viable population (MVP) of GHLTs (Zeigler et al. 2010), yet metapopulations had a substantially higher probability of extinction than a population on a single patch meeting MVP size requirements (Zeigler et al. 2010) because of the additional mortality imposed on individuals as they move through the matrix.

However, the amount of forest within a component was not a clear predictor of metapopulation extinction risk. For example, component 3 had a relatively small

amount of total forest area (610 ha) compared to many other components but one of the lowest metapopulation extinction risks at 39%. In comparison, components 2 and 6 had much larger areas of forest (1,007 ha and 991 ha, respectively) but 100% probabilities of extinction within 100 years. Most surprisingly, component 9 had a combined forest area of 1,307 ha and one patch that should have been large enough at 896 ha to support a viable population on its own (Zeigler et al. 2010) yet had a metapopulation extinction risk of 88%.

Metapopulation persistence seems to be, at least in part, associated with dispersal rates. Components 2, 6, and 9, which should have been large enough to support viable metapopulations, had high risks of extinction and rates of dispersal among patches. Components 3 and 10, which had relatively low probabilities of local extinction, also had low dispersal rates. In addition, models of components with high dispersal rates were significantly sensitive to the values of those dispersal rates (Table 10). In PVA models simulated here, dispersal rate was distance-dependent such that more dispersers entered the matrix, where they had higher mortality risks, in components with patches separated by short gaps. The result was a decline in metapopulation size as a higher proportion of the total population had a high mortality rate as compared to metapopulations where patches were separated by larger gaps, fewer dispersers entered the matrix, and a smaller proportion of the total population had high mortality rates. Because few observations on GHLT dispersal behavior have been made, it is unclear whether this is a biological phenomenon or merely a function of model parameterization. Finally, it should be noted that metapopulations on components 1, 7, and 8 had high extinction risks and low

dispersal rates while component 5 had a low extinction risk and a high dispersal rate. Thus, extinction risk is not solely associated with dispersal rate in my models.

In summary, because low rates of extinction were not always correlated with metapopulations on the largest components or with the lowest dispersal rates, the amount and configuration of habitat for metapopulation persistence is unclear. Further modeling will be required to determine the suite of characteristics required for metapopulation persistence.

Model Limitations and Parameter Uncertainty

Sensitivity analysis showed that certain PVA models were significantly impacted by variation in parameters for maximum reproductive age, Alleé parameter, percentage females breeding, and dispersal age, rate, and survivorship. These results are important because there is uncertainty surrounding the values used for these parameters in the PVA models simulated here. The maximum age of reproduction is known from captive golden lion tamarins (Holst et al. 2006), and the maximum age may be lower for individuals in the wild, which would increase extinction risk. Alleé effects (and their impact on the percentage of females breeding and other aspects of reproductive success) have yet to be explicitly observed for GHLTs, and the critical population size under which population decline is expected to accelerate is unknown. Finally, very little is known about GHLT dispersal behavior, including how far and how often individuals are willing to travel over what types of matrix. Further research on these areas of GHLT ecology and behavior will improve the predictive accuracy of PVA models in the future. However, despite the uncertainty in these parameters, metapopulations had a moderate to high risk of extinction across the

entire range of parameter values, and model results should not be discounted because of this uncertainty.

PVA models conducted here may also offer optimistic predictions of extinction risk. At the time of analysis, the only available survival and reproductive rates for GHLTs were based on studies of populations by B. Raboy in Una Biological Reserve, an area of optimal habitat for GHLTs. No published data on the demographic rates and group dynamics of GHLTs in small, degraded forest patches characteristic of the western portion of the species' range (and the components explored in this study) are currently available. In addition, for many of the stage-specific survival and reproductive rates, variability was attributed entirely to demographic variability and sampling error (Zeigler et al. 2010), and little variation attributed to environmental variability was incorporated into PVA models. If survival and reproductive rates are depressed or have high levels of variability in small, degraded forest patches, then extinction risk for the metapopulations modeled here may actually be higher. In addition, I did not incorporate the effects of catastrophes. Fire and disease are both major threats to GHLTs and would increase extinction risk, particularly for populations in the west that are surrounded by pasture that is routinely burned (Ballou et al. 1998; Holst et al. 2006).

Conclusions

GHLTs are threatened by both ultimate and proximate drivers of extinction. The majority of current forest cover within the GHLT range is moderately to highly vulnerable to deforestation, and metapopulations have a high probability of local

extinction if forest continues to be lost at its current rate. Even without continuing deforestation, small metapopulations are likely to go locally extinct due to the impacts of stochasticity, genetic deterioration, and Alleé effects. Immediate protection of large tracts of forest and the GHLT populations they support is of critical importance.

Chapter 5: Conclusions

Major Findings from Dissertation Research

The objectives of my dissertation research were to assess the vulnerability of golden-headed lion tamarins (GHLT; *Leontopithecus chrysomelas*) to habitat loss, fragmentation, and the threats related to small population size given past, current, and likely future trends in range-wide forest cover in Brazil's Atlantic Forest.

Specifically, I answered the following questions:

How did forest cover throughout the GHLT range change between 1987 and 2007?

In Chapter 1, I found that forest cover decreased by 13% (0.65% per year assuming constant rate of loss) between 1987 and 2007. During that time, the total number of forest patches decreased by 1,419 patches, and the mean size of those patches contracted by 10 ha.

How much forest remains currently as habitat for GHLTs?

Currently, 965,861 ha of forest (880,179 ha at elevations below 500 m) remain in 15,713 patches throughout the GHLT range. However, the majority of these patches are too small to support a group of GHLTs with any permanence; only 5% of patches were greater than 36 ha (the smallest recorded GHLT territory size at the time of analysis).

How vulnerable is current forest cover to future deforestation?

In Chapter 4, I found that much of the deforestation between 1987 and 2007 occurred in areas of low elevation, high human population density, and short distances from

previously cleared areas. These characteristics describe much of the landscape where forest still occurs, and thus the majority of forest has a medium (65% of forest area) or high (34% of forest area) relative vulnerability to future deforestation.

How many forest patches currently exist throughout the species range that are large enough to support a minimum viable population of GHLTs under varying levels of risk?

Population viability analysis (PVA) in Chapter 1 showed that a stable, self-sustaining minimum viable population of GHLTs would require 70 to 250 individuals, depending on density and the consideration of additional risks like disease and fire. A genetically viable population would require 780 to 960 individuals. Assuming a medium GHLT density, populations at these sizes would require 1,045 to 3,731 ha (for viable populations) and 11,642 to 14,328 ha (for genetically viable populations). Currently, there are between 1 - 22 forest patches meeting these size requirements and able to support a viable or genetically viable population of GHLTs.

What is the current level of functional connectivity between habitat patches for GHLTs?

Functional habitat connectivity throughout the species' range, based on the results of Chapter 3, was low at small Euclidean distance and movement cost thresholds, the likely necessary conditions for this arboreal primate to travel through non-forest matrix separating forest patches. Many forest patches were isolated at dispersal distances less than 100 m (95%- 96% of patches) or 1 km (23%-27% of patches). The average component size (not including the component containing the largest

patch on the landscape) ranged from 255 - 267 ha at dispersal distances up to 100 m and from 277 - 490 ha at dispersal distances up to 1 km. Thus, even allowing for resource acquisition by movement between patches, the combined forest area available for most populations of GHLTs is likely much lower than the 1,045 ha required to support a viable population of GHLTs.

Could conspecific or heterospecific attraction alter measurements of functional connectivity patterns for this social species?

Social species like GHLTs may use cues from conspecifics or heterospecifics to motivate dispersal decisions, and measurements of connectivity change when social behaviors are incorporated into analyses of functional connectivity according to the results of Chapter 3. Within the GHLT range, where only a small fraction of patches are known to be occupied, I found that functional connectivity would substantially increase if dispersers travel over more hostile matrix to reach an occupied patch and would decrease if dispersers only travel to occupied patches.

How viable are GHLT metapopulations on small, relatively isolated habitat patches?

According to the results of Chapter 4, the majority of metapopulations modeled (7 out of 10) had a greater than 80% probability of local extinction within 100 years, and no metapopulation was considered viable under the standard of less than 2% extinction risk set by Holst et al. (2006). The metapopulations that did persist to 100 years had very low final abundances (less than 20 individuals) and genetic diversity.

Metapopulation declines and extinction risks increased substantially when continuing forest loss was also considered; only two populations had a less than 80% probability

of local extinction under current deforestation rates (0.65% loss per year) and all populations had a 100% probability of extinction under double the current rate of deforestation (1.3% loss per year).

In summary, with an estimated population size over 6,000 individuals and a large percentage of habitat remaining, GHLT have been considered relatively secure from a conservation standpoint, especially compared to the three other lion tamarin species endemic to the Atlantic Forest of Brazil. However, my dissertation research illustrates that forest cover has declined throughout the range of the species over the last 20 years. Functional landscape connectivity, which is important for the acquisition of resources and gene flow, is low at the distance and movement cost thresholds likely associated with this arboreal species that is rarely seen in non-forest matrix, and only one habitat patch is large enough on its own to support a genetically viable GHLT population able to recover from extrinsic threats such as fire and disease. The majority of remaining forest cover throughout the species' range is found in patches that are either (1) too small to support even a single group of GHLTs or (2) found at low elevations, in areas of high human population density, and close to previously cleared areas—conditions that are associated with past deforestation patterns and that make current habitat vulnerable to loss in the future. Finally, many of the known GHLT populations (10 examined here out of 21 known occupied patches) have a moderate to high risk of local extinction even assuming no further forest loss, and their presence may represent extinction debt. Continued deforestation will accelerate population declines and local extinction events. The results of my

dissertation research suggest that GHLTs and their habitat face significant threats and low viability in the future due to both ultimate and proximate drivers of extinction.

Priorities for Conservation

Because the majority of available habitat is vulnerable to deforestation and because metapopulations on small forest patches have a moderate to high risk of local extinction, implementing strong protective measures as part of a proactive conservation program is of immediate importance. To synthesize the results of the dissertation research described in this volume, I provided a simple ranking scheme to prioritize forest patches throughout the range of the species (Figure 20). I gave each forest patch a point if it was (1) large enough to support a minimum viable population, (2) large enough to support a genetically viable population, (3) indicated as important for maintaining functional connectivity in Conefor Sensinode, or (4) known to be occupied based on positive survey results (Raboy et al. 2010). Under this ranking, forest patches could have a value ranging from zero (not meeting any of the above conditions) to four (meeting all of the above conditions). Forest patches with the highest values are critical to the persistence of GHLTs and should first be prioritized for surveys and research to determine habitat quality and GHLT occupancy (if not already known). Patches that are of high quality should be further prioritized for protection either through federal or state protection or through private reserves. Because no protected areas currently exist in the west where deforestation and relative deforestation vulnerability were highest, large patches meeting one or more of these criteria in the western portion of the GHLT range should be of

particular interest for formal protection to ensure that redundant populations and that the full spectrum of the species' genetic diversity are conserved.

Forest patches of high quality that meet one or more of the four criteria should also be prioritized as potential reintroduction sites for captive-bred GHLT populations. A large and well-managed captive breeding program currently exists for GHLTs (Ballou et al. 2002), yet these captive populations have not yet contributed to wild populations. Reintroductions of captive golden lion tamarins (*Leontopithecus rosalia*) have significantly improved the status of the wild population, contributing to the species' downlisting from Critically Endangered to Endangered in recent years (Ballou et al. 2002; Kierulff et al. 2008a). A similar program for GHLTs, where captive individuals are reintroduced into large forest patches highlighted in Figure 20 (particularly in the western portion of the species' range), could also provide substantial conservation benefits for this species.

Finally, only one patch meets all four criteria and is of highest priority for protection (Figure 20). However, this patch was primarily composed of cabruca as of 1995 (Landau et al. 2003) and is vulnerable to forest loss and fragmentation as the low price of cocoa and fungal epidemics make it more profitable for farmers to clear cut their land for timber sale (Alger & Caldas 1994) or for conversion to cattle pasture (Schroth & Harvey 2007). Government subsidies, price premiums for "shade" or "fair-trade" cocoa production, and other incentives for maintaining cabruca plantations over cattle pasture will be critical for the persistence of GHLTs and their habitat and should be promoted. Such mechanisms will allow farmers to be profitable while supporting biodiversity conservation.

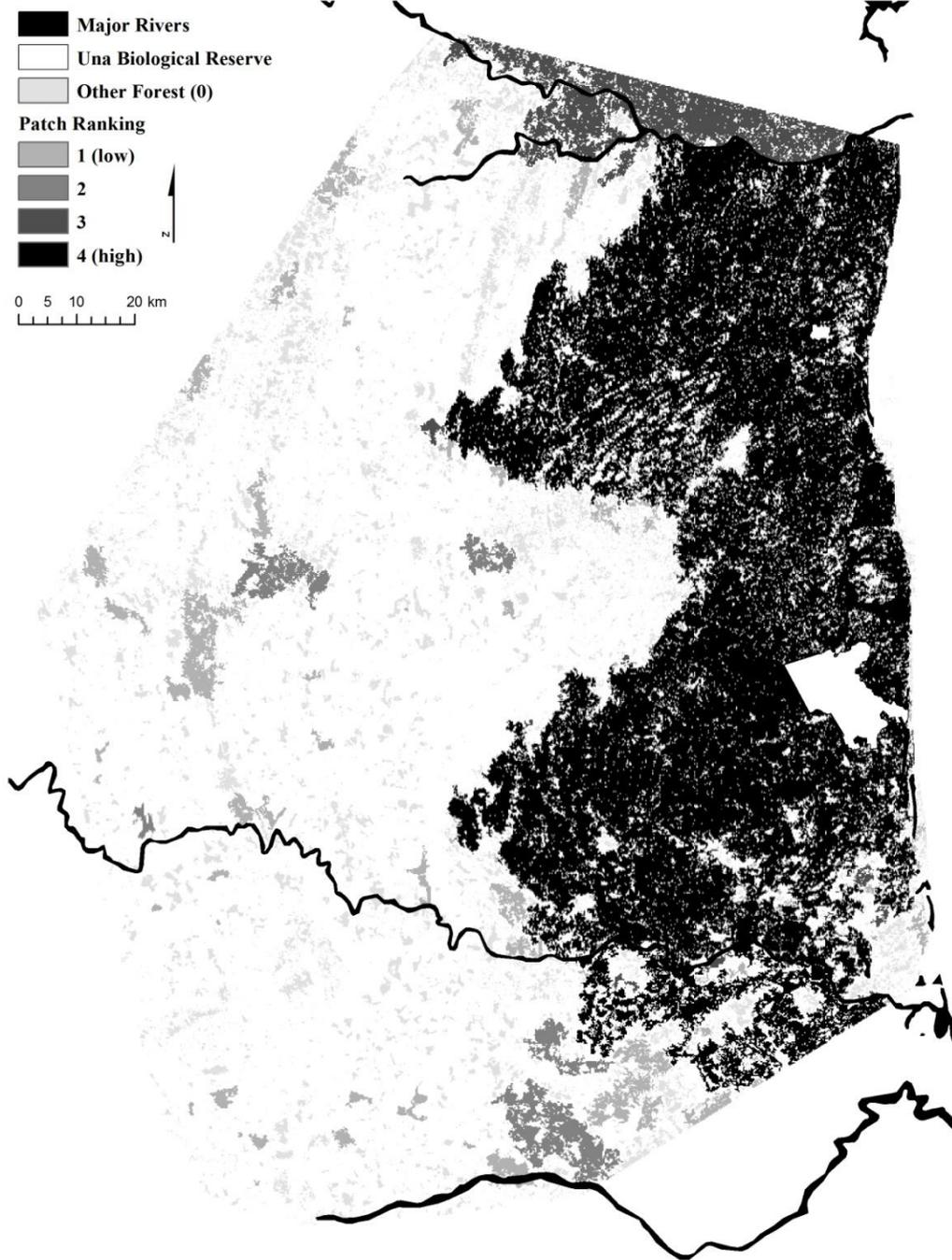


Figure 20. Priority forest patches for the conservation of golden-headed lion tamarins (GHLT). Each patch was given a point if it was (1) large enough to sustain a minimum viable population, (2) large enough to support a genetically viable population, (3) important for promoting functional landscape connectivity, or (4) occupied based on positive survey results (Raboy et al. 2010). Patches meeting all of these requirements (patch ranking = 4; shown in black) may be disproportionately important for GHLTs and should be prioritized for further research and protection.

Recommendations for Ecological Research

In the course of parameterizing PVA models in Chapters 2 and 4, I determined areas of GHLT behavior and ecology for which information is lacking. Models were parameterized with survival and reproductive rates collected by B. Raboy in Una Biological Reserve, an area of optimal habitat for GHLTs. Trends were assessed based on a relatively small sample size; 2 of the groups were followed for 12 years, 1 group was followed for 9 years, 1 group was followed for 7 years, and 2 groups were followed for 5 years. No published data on the demographic rates and group dynamics of GHLTs in small, degraded forest patches characteristic of the western portion of the species' range are currently available. In addition, for many of the survival and reproductive rates, I found that variability was attributed entirely to demographic variability or sampling error due to small sample sizes/short observation time scales; little variation due to environmental variability was incorporated in my PVA models. Other studies have found that at least 15-20 years of population-level data are necessary to capture natural variability in a system and to correctly estimate population growth rates (Che-Castaldo & Inouye In Prep; Doak et al. 2005; Fagan et al. 1999; Holmes et al. 2007). Thus, because I used survival and reproductive data with little variability and that may correspond to the upper range for the species, the risk of local extinction for small populations as determined in my dissertation research may actually be optimistic.

I also found that information on dispersal behaviors for any lion tamarin species is lacking. Aside from occasional anecdotal evidence and expert opinion, no

statistically supported data currently exist on the survival rate of GHLTs in non-forest matrix or on how often or far GHLTs move between forest patches. Sensitivity analysis of my PVA models showed that disperser survival rate and dispersal rate significantly impacted estimates of extinction risk for some metapopulations. A stronger body of evidence on dispersal behavior for the species would increase the predictive ability of PVA models for metapopulations in this fragmented landscape.

Finally, sensitivity analysis of PVA models also showed that extinction risk was significantly impacted by the Alleé parameter used. Alleé effects have been highlighted as a key factor in population dynamics and extinction risk for a variety of species, particularly primates (Dobson & Lyles 1989; Stephens & Sutherland 1999). While I was unable to detect a reduction in survival or fecundity with decreasing group size in the data available for the species, it is reasonable to believe that reproduction and survival may decrease with decreasing population size for this social, cooperatively-breeding species. Understanding the population size threshold at which this occurs is particularly relevant for populations of GHLTs on small, isolated forest patches.

In general, an open and important niche exists for the study of small GHLT populations on degraded habitat patches in the western portion of the species range. Observations of demographic rates, dispersal behaviors, and Alleé thresholds would fill major knowledge gaps and help conservationists to better understand extinction risk for this species.

Future Directions

The work presented here as part of my dissertation is just the beginning for assessing risks, prioritizing habitat for protection, informing conservation decisions (e.g. translocation and reintroduction locations), and planning habitat restoration for GHLTs. Future directions for research could include the following::

1. Previous studies have found that predictive models of GHLT presence/absence on forest patches were moderately correlated with landscape metrics for the amount of core area and overall patch area; although these models could not completely explain conditions required for GHLT presence or the distribution observed for the species (Raboy et al. 2010). Their analysis could be repeated using the updated forest cover maps created in my dissertation research and additional metrics for distance from the largest patch and distance from other occupied patches in order to explain the structural and social requirements for GHLT occupancy. This information is important for habitat restoration and prioritization for GHLTs.
2. A substantial range reduction has been observed in the southwestern portion of the GHLT distributional range. Reasons for this reduction have not been thoroughly addressed, and an analysis of how changes in forest cover and connectivity specific to this sub-region may be driving local extinctions is an important avenue of future research. This information can be used to assess the risk of local extinctions in similar areas that may still be occupied.
3. PVA modeling in Chapter 4 showed that some metapopulations had a higher risk of extinction than others but that the conditions for why one

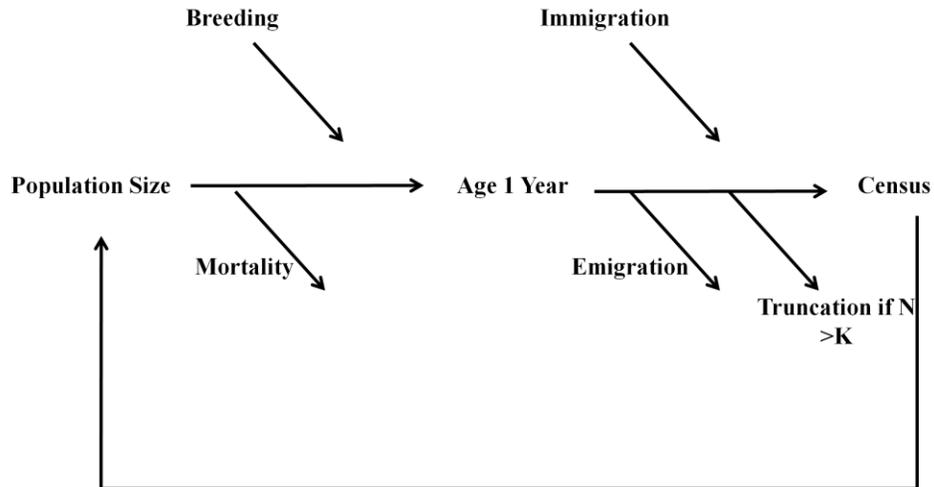
metapopulation may persist as compared to another are unclear. Continued use of PVA to explore the hypothetical conditions (e.g. required habitat amount and configuration) under which metapopulations have the lowest extinction risk could be used for prioritizing habitat for GHLT conservation.

4. I examined the population viability of metapopulations on only a subset of forest patches that are known to be occupied in Chapter 4. I made the assumption that populations on other small occupied patches were secure because they were functionally connected to the large eastern patch that is able to support a genetically viable population of GHLTs; continued immigration from individuals on the large patch would provide a demographic and genetic rescue effect that would prevent the local extinction of populations on these small patches. PVA could be used to explore the validity of this assumption and to understand what levels of immigration would have to occur to prevent the local extinction of these populations.
5. Finally, PVA models conducted through my dissertation research should be updated as new observations of GHLT demography, ecology, and behavior are released in order to improve the predictive accuracy of models of GHLT risk assessment.

Appendices

Appendix I. Program algorithm for Vortex ver9.72.

The population viability analysis program Vortex ver9.72 was used to simulate demographic processes in Chapters 2 and 4. The program models population dynamics as discrete, sequential events that occur based on user-specified probabilities. Events take place according to the following timeline and algorithm (adapted from Miller & Lacy 2005):



Program Initiation:

- Calculates deterministic rates (growth rates, initial age distribution, etc)

Starting Point for Each New Iteration

Starting population assigned age, sex, and genetic structure

- 50/50 sex ratio
- Stable age distribution
- 2 unique alleles at hypothetical neutral genetic locus assigned to each individual
- For each of the 10 alleles at the 5 non-neutral loci, each founder is assigned a lethal allele with probability = $0.1 * \text{mean \# of lethal alleles per individual}$

Starting Point for Each New Time Step (Year)

Number of Females Breeding

- Adjusts percentage to account for density dependence in reproduction:

$$P(N) = (P(0) - [(P(0) - P(K)) (N/K)^B]) * (N/(N+A))$$

P(N): % females breeding at pop size N
P(0): % females breeding at low pop size
P(K): % females breeding at high pop size
B: Shape of curve (1 = linear)
A: Allee effect

Environmental Stochasticity and Carrying Capacity (K)

- Adjusts birth rate, percentage females breeding, and survival rate by choosing rate from binomial distribution
- Adjust K by choosing from a normal distribution with mean/standard deviation specified by user (if applicable)
- Determines K for year by decreasing (or increasing) according to amount specific by user

Catastrophes (if applicable)

- Adjusts birth and survival rates for catastrophes

Reproduction

- Selects breeding males for the year (independent each year)
- Pairs each breeding female with one breeding male
- Size of litter produced per pair is chosen by comparing probability of each potential litter size with random number
- Offspring are randomly assigned 1 allele at the hypothetical neutral locus from each parent

Inbreeding

- Calculates kinship of each new offspring to each other living animal in the population
- Calculates inbreeding coefficient for each individual (kinship between parents)

Mortality

- Compares survival probability to random number
- For individuals < 1 year, applies the effect of inbreeding depression on survival:
 $S = S_0 * e^{(-b * F)}$
S₀: Survival of non-inbred individuals
b: Average number of lethal alleles per haploid genome
F: Inbreeding coefficient

Age Individuals by 1 Year

Dispersal

- Moves individuals between populations w probability from dispersal matrix

Population Growth

- Calculated as (N_t / N_{t-1})

Density Dependence (Ceiling Model)

- Pop size truncated if $N > K$
- Prob of animal dying due to truncation = $(N-K)/N$

Summary Stats Calculated for Year

Summary Stats Calculated for Iteration

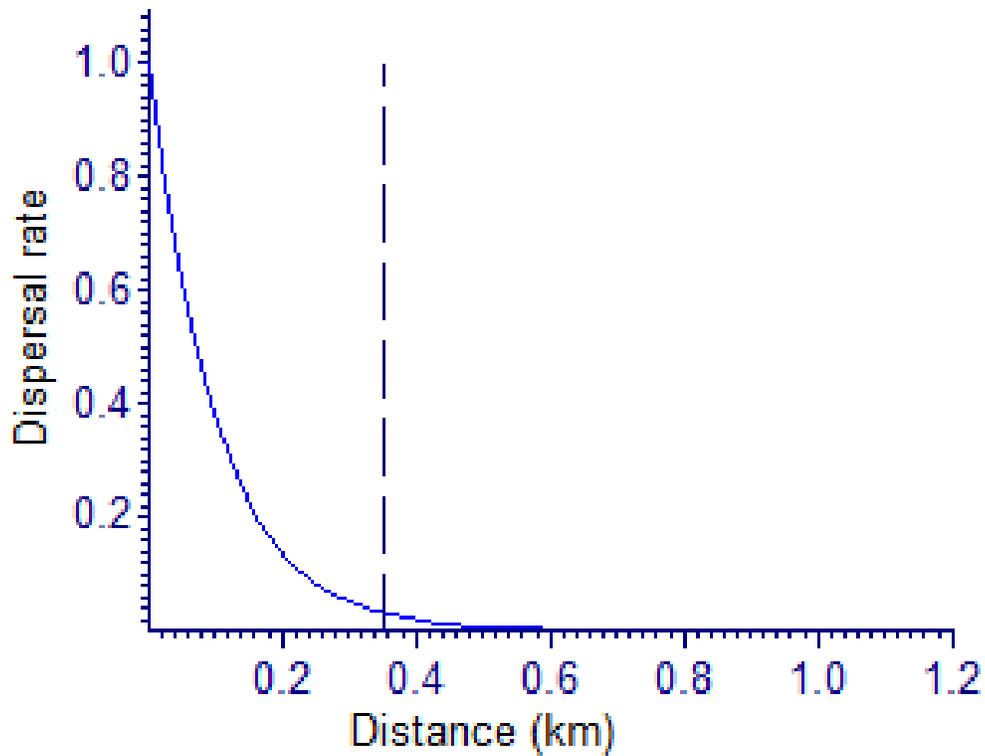
Iterations Averaged

Dispersal rates were calculated in RAMAS GIS ver5.0 and assumed to be distance-dependent based on the function:

$$M_{ij} = e^{-\frac{D}{b}} \quad \text{up to } D_{\max}$$

where M is the dispersal rate between populations (patches) i and j , D is the distance between populations (patches) i and j , b is the average dispersal distance (100 m), and D_{\max} is the maximum dispersal distance (1 km).

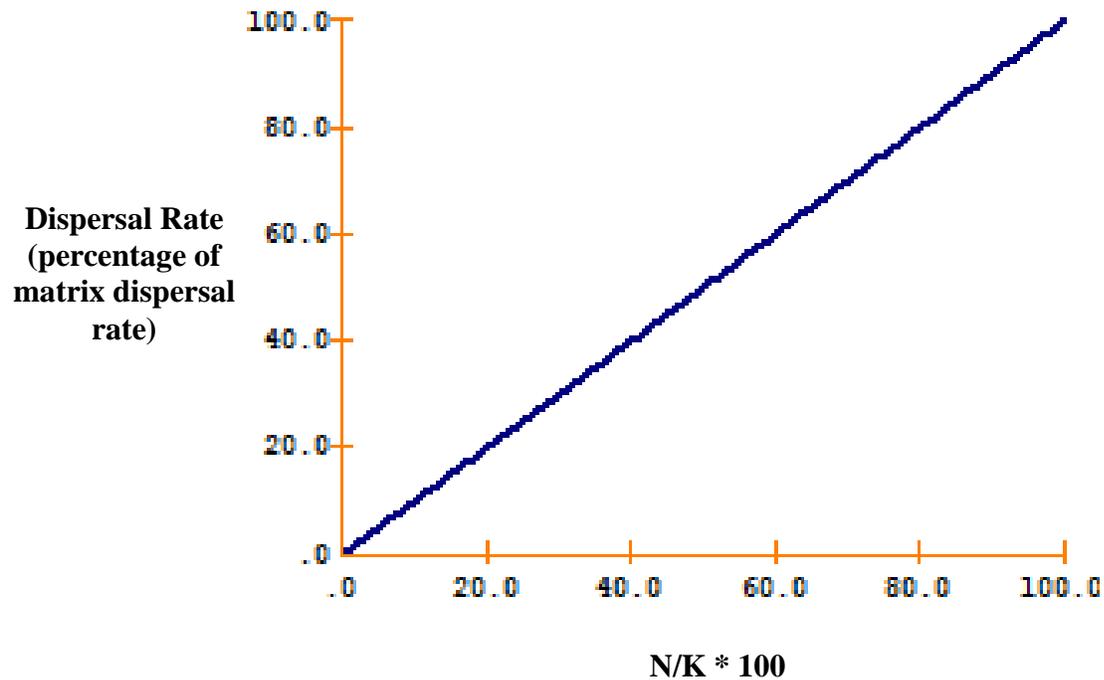
Dispersal-distance



Dispersal was also assumed to be density-dependent such that dispersal rates declined with decreasing population density according to the equation:

$$D_{ij} = D_{\text{matrix}} * (N/K)$$

where D_{ij} is the dispersal rate between populations i and j , D_{matrix} is the dispersal rate given in the dispersal matrix (defined by distance-dependent dispersal function), N is the population size, and K is carrying capacity.

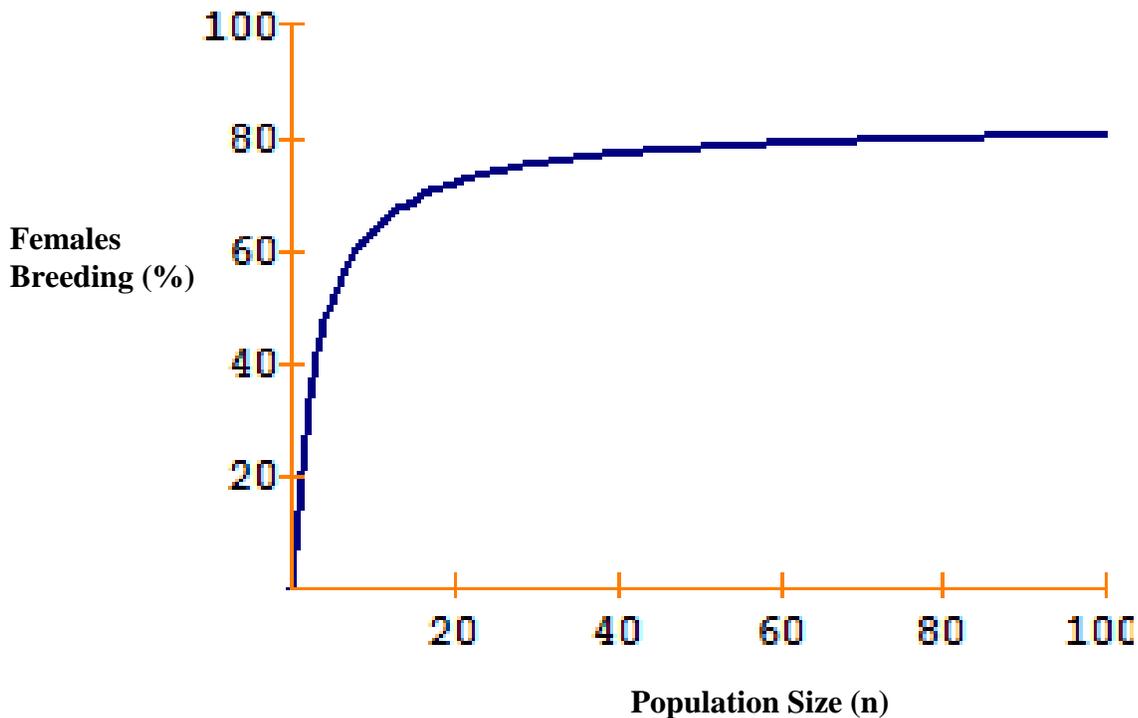


Reproduction was density-dependent such that, due to Alleé effects, the percentage of females breeding was reduced at low population sizes based on the equation:

$$P(N) = ((P(0) - [(P(0) - P(K)) * (N/K)^B]) * (N/(N+A)))$$

$$P(N) = 82.9\% * (N/(N+3))$$

where P(0) is the percentage females breeding at low population density (assuming no Alleé effect), P(K) is the percentage females breeding at high population density, B is the shape of the curve, and A is the Alleé parameter (population size at which the percentage of breeding females is half of what it would be without an Alleé effect). I assumed the percentage females breeding at both high and low densities was 82.9% as observed in the field, B was 1 (linear relationship), and A was 3 individuals.



Appendix II. Parameterization of population viability analysis models for golden-headed lion tamarins simulated in Vortex ver9.72 as part of Chapter 4.

Parameter	Baseline Value	Equation	Description
<i>Model</i>			
Years	100		Population viability was simulated over 100 years.
Iterations	1000		Because this is a stochastic model, I ran each simulation 1,000 times to determine average population trends and local extinction risk. With 1,000 replications, the risk curves have a 95% confidence interval of about +/- 0.03 (Akçakaya 2005).
Time Step	1		Each time step was equivalent to 1 year.
<i>Inbreeding Depression¹</i>		$S = S_0 * e^{(-b * F)}$	Vortex models inbreeding depression as an exponential reduction in first-year survival for inbred individuals.
b; Number of Lethal Equivalents ¹	4.07		The number of recessive alleles per haploid genome that would cause the observed rate of inbreeding depression; incorporates the severity/nature of inbreeding depression.
F; Inbreeding Coefficient	Calculated by Vortex		The inbreeding coefficient for each individual is calculated as the kinship between that individual's parents.
<i>Dispersal (D)</i>			
Dispersal Age	2-16 years		Age range at which individuals can disperse between populations (Raboy 2002; Raboy unpublished data).
Dispersal Mortality	50%		I assumed that half of all dispersers would die in non-forest matrix before reaching the target population.
Dispersing Sexes	Males, Females		I assumed both sexes are equally likely to disperse.

Dispersal Modifier	N/K	$D = D * N/K$	Dispersal rate decreases linearly as population size declines from carrying capacity (Appendix I).
Dispersal Rates	Calculated in RAMAS GIS	$M_{ij} = e^{(-D/b)}$ up to D_{max}	Distance-dependent dispersal was calculated in RAMAS GIS such that the rate of dispersal (M) between populations on patches <i>i</i> and <i>j</i> was a negative exponential function, D was the distance between patches <i>i</i> and <i>j</i> , D_{max} is the maximum dispersal distance (1 km), and b is the average dispersal distance (100 m; Appendix I). Distance-dependent dispersal rates were decreased to 25% in cases where the total rate emigration exceeded 25% of individuals in the source population.
<i>Reproductive System and Rates</i>			
Reproductive System ²	Monogamous		Under monogamous mating, there must be one male for each female for breeding to occur, and both sexes are limiting.
Age First Offspring (female) ²	4 years		Age at which females begin breeding.
Age First Offspring (male) ²	4 years		Age at which males begin breeding.
Max Age Reproduction ²	16 years		Age at which individuals are removed from the breeding pool.
Max # Progeny ³	4 offspring		Largest number of offspring a single female can produce in a given year.
Litter Size			Probability of females having specified number of offspring per reproductive year.
1 offspring	33.3%		
2 offspring	45.5%		
3 offspring	4.5%		
4 offspring	16.7%		
Sex Ratio at Birth ²	50% males		Average percentage of newborn males born per year.
% Adult Females Breeding ³	82.9%		Mean percentage of females that breed in a given year. I assumed this rate was density-dependent (see density-dependent reproduction; Appendix I).

Density-Dependent Reproduction	P(0), P(K) = 82.9%	$P(N) = ((P(0) - [(P(0) - P(K)) * (N/K)^B]) * (N/(N+A)))$ $P(N) = (82.9 - (N/K)) * (N/(N+3))$	Vortex models density dependence in reproduction by modifying the percentage of females breeding. I assumed that reproduction did not decline at high population densities, but that the probability of reproduction (and thus the percentage of breeding females) was lower at low population densities due to Alleé effects (Appendix I).
A	3		Magnitude of Alleé effect, modeled at the population size at which the percentage of breeding females falls below 50%.
B	1		Determines the shape of the curve for density-dependent reproduction. I used B = 1 so that the percentage of breeding females declines linearly with population size.
% Males Breeding ²	100%		Mean percentage of males that breed in a given year.
Mortality			Vortex models mortality as the percentage of individuals of age X that die before reaching age X + 1
			Sex- and Age-specific Mortality Rates ³ (Environmental Variation ⁴)
Age Class:		Males (EV)	Females (EV)
0-1 year old		35.0% (0%)	35.0% (0%)
1-2 years old		13.9 (0)	14.8 (13.0)
2-3 years old		4.0 (3.0)	26.5 (0)
3-4 years old		5.4 (0)	28.1 (12.1)
> 4 years old		16.2 (1.6)	13.3 (0)

¹J. Ballou personal communication, Ralls et al. 1988

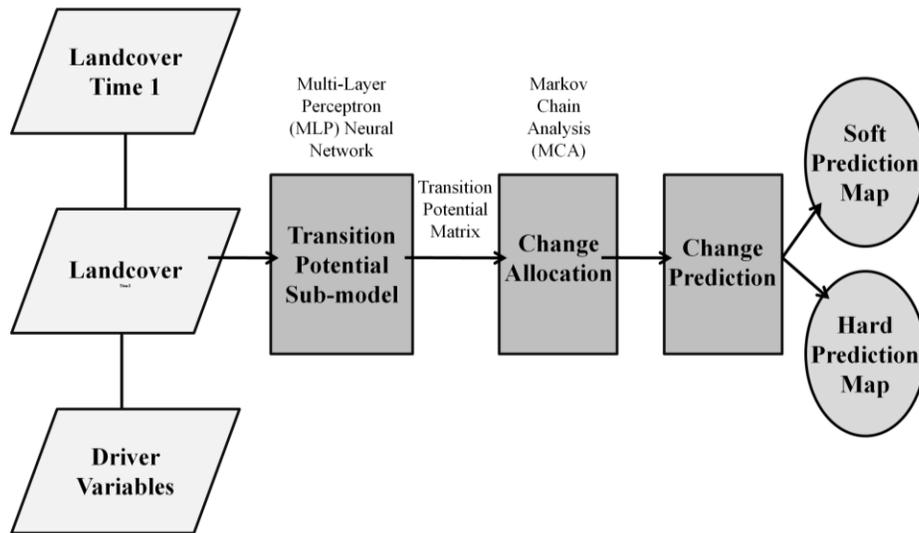
²Holst et al. 2006

³Raboy unpublished data; see Zeigler et al. for calculations

⁴Value of 0 indicates all variation accounted for by demographic variance, which is automatically incorporated in Vortex

Appendix III. Parameterization of Land Change Modeler (Clark Labs).

Land Change Modeler (LCM; Clark Labs) is software for landcover change analysis and prediction and is available through IDRISI GIS and Image Processing software (Clark Labs) or as an extension in ArcGIS (ESRI). I used the ArcGIS extension to model landcover change throughout the range of the golden-headed lion tamarin (GHLT, *Leontopithecus chrysomelas*) in Bahia, Brazil. LCM evaluates and predicts change through three steps: change analysis, transition potential, and change prediction.



The first step is an exploration of historical change between the two landcover maps input by the user. In my analysis, change was analyzed between landcover maps derived from a supervised classification of Landsat 5TM satellite imagery captured in 1987 and 2007 (see Zeigler et al. 2010 for details on how these maps were

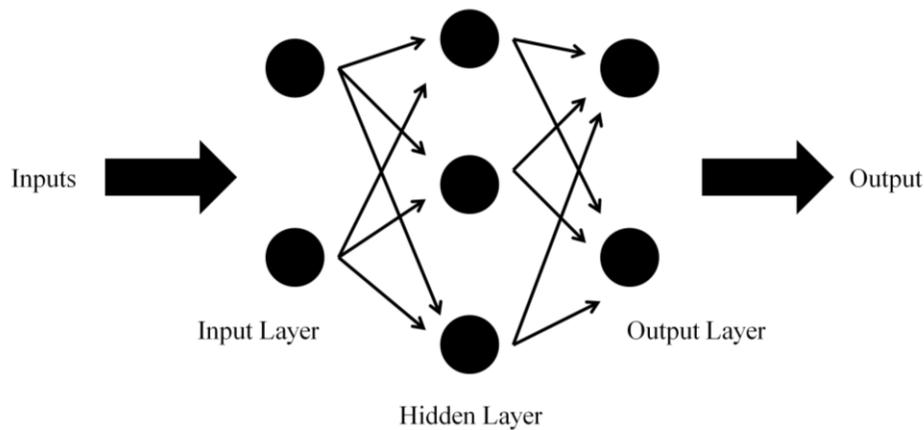
created). Cells (30 m) were classified as (1) forest, (2) non-forest, (3) water, and (4) clouds and shadows. Because I was interested in deforestation, I chose to focus solely on the change of forest pixels in 1987 to non-forest pixels in 2007. I called this the 'Forest Loss' sub-model and proceeded with this model for subsequent change allocation and prediction.

LCM then allows the user to test potential drivers of landcover change by using the Cramer's V statistic to test the association of a given landscape characteristic to the distribution of landcover types in the later landcover map. LCM bins quantitative variables into 256 categories and calculates a Cramer's V score between each test characteristic and landcover category. Cramer's V scores greater than 0.15 are considered useful and greater than 0.4 are considered good (Clark Labs 2007). I predicted that the forest that persisted from 1987 to 2007 would be in areas of high elevation and low human population density and at large distances from roads, rivers, and cities; forest in these areas should be less vulnerable to deforestation in the future. I tested the power of these landscape characteristics using Cramer's V and found that elevation, human population density, and distance from previously cleared areas were correlated while distance from roads and cities were uncorrelated with forest patterns (Table 9). Correlated landscape characteristics were considered 'potential drivers of change' and subsequently included in the transition potential sub-model.

LCM then uses the landcover maps and potential drivers of change to create a transition potential matrix, which indicates the probability of each cell on the landscape changing to a different landcover type, using a multi-layer perceptron

(MLP) neural network. The MLP neural network is the default model in LCM since this model has demonstrated the ability to perform rapidly and accurately, to incorporate a priori knowledge and realistic physical constraints, and to incorporate different types of data (reviewed in Atkinson & Tatnall 1997).

In general, the MLP architecture consists of three types of layers (input, hidden, and output) comprised of nodes:



In the input layer, nodes are elements of a feature vector that, in this model, include the maps for landcover in 1987, landcover in 2007, and landscape characteristics associated with forest/non-forest cover. The hidden layer(s) is internal and consists of the nodes where learning occurs. The output layer represents all output data, in this case the change prediction map. Nodes in each layer of the network are interconnected to nodes in both the preceding and following layers by connectors with associated weights. Signals are fed-forward, or passed from the nodes in the input layer to nodes in the hidden layer, after being modified by connection weights. The receiving node sums the weighted signals from all nodes to which it is connected in the preceding layer, applies a non-linear sigmoid function to the weighted sum, and

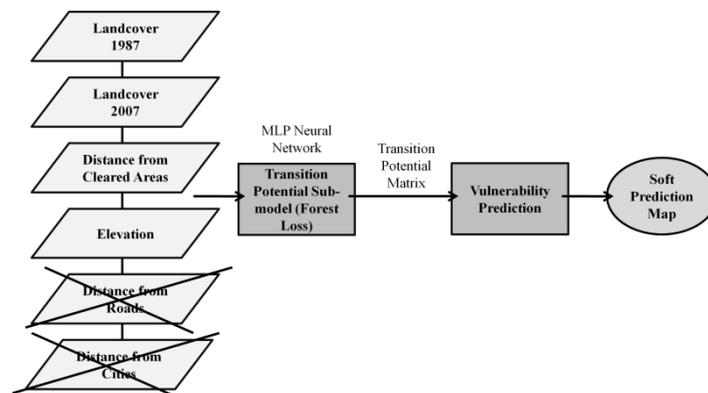
passes the new, modified signal to the next layer. This is repeated through all internal hidden layers until the signal is finally passed through the nodes in the output layer as the network output. The network output is then compared to the desired output (based on known validation data), and error is computed. The model then back-propagates the error through the network, altering the weights of connections according to the generalized delta rule:

$$\Delta \omega_{ji}(n + 1) = \eta(\delta_j o_i) + \alpha \Delta \omega_{ji}(n)$$

where η is the learning rate parameter, δ_j is the index of rate of change in error, and α is the momentum parameter. The process of feeding forward and back-propagating error is repeated iteratively until error within the network is minimized or reaches some acceptable magnitude as specified by the user (Atkinson & Tatnall 1997). In LCM, I used a sample size of 10,000 cells, learning rate of 0.001, momentum factor of 0.5, and 10,000 iterations of back-propagation. The model ultimately created a multivariate function with weights for the driver variables determined through the weights of connections in the neural network. It also produced an associated transition potential matrix describing the likelihood of each 30 m cell in the 2007 landcover map changing to any other landcover type in the future. Because I modeled only one transition, the transition potential matrix describes the potential of a cell that was forest in 2007 to transition to non-forest in the future.

Finally, transition potential matrix and landcover maps are analyzed in the change prediction sub-model in LCM to create maps depicting (1) the landscape's

vulnerability to change in the future (soft prediction map) and (2) the predicted forest cover at a specified future date (hard prediction map). The soft prediction map is a continuous map of relative vulnerability to change that establishes the degree to which areas have the right conditions to precipitate change and thus the highest transition probabilities in the transition potential matrix. In my model, forested areas at low elevations, near previously cleared areas, and/or near areas of high human population density have the highest probability of being converted to non-forest and thus have the highest relative vulnerability index (approaching 100) on the soft prediction map (Figure 14). The hard prediction map shows one realization of many possible future outcomes of continued landcover change. After considering the ‘end’ prediction date to be modeled, LCM analyzes the earlier and later landcover maps in a markov chain analysis to determine the quantity of change that will occur. LCM then uses the transition potential matrix to allocate this quantity of change to the cells with the highest probability of change based on a competitive land allocation model. In my model, LCM would have allocated change to forested cells with the highest probability of being converted to non-forest. However, because many more cells with a high probability of change may exist relative to the actual quantity of change, the exact location of cells that transition in the hard map may be different in different hard maps. For this reason, I did not create hard prediction maps of the GHLT range.



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