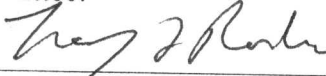
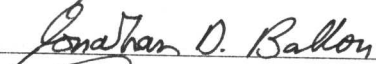
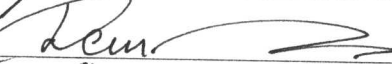
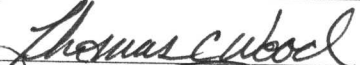
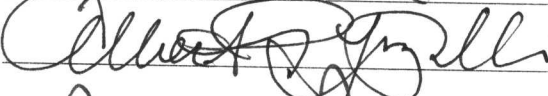
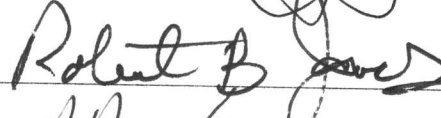

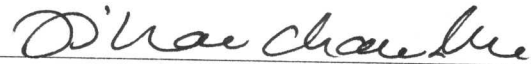


UNDERSTANDING AND MANAGING ISOLATION IN A FRAGMENTED
POPULATION OF GOLDEN LION TAMARINS, *LEONTOPITHECUS ROSALIA*

by

Jennifer L. Mickelberg
A Dissertation
Submitted to the
Graduate Faculty
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The Requirements for the Degree
of
Doctor of Philosophy
Environmental Science and Public Policy

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Understanding and Managing Isolation in a Fragmented Population of Golden Lion
Tamarins, *Leontopithecus rosalia*

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DEDICATION

To my mother, Cheryl Nash, and esteemed mentor, Devra Kleiman—two strong, inspirational women I greatly admire who have taught me the meaning of independence and perseverance.

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ABSTRACT

UNDERSTANDING AND MANAGING ISOLATION IN A FRAGMENTED POPULATION OF GOLDEN LION TAMARINS, *LEONTOPITHECUS ROSALIA*

Jennifer L. Mickelberg, Ph.D.

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Habitat fragmentation is one of the most pervasive threats affecting wildlife populations around the world. The resulting fragments are often small and isolated, increasing a population's risk of extinction. Demographic variation, such as fluctuation in birth or death rates, can cause a small population's numbers to plunge so low that recovery is impossible. Due to lack of gene flow, small, isolated populations eventually lose genetic diversity, become inbred, and suffer from inbreeding depression. These threats, however, can be reduced if there is some movement of animals, and gene flow, between populations. Unfortunately, movement of individuals between populations is restricted due to often unsuitable or even hostile environments separating the populations. Improving connectivity in these cases is vital for long term population persistence and viability. Therefore it is critical for conservation planning to include strategies that promote gene flow and metapopulation management strategies. The path to creating

these successful plans begins with an understanding of the population's status and the factors that affect movement in a fragmented landscape. The golden lion tamarin (*Leontopithecus rosalia*; GLT), an endangered primate native to the Atlantic Coastal forest in Brazil, lives in a landscape that is highly fragmented providing a perfect platform to investigate the effects of fragmentation and isolation on genetic status, movement, and long-term population viability. Currently around 1,600 GLTs are divided among at least 7 isolated populations (management units).

The first study in this dissertation evaluates the genetic status of the reintroduced population of golden lion tamarins and determines if future reintroductions from captivity could further contribute to the wild population's genetic diversity. Results indicate that the overall genetic status of the reintroduced GLT population is favorable; the population is currently maintaining relatively high levels of genetic diversity. However, this population is small and fragmented and is still at risk. Further reintroductions could enhance the genetic diversity and carefully selected translocations could help increase the genetic diversity of the isolated management units. This study demonstrates the power of using pedigree analysis for assessing wild populations and further using this information to make management recommendations for the conservation of the species.

The second study investigates the level of connectivity in the GLT reintroduced population as well as factors that affect movement by examining the movements that occurred between groups and populations. This study demonstrates that distance is the most important factor that will affect movement in this fragmented population.

Additionally, movement within seemingly connected habitats can actually be quite

limited such that within a single management unit, there may be functional units that do not have movement between them despite their structural connectivity. From the 7 management units that have been classified, this study demonstrates that there are actually a minimum of 11 functional units.

Based on the population structure as defined by the second study, the third study uses *VORTEX*, an individual based modeling program, to model the long term metapopulation and functional unit viability, measured by probability of extinction and retained genetic diversity. The model indicates that the metapopulation is viable for the 100 years modeled. Notably however, only the two largest units were needed to meet the minimum requirements for population viability. The smaller units were vulnerable to the loss of genetic diversity and require an increase in gene flow to meet the genetic target for viability. Even with an increase in connectivity however, the genetic diversity of the 11 isolated units is not able to match that of the metapopulation modeled as a panmictic population. Collectively, these studies contribute to the understanding of the effect of isolation on population viability, genetic status, and movement. Specifically, this information helps form the scientific basis on which effective management strategies can be based to promote population persistence in the fragmented population of golden lion tamarins.

INTRODUCTION

Wildlife populations around the world are threatened by habitat loss and fragmentation. These threats often lead to small, isolated populations that are increasingly vulnerable to extinction. Variation in demographic rates such as birth or death rates can push a small population to become even smaller, making recovery nearly impossible (Drake and Lodge 2004). Additionally, due to inbreeding and genetic drift, small, isolated populations eventually suffer from low genetic diversity and inbreeding depression (Frankham et al. 2010). These threats can overwhelm small populations if they are not properly managed. When populations are not able to be expanded through an increase in habitat, increasing gene flow between populations is one method to help buffer against demographic variation and the loss of genetic variation (Hanski and Gilpin 1997). In many cases, however, movement between populations is restricted due to hostile matrix separating the populations. Improving connectivity in these cases is critical for long term population persistence and viability (Crooks and Sanjayan 2006). For example, using forest corridors to connect isolated forests can promote gene flow and support a metapopulation structure (Beier and Noss 1998). Conserving endangered species will likely depend on using such techniques to ensure small populations do not go extinct. Therefore it is critical for conservation planning to include strategies that promote gene flow and metapopulation management strategies. The path to creating these successful

plans begins with an understanding of the population's status and the factors that affect movement in a fragmented landscape.

Metapopulation Ecology

With an increase in fragmented populations, metapopulation biology has become increasingly important in developing long-term conservation strategies. A metapopulation structure, where an overall population is composed of a number of smaller populations with some level of migration between them, can help reduce genetic and demographic deterioration (Hanski and Gilpin 1997). Levins (1969) was the first to examine the characteristics of a metapopulation, considering the interactions among an infinite number of small populations with the same quality and size of habitat. Under this model, extinction and immigration probabilities were identical for every population and the number of patches occupied in the metapopulations was determined by both of these factors (Levins 1969). Metapopulation theory was further modified by Hanski and Gilpin (1991) who considered a metapopulation consisting of a finite number of populations of varying quality and size. These more realistic models have populations with immigration and extinction probabilities depending on their degree of isolation (Armstrong 2005).

Several patch models have been developed to predict metapopulation dynamics one of which is the Incidence Function Model (IFM) developed by Hanski (Hanski 1994, Rockwood 2006). This is a stochastic patch model where only the presence or absence of a species in habitat patches is modeled to predict metapopulation dynamics. These data

can be taken from a single field survey of patch occupancy data. Hanski et al. (1996) conducted a study to test the IFM using an endangered butterfly (*Melitaea cinxia*) population and found that this model was able to predict the patch occupancy in over half of the study area. The model proved to be less accurate in an area of the study site where there was variation in habitat quality (Hanski et al. 1996). While the IFM is a practical tool to examine metapopulation dynamics allowing a manager to see what patch network would be most likely to survive, Hanski recommends that caution be taken when applying any model (Hanski et al. 1996).

Metapopulations also vary in structures. Harrison (1991) defined 4 distinct metapopulation structures; classical (Levins), mainland-island (source-sink), non-equilibrium, and patch. Through modeling these different types of metapopulation structures, some generalizations on metapopulation dynamics can be made.

Metapopulations that are limited to a small number of populations face a real possibility of all subpopulations going extinct simultaneously, resulting in the extinction of the metapopulation (Nisbet and Gurney 1982). In terms of genetics, metapopulations that have low rates of extinction and high levels of migration behave like one large contiguous population (Frankham et al. 2010).

In cases where natural dispersal is not possible, creating a metapopulation management strategy to systematically transfer animals among habitat fragments as if they were dispersing naturally can lessen the risk of extinction (Frankham et al. 2010). As

populations become more isolated, conservationists are in search of methods that help facilitate dispersal and increase connectivity, optimizing the metapopulation structure.

Increasing Connectivity: Corridors and Translocation

One such method for increasing connectivity between fragments is the creation of corridors. Wilson and Willis (1975) were the first to propose the use of corridors to facilitate movement based on Island Biogeography Theory. From there, the idea of corridors expanded with little evidence to support them. Simberloff et al. (1992) discussed a blind acceptance of corridors and their presumed benefits despite the lack of evidence to support these claims. In their review they found four major rationales for maintaining corridors: increasing immigration, providing movement routes for wide ranging species, decreasing inbreeding depression and reducing demographic stochasticity. At that point, very little data were available to support these rationales. In 1998, Beier and Noss published a literature review on corridors investigating whether or not they provide connectivity and therefore improve population viability. They found that while there still was a lot of research to be conducted, those studies that were well designed suggested that corridors are valuable (Beier and Noss 1998). The debate on the effectiveness of corridors continues. Some argue that corridors can aid in the spread of disease (Hess 1994), catastrophic disturbances, and the movement of exotic species (Downes et al. 1997) which all have a negative impact on population viability (Simberloff and Cox 1987, Simberloff et al. 1992). In the last 10 years, there has been a number of papers published arguing both sides of this debate. For example, Tewksbury

et al. (2002) conducted an elaborate study which examined the effects of corridors on animals as well as plant-animal interactions at a landscape scale. Findings from this study show that corridors benefit both plant population and community interactions.

Translocation, the deliberate movement of wild individuals from one part of their range to another, is another conservation tool used to increase connectivity (Griffith et al. 1989, Molony et al. 2006, IUCN 2008). As in the case with corridors, there are possible negatives that need to be considered. Increase in aggression, possible disease introduction and outbreeding depression are all cited as possible detrimental effects (Molony et al. 2006). Financial costs are also high for most translocations (Kleiman 1989). Despite these risks, translocations can be used to reintroduce animals to their former range, increase numbers when populations are in decline or to speed up recovery rates (Griffith et al. 1989, Bright and Morris 1994). They can also be used to decrease the risk of extinction by catastrophes and can be critical in small populations to increase genetic diversity and maintain stable demographic rates (Griffith et al. 1989, Bright and Morris 1994).

There are several factors that can contribute to the success of translocations such as season and habitat quality of release site, number of animals released, release methods (soft or hard release) and level of competition in the release site (Griffith et al. 1989, Bright and Morris 1994, Letty et al. 2000). While studies have been done examining these variables, there seems to be no consensus on identification of the most important

factor for success and it can be species specific. For example, Letty et al. (2000) found that handling stress did not affect the survival or translocation of rabbits (*Oryctolagus cuniculus*) and acclimation success was correlated to sex. Bright and Morris (1994) found that pre-release conditioning and animal origin (captive or wild caught) were important for translocations of the dormouse (*Muscardinus avellanarius*). In otters (*Lutra lutra*), resource availability and location of conspecifics were important factors to translocation success (White et al. 2003). A study conducted by Molony et al. (2006), found that hedgehogs (*Erinaceus europaeus*) held temporarily in captivity before translocation were able to build up fat reserves and had an improved survival rate. Given the wide variety of results, more research is needed to better understand the factors that contribute to successful translocations. When successful, translocations can be used as a conservation tool to ultimately increase connectivity between populations, thereby increasing population viability.

Genetic Diversity

One component of population viability is genetic diversity. Genetic diversity is critical for both short and long term fitness and for maintain evolutionary potential (Frankham et al. 2010). Small populations are vulnerable to a loss in genetic diversity through the processes of inbreeding and genetic drift (the change in frequency of alleles as they are randomly passed from one generation to the next, ultimately leading to fixation of one allele). The smaller the population, the larger the impact from genetic drift (Frankham et al. 2010). In small populations, genetic drift can overwhelm selection such that alleles

that have effects on fitness behave just as those that are neutral, randomly being passed from one generation to the next. Inbreeding can increase homozygosity and the frequency of exposed deleterious alleles which can lead to reductions in reproduction and survival (Ralls et al. 1988, Frankham et al. 2010).

Genetic diversity is lost at a rate that depends on the effective population size (N_e), rather than the actual population size. Heterozygosity decays exponentially over generations at a rate that is inversely proportional to N_e (Frankham et al. 2010). Several factors affect N_e such as the fluctuation of population sizes over generations, variance in family size, and unequal sex ratios (Frankham et al. 2010). In most cases, the effective population size is much less than the actual population size, averaging only about 11% of the actual population. This is especially pertinent for threatened species that may have an effective population size of only a few hundred individuals making them vulnerable to the loss of genetic diversity.

Connectivity in landscapes affects the genetic diversity in populations. Fragments that are completely isolated have lower genetic diversity and higher rates of inbreeding (Crooks and Sanjayan 2006, Frankham et al. 2010). Increasing gene flow between isolated populations can help to reduce the loss of genetic diversity and decrease the risk of extinction. Even one migrant per generation can have a significant impact on the genetic of the recipient population (Spielman and Frankham 1992, Crooks and Sanjayan

2006). Therefore the strategies described above to increase connectivity can have a positive impact on genetic diversity for small, fragmented populations.

Given its impact on extinction, assessing the genetic status for species living in small populations is a valuable tool for their conservation. There are different types of genetic diversity; the two most common are allelic diversity and heterozygosity. Allelic diversity is the number of alleles at any given locus in the population. The greater the allelic diversity the more equipped a population may be to adapt to future changes; allelic diversity is important for evolutionary potential. Heterozygosity is the percentage of loci that are heterozygous in an individual or population and is important for short-term health. Average heterozygosity is the most commonly used indicator for genetic diversity in a population.

In wild populations, measuring genetic diversity is most frequently assessed using molecular techniques where DNA is collected from an organism or from several individuals in a population, and the frequency of alleles or heterozygosity at a set of loci is measured. These measures are then used to compare levels of genetic diversity among populations and estimate degrees of relationship between populations and individuals. However, these can only be rough estimates as even at the most rigorous level, only a few of the loci can be sampled out of the tens of thousands that exist.

Another method for measuring relative genetic diversity and relationships between population and individuals is through pedigree analysis (Haig and Ballou 2002). When data are available to construct pedigrees, levels of genetic diversity and relationships can be estimated by calculating kinships among individuals. These can then be used to calculate gene diversity, expected heterozygosity, population and individual levels of inbreeding, and changes in genetic diversity over time. There are distinctive differences between molecular and pedigree-based estimates. Whilst molecular measures provide absolute empirical (but only very rough) estimates of these, pedigree-based calculations provide relative statistical estimates of the same measures, relative in the sense that they are relative to those measures in population from which the founders of the pedigree derive (e.g., a pedigree-based heterozygosity of 0.92 means that the heterozygosity in the pedigree is 92% of the heterozygosity in the population from which the founders of the pedigree were derived – often referred to as the “source” population). Thus, using molecular analysis provides an empirical estimate of genetic diversity at only a few loci, while pedigree analysis provides a statistical measure of genome-wide level of diversity that is relative to the source population. Managing populations based on molecular techniques can result in populations that have high diversity in the loci that were sampled, but loss of diversity at all other loci; therefore, management based on pedigree analysis is more effective at maintaining genetic diversity than molecular methods (Slate et al. 2004, Fernandez et al. 2005).

Golden Lion Tamarins

The highly fragmented population of golden lion tamarins (*Leontopithecus rosalia*: GLT), an endangered primate endemic to the Atlantic Coastal forest of Brazil, provides an ideal situation for studying how a fragmented landscape affects the population structure in primates. Over the last 50 years, the Atlantic Coastal forest has been faced with increasing development pressure from the large cities that thrive within it; it is estimated that the Atlantic Coastal forest initially covered over 1.2 million squared kilometers of forest in pre-Columbian times (Dean 1995). It has since been reduced to less than 7% of its original area where most of this forest is in very small fragments, unsuitable for long term viability of most organisms (Ballou 1992, Kleiman and Rylands 2002, Wuethrich 2007).

The golden lion tamarins have become ambassadors for the Atlantic Coastal forest. They are found just 70 kilometers northwest of Rio de Janeiro and were first described in 1519 as “beautiful simian-like cats similar to small lions” by a priest, Antonio Pigafetta, who had been chronicling Magellan’s voyage around the world (Kleiman and Rylands 2002). It was not until 1766 that they were fully described by the Swedish scientist Carolus Linnaeus (Linnaeus 1766). At this time and for the next couple hundred years, the species was thought of as common. It was a Brazilian primatologist, Ademar F. Coimbra-Filho, who first recognized the plight of the golden lion tamarin in the early 1960s. In his 1969 paper, he described the species, which he estimated had a population size of around 200 (Coimbra-Filho 1969). He also described the threats to this species

which at that time included habitat loss and the pet trade. Due to the rapid decline in the population, several conservation efforts were initiated in the mid 1970s to restore this habitat and to protect the golden lion tamarin (Kleiman et al. 1987a, Kleiman and Rylands 2002). As a result of these conservation efforts, the population now stands at approximately 1,600 individuals divided into as many as 18 mostly isolated smaller populations of varying size (Holst et al. 2006, AMLD 2009a). In many cases, the habitat that surrounds the forest islands is pasture, likely inhibiting dispersal between populations. As part of their long-term conservation program, the Golden Lion Tamarin Association, the principal non-governmental organization conducting research on and implementing conservation actions for golden lion tamarins, has begun to construct forest corridors that connect many of these small fragments within these areas in efforts to increase natural migration between populations (AMLD 2009a). In many cases however, the populations are isolated and dispersing is risky. Most dispersers probably die trying to disperse, how many succeed is not known as little is known about how tamarins, or arboreal mammals in general, disperse in a highly fragmented landscape (Palomares et al. 2000, Anderson et al. 2007).

Tamarin Biology and Behavior

Golden lion tamarins are squirrel sized, arboreal primates that live in monogamous family groups. Family group range in size from 2 to 10 individuals (average 6 individuals) and typically consist of a breeding pair and their offspring (Coimbra-Filho and Mittermeier 1973, Kleiman 1981). Characteristic of the callitrichid family, GLTs

most commonly give birth to twins and all family member participate in the rearing of offspring (Kleiman 1981).

Golden lion tamarins are omnivorous with most of their diet composed of fruit and insects. As fruit eaters, they play an important role in the lowland forest ecosystem as seed dispersers (Coimbra-Filho and Mittermeier 1973, Lapenta et al. 2008, AMLD 2009a). They will also prey on small mammals, snakes, and amphibians (Kleiman 1981). Tamarins rely on bromeliads that are characteristic of the Atlantic Coastal forest as a source of water and as a prime foraging location due to the large number of frog and insects which use bromeliads as a breeding ground (Coimbra-Filho and Mittermeier 1973, Kleiman 1981). Family groups use hollowed out trees as sleeping sites and they often have many tree holes in their territory, which is around 40 hectares (Coimbra-Filho and Mittermeier 1973, Dietz et al. 1997, Hankerson and Dietz 2005). They are very territorial and will mark their territory with scent marks and defend it against other family groups (Kleiman 1981).

Tamarin Dispersal

At around two years of age, GLTs become sexually mature and normally disperse from their natal group (Baker and Dietz 1996). Both sexes disperse, with the highest rates from March through July (Baker 1991). Dispersal is a very risky behavior for a golden lion tamarin as they may be more vulnerable to predation and other physiological stressors. Mortality rates are some of the highest during this age class and are surpassed

only by tamarins of extremely young or old ages (Baker and Dietz 1996). Females will disperse alone and occupy the first available habitat they encounter, while males have been observed to disperse alone or with a male sibling. Occasionally, lone males dispersing from different groups will travel together until they encounter an available female (Baker 1991).

Very little is known about how GLTs move in this fragmented landscape and what factors contribute to successful movement. Patterns of habitat exploration are likely to be affected by such things as the number of other GLTs in the fragment, the size and shape of the fragment, the proximity of other fragments, the complexity of the matrix between fragments and the length of time since dispersing from the natal group (Chepko-Sade and Halpin 1987). More research is needed to better understand movement in this heavily fragmented landscape.

GLT Population Structure

The population of golden lion tamarins is fragmented into several small and medium size populations primarily located in the Sao Joao watershed in Rio de Janeiro State. These populations were reclassified during a Metapopulation Workshop in 2009 into 7 different management units (MU) as described below (AMLD 2009b).

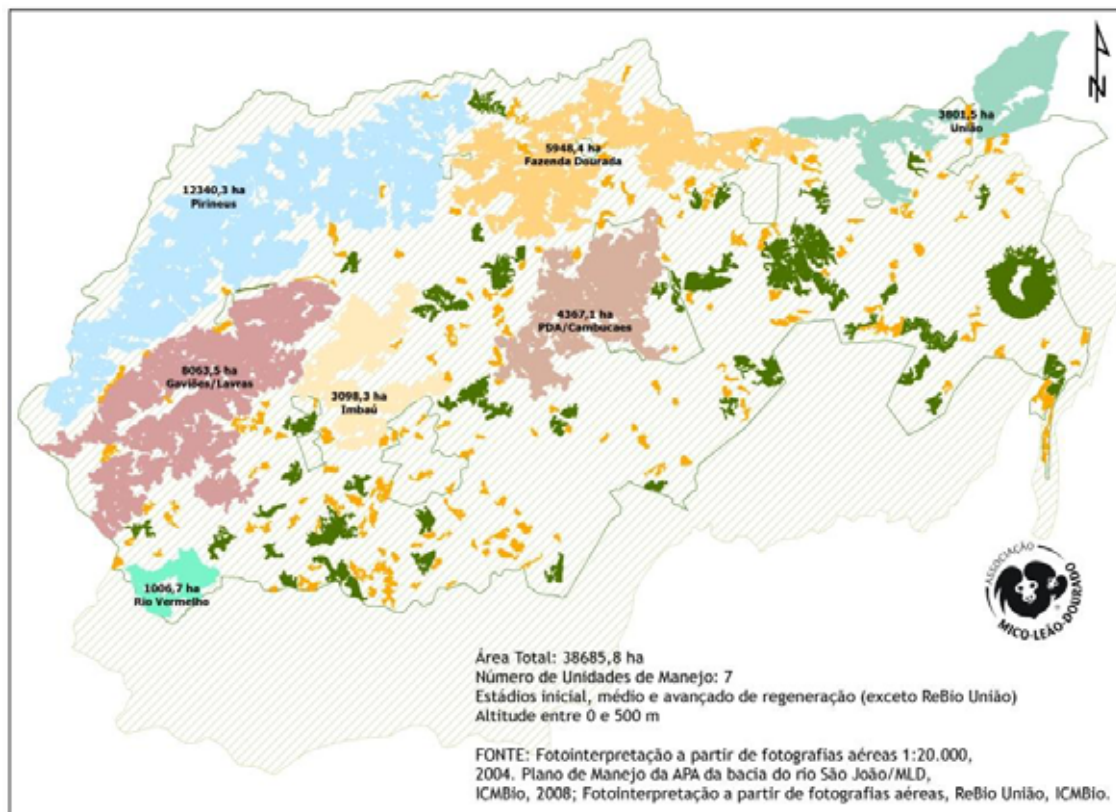


Figure 0.1. Map with GLT metapopulation management units (MUs). The size of each MU is shown in hectares. Image from AMLD 2009b

Poço das Antas: In 1974, Poço das Antas (PDA), the first biological reserve in Brazil, was created with the goal of protection and conservation of the golden lion tamarin (Kleiman and Rylands 2002). This population of golden lion tamarins has been extensively monitored since the 1980s with emphasis on the natural ecology, biology, and behavior of GLTs (Baker 1991, Dietz et al. 1997).

União: This population is primarily composed of descendents from a translocation program that began in 1994. The program identified 12 groups of GLTs that were living in fragments that were either too small to support a healthy population or were in danger of being destroyed (Kierulff and Rylands 2003). The animals living in these forest fragments were thought to be genetically valuable since they were located outside of Poço das Antas and had likely been separated from the primary population for many years (Grativol et al. 2001). In an effort to preserve the highest possible amount of gene diversity, the goal was to relocate these groups to a safer, larger forest (Kierulff and DeOliveira 1996). To date, six groups have been translocated to União. This area was initially owned by the Brazilian Federal Railway Company, but after five years of negotiations became the União Biological Reserve in April 1998 (Kierulff and Rylands 2003). This reserve has the second largest block of lowland Atlantic forest in the state, with Poço das Antas being the largest (Kleiman and Rylands 2002).

Imbaú, Dourada, and Rio Vermelho: GLTs living in these three MUs are descendents of animals that were reintroduced from the captive population between 1984 - 2000 (Beck and Martins 2003). Both Imbaú and Dourada are composed of several privately owned farms where reintroductions have occurred. Many of these farms and ranches are officially registered as Private Natural Heritage Reserves (RPPN), giving legal protection to this habitat. Rio Vermelho is the largest privately owned ranch where tamarins have been released.

The GLT Reintroduction Program began in efforts to increase the number of GLTs in the population, increase the genetic diversity through careful selection of reintroduction candidates and also increase habitat (Beck and Martins 2003). This program has met each of these goals (Beck and Martins 2003) and is often regarded as one of the most successful programs for returning endangered captive-born individuals to the wild. This success is in part due to the extensive post-release monitoring that occurred (Beck et al. 1991, Kleiman and Rylands 2002). Once released, the GLTs were monitored, given food and water, a nestbox and support as needed. This intensive support continued until the animals were acclimating to their new environments at which point monitoring continued, but the level of support was decreased. Reintroduction ended in 2000 after a total 147 captive animals and 6 confiscated animals had been released, largely due to the program's success; the population was growing well on its own and there was no longer suitable habitat within commuting distance. The reintroduced animals have left a descendant population of about 700 individuals (Beck and Martins 2003).

Pirineus and Gaviões: These two units are located in the mountainous northwestern boundary of the Sao Joao Watershed. They have not historically been monitored by the GLT Association and little is known of the characteristic of these two MUs, although it is suspected that they live at much lower densities in these areas. Research is now being conducted to get more information important to effectively conserve GLT in these areas.

Research Objectives

The purpose of this project is to understand how habitat fragmentation impacts movement between forest fragments in an arboreal primate (the GLT) and use this information to create a long-term management plan to increase population viability. The current landscape and population structure provide an excellent opportunity to examine isolation and movement in a fragmented landscape. Additionally, the information already available on the GLT population and the infrastructure in place in Brazil make this study possible.

This dissertation has three components:

1) An examination of the genetic status of the reintroduced populations of GLTs using pedigree analysis.

As the reintroduced population has been monitored for the last 20 years, those data can be used to construct a pedigree. The pedigree will be analyzed to determine the genetic status in the three reintroduced MUs (Imbaú, Dourada, Rio Vermelho). Pedigree analysis is a powerful tool for accessing genetic status and monitoring loss of genetic diversity over time (Haig and Ballou 2002). It provides an estimate of genomic-wide diversity whereas molecular analysis estimates diversity using just a few loci out of the tens of thousands genes that make up the genome. Therefore, when pedigree data are available as they are in this case, pedigree analysis is better suited to guide management strategies to maintain genetic diversity (Slate et al. 2004, Fernandez et al. 2005).

2) An examination of the movement of golden lion tamarins in the fragmented landscape.

The movement data available for the reintroduced populations in Imbaú, Dourada, and Rio Vermelho will be analyzed to determine which factors affect movement, specifically examining the effect of distance, fragment size, and population size and density.

Movement data will also be used to evaluate the connectivity in the population, particularly the functional connectivity in these management units to confirm if tamarins are moving freely within them.

3) The use population viability analysis to assess the long-term viability of the population in terms on probability of extinction and the maintenance of genetic diversity.

The individual based population viability analysis program *VORTEX*, will be used to examine the long term status of the metapopulation. *VORTEX* will be used to determine the value of each unit to overall metapopulation persistence and the minimum number of units needed to maintain a viable population. For any unit not viable, strategies will be modeled in efforts to rescue the units. Finally, differently levels of connectivity between units will be modeled to determine the minimum needed to meet viability goals and determine if it is possible to maintain the same level of genetic diversity within the units as with the population as a whole. For this study, viability includes maintaining populations with no risk of extinction as well as high levels of genetic diversity.

CHAPTER 1

Evaluation of the Reintroduced Golden Lion Tamarin Population Using Pedigree Analysis

Introduction

Deforestation and habitat fragmentation are two of the most pervasive threats affecting wildlife populations around the world. The resulting habitat fragments are often small and isolated, increasing a population's risk of extinction due to stochastic changes in demographics and genetic variation (Frankham et al. 2010). Maintaining genetic diversity is vital in the fight against extinction and has been identified as one of the primary levels of conservation by IUCN (McNeely et al. 1990). High levels of gene diversity are important for fitness of a population (Reed and Frankham 2003), disease resistance (Frankham et al. 2010) and the maintenance a population's evolutionary potential (Franklin 1980, Burger and Lynch 1995, Frankham et al. 1999). Genetic variation is lost through selection and random genetic drift, but in small populations, unless selection is strong, genetic drift is the primary mode of loss (Lacy 1987). While both small and large populations lose genetic variation through genetic drift, the smaller the population, the faster its gene diversity is lost and the more inbred the population becomes (Frankham et al. 2010). Inbreeding between related individuals over multiple

generations has been shown to decrease survival and reproduction rates in several species (Ralls et al. 1988). Therefore, maintaining high genetic diversity and low inbreeding is critical for the long term viability of small populations.

Because of its importance, maintaining genetic health is frequently a principal conservation goal for managed populations. Genetic management of wild populations can prove to be a challenge, but a model exists in captive population management where techniques have been developed to maximize genetic diversity and minimize inbreeding (Ballou and Lacy 1995, Ballou and Foose 1996). Genetic diversity is retained through the equal retention of founders and minimizing kinship (Ballou and Lacy 1995, Caballero and Toro 2000). Kinship levels are calculated and used to ensure that animals that are under-represented receive breeding recommendations and those with many relatives in the population do not. Captive populations are managed at the level of individuals to ensure long-term health of the population and if necessary, can serve to enhance or create a new population through reintroduction (Kleiman et al. 1987b, Kleiman 1989, Ballou 1992). This individual level of management is not possible or practical for wild populations; nevertheless the tools and techniques for captive management can provide insight and guidance into assessing and managing genetic diversity in wild populations. This is especially true in reintroduced populations derived from captive populations previously managed under such intense guidelines. If similar genetic monitoring can continue post reintroduction, this can provide valuable information for guiding future *in situ* management strategies.

One method available to measure genetic diversity in populations is through pedigree analysis. While pedigrees are frequently used for captive and domestic population management, they are rarely used for wild populations (Haig and Ballou 2002).

Although pedigree analysis may not be feasible for all wild populations given the amount of data needed for their construction, they can be a valuable tool for analysis. Pedigree analysis provides information on the genetic micro-structure of populations and allows the examination of the relative changes in genetic diversity over time through the simulation of the passage of genes across generations (Haig and Ballou 2002). Pedigree analysis also allows for the identification of which founder lines have contributed to population structure (Haig and Ballou 2002). Given the value of pedigree analysis and the life history information available, this technique was used to evaluate the genetic status of the reintroduced population of golden lion tamarins.

The golden lion tamarin (*Leontopithecus rosalia*: GLT) is a small, endangered primate endemic to the Atlantic Coastal Forest of Brazil. Living just 70 kilometers northwest of the city of Rio de Janeiro, the golden lion tamarin lives in a highly fragmented forest where less than 7% of the original forest remains (Coimbra-Filho and Mittermeier 1973, Wuethrich 2007). Due to deforestation and the pet trade, only a few hundred animals were estimated to be living in the early 1970s when a conservation program to protect GLTs began (Coimbra-Filho and Mittermeier 1973, Kleiman and Rylands 2002). The primary objective of this program was to prevent the extinction of golden lion tamarins

and further loss of their habitat, the lowland coastal forest. Several conservation actions have taken place including the establishment of two federal biological reserves (Poço das Antas and União) and field studies to examine the ecology and behavior of wild golden lion tamarins (Baker and Dietz 1996, Dietz et al. 1997, Kleiman and Rylands 2002). In addition, the captive program was strengthened through better husbandry, and managed to maintain genetic diversity (Kleiman and Rylands 2002). In 1984, with the stabilization of the captive population, a reintroduction program was started with the objective to increase the population of GLTs as well in increase genetic diversity through the introduction of captive animals to the wild (Beck et al. 1991, Beck and Martins 2003). Reintroductions took place until 2000 at which point the suitable habitat within commuting distance of the field team was occupied. Cumulatively, these conservation efforts have increased the population of golden lion tamarins to approximately 1,600 individuals (Kleiman and Rylands 2002, AMLD 2009a).

Given these intensive conservation strategies, the population of golden lion tamarins is among one of the best studied primates in the world. These long term studies have contributed to the overall knowledge of golden lion tamarins, but have also been important for developing effective conservation strategies using adaptive management. Management goals for the golden lion tamarin include optimizing genetic diversity (Kleiman and Rylands 2002, Holst et al. 2006). In order to meet this goal and develop successful conservation programs, an understanding of the population's genetic characteristics is required.

The purpose of this study is to evaluate the genetic status of the reintroduced population of golden lion tamarins and to determine if future reintroductions could further contribute to the wild population's genetic diversity. This study demonstrates the power of using pedigree analysis for assessing wild populations and then using this information to make additional management recommendations for the conservation of the species.

Study Site and Population

The current golden lion tamarin population is confined to 8 municipalities in Rio de Janeiro state all within the Sao Joao watershed. There are over 25 private land reserves where golden lion tamarins have been reintroduced (AMLD 2009a). These Private Natural Heritage Reserves (RPPNs) and the tamarins that inhabit these small forests are a result of the reintroduction program which ran from 1984 until 2000 (Figure 1.1).

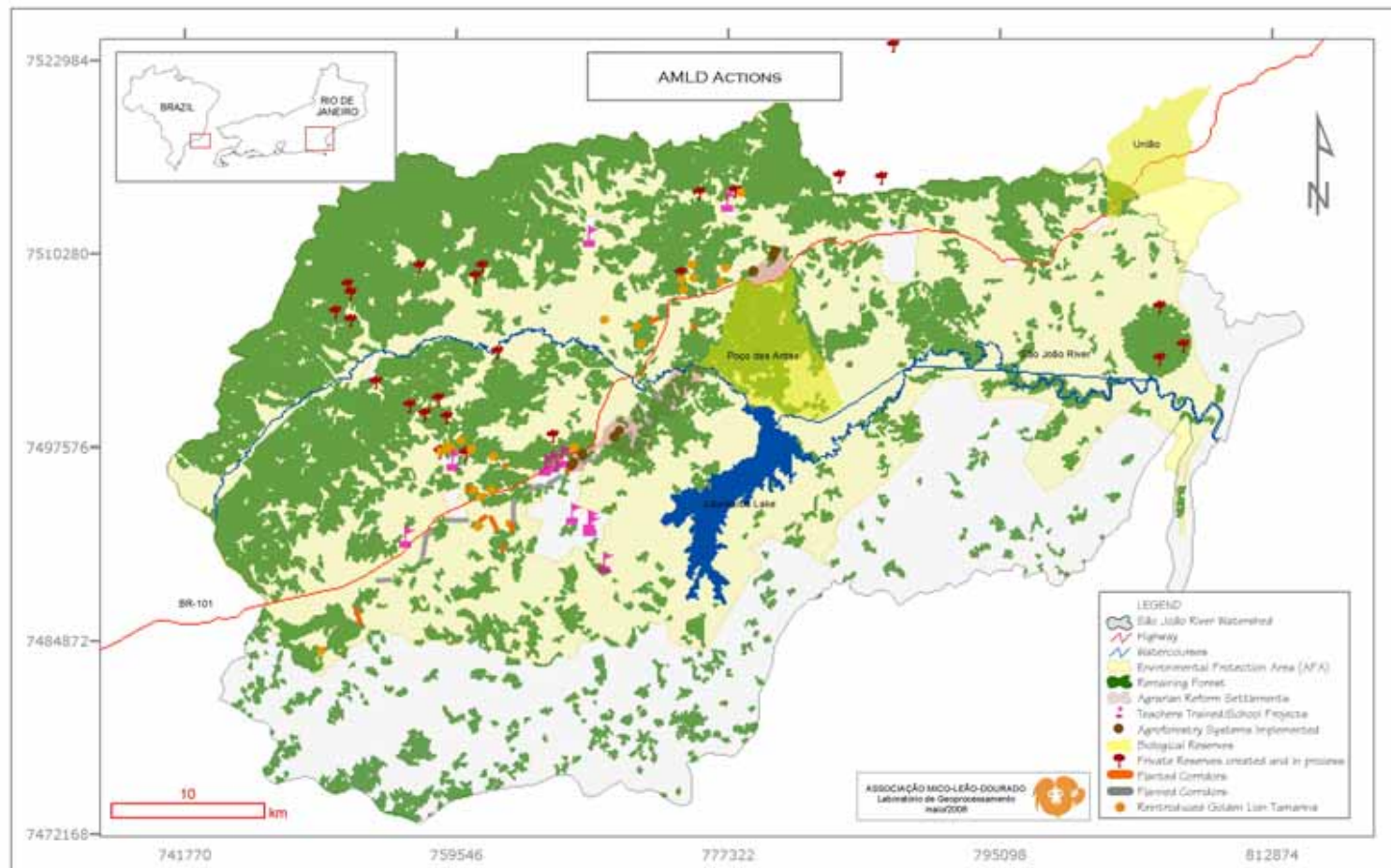


Figure 1.1: Map of GLT occurrence area. Image from AMLD 2009a.

A total of 146 captive-born and 7 confiscated golden lion tamarins have been released (Beck and Martins 2003). The current reintroduced population is made up of over 99% wild-born tamarins and is estimated to be between 550 and 750, making up more than a third of the entire wild population (Beck and Martins 2003).

At a metapopulation workshop held in 2009, the population of GLTs was classified into 7 different metapopulation management units (AMLD 2009b). These management units (MU) were defined based on degree of isolation and suitability for golden lion tamarins. Fragments 50 hectares or larger and within 100 meters of each other were categorized in the same MU as it is believed that GLTs can easily cross a distance of 100 meters. Therefore, in most cases, the MU is composed of several fragments that are separated by a distance of less than 100 meters. Three of these units are composed of reintroduced GLTs (Rio Vermelho, Imbaú, Dourada), two composed of “wild” (i.e. naturally occurring) GLTs in the biological reserves (Poço das Antas and União) and two MUs that are wild populations that have not historically been monitored or managed (Figure 1.2). There are a few small populations of GLTs outside of these MUs. For the purposes of this study, the location of those tamarins was classified as “Other”. These are tamarins living on farms that are outside the management areas or had groups of tamarins that have not been monitored for over 20 years.

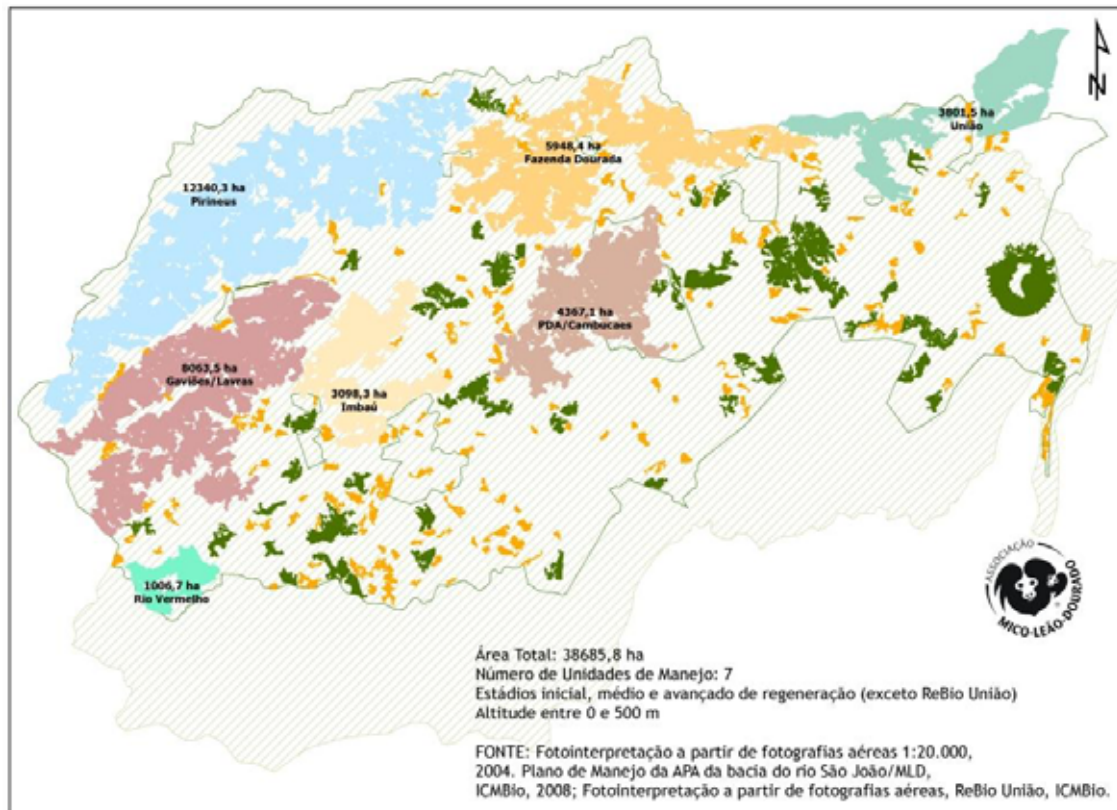


Figure 1.2: Map with GLT metapopulation management units (MUs). The size of each MU is shown in hectares. Image from AMLD, 2009b.

Methods

The population of reintroduced GLTs has been extensively monitored for the last 25 years (Baker and Dietz 1996, Dietz et al. 1997, Kleiman and Rylands 2002). A large percentage of the groups living in these areas have been monitored and captured every six months to determine group composition and for the placement of radio telemetry collars, permanent tattoos and temporary dye markings. These historical records provide continuous data on group composition, births, deaths, and migrants to and from the study

groups. Data from the reintroduced GLT population inventory was used, kept since the program began in 1984, to construct a pedigree database. The database program, Single Population Animal Records Keeping System (SPARKS version 1.52; International Species Information System, Eagan, MN) was used to generate the complete studbook. Parents, gender, birth date, death date, location, and any other life history information were entered for every individual (living and deceased) recorded in the inventory. Animals where parents were unknown were recorded as such and animals where the parents could not be determined between multiple options were recorded as “mult” and each possible parent was assigned a probability based on the likelihood that it sired that offspring. In most cases, the probabilities were divided up equally among all possible sires since there was no detailed information to indicate otherwise. Those probabilities were used to calculate its genetic contribution to the offspring (details below). Birthdates of individuals in the reintroduced population were frequently recorded as estimates since most of the births occurred between group visits. All records were validated and examined for errors and any uncertainties were checked against historical records. To include the reintroduced animal’s captive founders, the lineage of reintroduced animals was traced back to the original captive founder and those data were merged with the reintroduced studbook. Thus, the founder population for the reintroduced population is traced back to the same founders as the captive population. Founders were assumed to be unrelated unless known otherwise.

Once validated, the data were exported and analyzed using PMx (Ballou et al. 2010), a population management program that performs demographic and genetic analysis on pedigree data. The founder representation, defined as the proportion of genes in the living descendent population that are derived from that founder (Lacy 1995), the level of genetic diversity maintained relative to the population from which these founders were derived, and inbreeding overtime were evaluated. Inbreeding is measured in terms of inbreeding coefficients (F) which is defined as the probability that two alleles at homologous loci in an individual are identical by descent from a common ancestor of the parents (Lacy 1995).

Genetic diversity is measured in pedigree analysis using a gene drop technique where alleles are tracked through a known pedigree (Lacy 1989). Each founder is assigned two unique alleles which are then randomly passed from parent to offspring assuming Mendelian segregation. An offspring receives an allele from its father and one from its mother. When multiple parents (i.e. two possible sires) are present, the probability assigned to each possible parent is multiplied by the probability of the allele being passed on. At the end of the gene drop simulation, the frequency of the founder alleles was used to calculate gene diversity using the formula for expected heterozygosity: $H = 1 - \sum p_i^2$. The simulation is run 1,000 times to simulate broad sampling across an individual's genome (Ralls et al. 2000). Since genetic parameters are measured relative to a population from which the founders were derived, measures of genetic diversity are calculated as a proportion; the proportion of heterozygosity in the source population that

is retained in the extant populations (Lacy 1989, Lacy 1995, Ralls et al. 2000). This analysis was completed for the reintroduced population as a whole and then also for each of the three management units that consist of reintroduced GLTs (Rio Vermelho, Imbaú, and Dourada).

The population sizes listed in this study are reflective of the individuals listed on the animal inventory, but it is likely that there are other GLTs in these habitats that may not be counted in this analysis. Likewise, there could be deaths or births that were missed by the field team; therefore, population sizes reported here should be considered estimates. There were 716 animals considered living at the time of this study. Removed from these analyses were animals that had disappeared (at the time they disappeared) and animals located outside the reintroduced populations (i.e. Poço das Antas animals). Animals that entered the population from an unknown origin were treated as new founders. These animals could be from the reintroduced population, but could not be identified as such (no markings). Analysis of these unknown individuals was compared both by counting them as unique founders (Ballou and Lacy 1995) and by not counting them as founders. While counting them as founders may give a slightly higher level of GD and lower F values, overall treating the unknown animals as founders provides a more accurate representation of the status of the reintroduced population.

The affect that future reintroductions could have on the captive and reintroduced populations were also examined. Using PMx, the levels of kinship among the population

using mean kinships (MK), which is the average relatedness of an individual to every individual in the population (Ballou and Lacy 1995) were calculated. Individuals with high MK values have many relatives in the population whereas individuals with low MK values have few relatives in the population and are considered genetically valuable. Mean kinship is directly related to gene diversity ($GD = 1 - \text{average MK}$) and can be used to measure the change in genetic diversity in both recipient and donating populations as a result of reintroductions. The best reintroduction candidates would be those individuals that were overrepresented (i.e. had large MK values) in the captive population and underrepresented (i.e. had low MK values) in the reintroduced populations; these individuals would have the greatest positive impact on the genetic diversity in both the captive and reintroduced populations if reintroduced. A similar method was followed using MK to identify if there were any animal translocations that could occur between management units that would benefit the genetic diversity of the MUs. Those movements were then simulated and the cumulative effect on the population's genetic diversity was determined.

Results

Population Analysis

The current pedigree consists of 1572 individuals (living and deceased). Although it was not possible to identify the parents for every offspring, 85% of the individuals have known ancestors. This percentage known drops to 81% once the animals that have disappeared and those that are no longer considered part of the managed population are removed. Of the total 716 that are considered living in the managed population, 88

individuals or 12% are completely unknown (Figure 1.3). These unknown animals appeared in the managed population from a neighboring GLT population. They likely came from the reintroduced population, but since they were not tattooed and their origin is unknown, the parents are listed as unknown. Fifty percent of the population has 90% or more of their pedigree known.

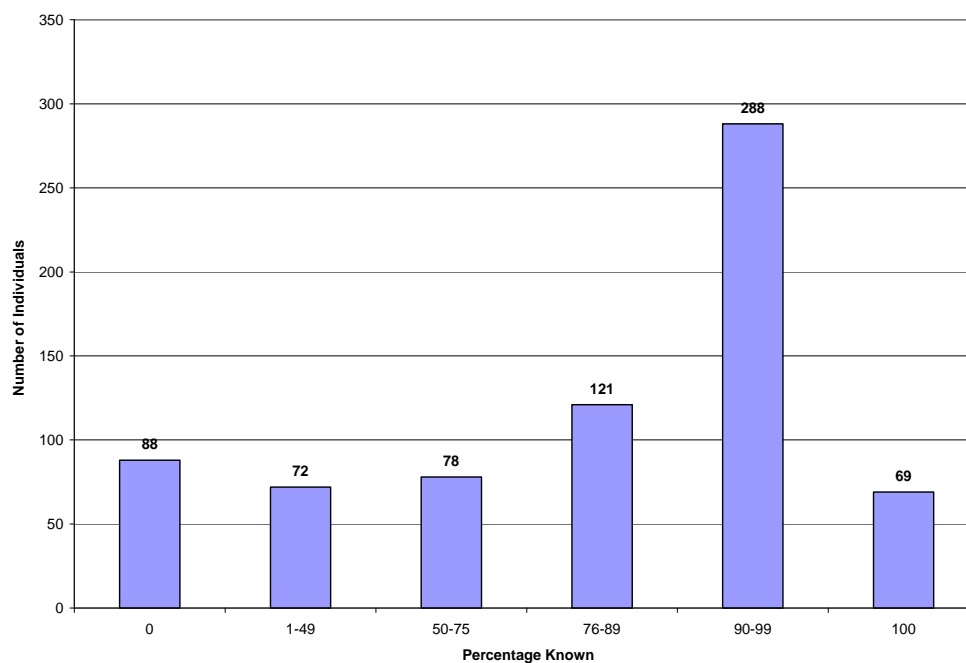


Figure 1.3: The distribution of animals with percentage of their pedigree known.

The current reintroduced population can be traced back to 46 founders, with 13 founders that entered the reintroduced population from the neighboring wild population. The representation of founders is relatively equal among the founders, that is, the representation is not dominated by any one or any small group of founders (Figure 1.4).

The captive population has 51 founders of which all but 18 are represented in the current reintroduced population (Figure 1.5). However, of those 18 not represented, 11 of those founders came into the captive population after reintroductions ceased in 2000 and 9 of them have not yet bred in captivity. The captive founders that are not represented in the reintroduced population never had decedents reintroduced (Figure 1.6) and all of the founders that are represented in the original reintroduced animals, are still represented in the reintroduced population today (Figure 1.7).

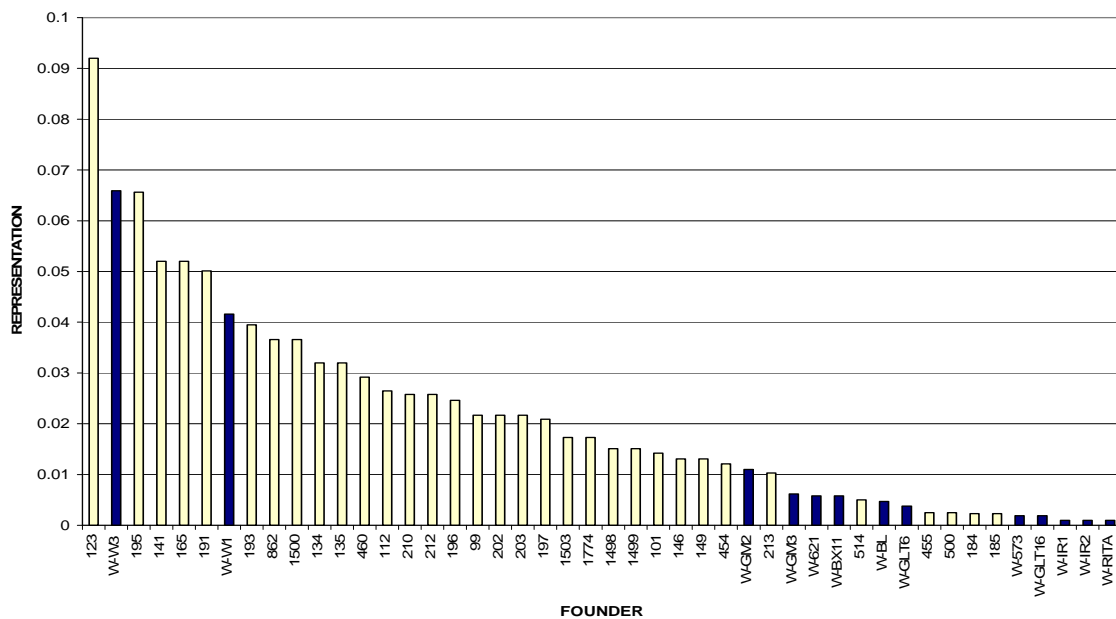


Figure 1.4: Proportion of genes in living descendant population that are derived from founders. There are 46 founders that contributed to the reintroduced population, 13 of those came from nearby wild populations. Those wild founders are marked with a “W” before their identification code and their representation bars are blue.

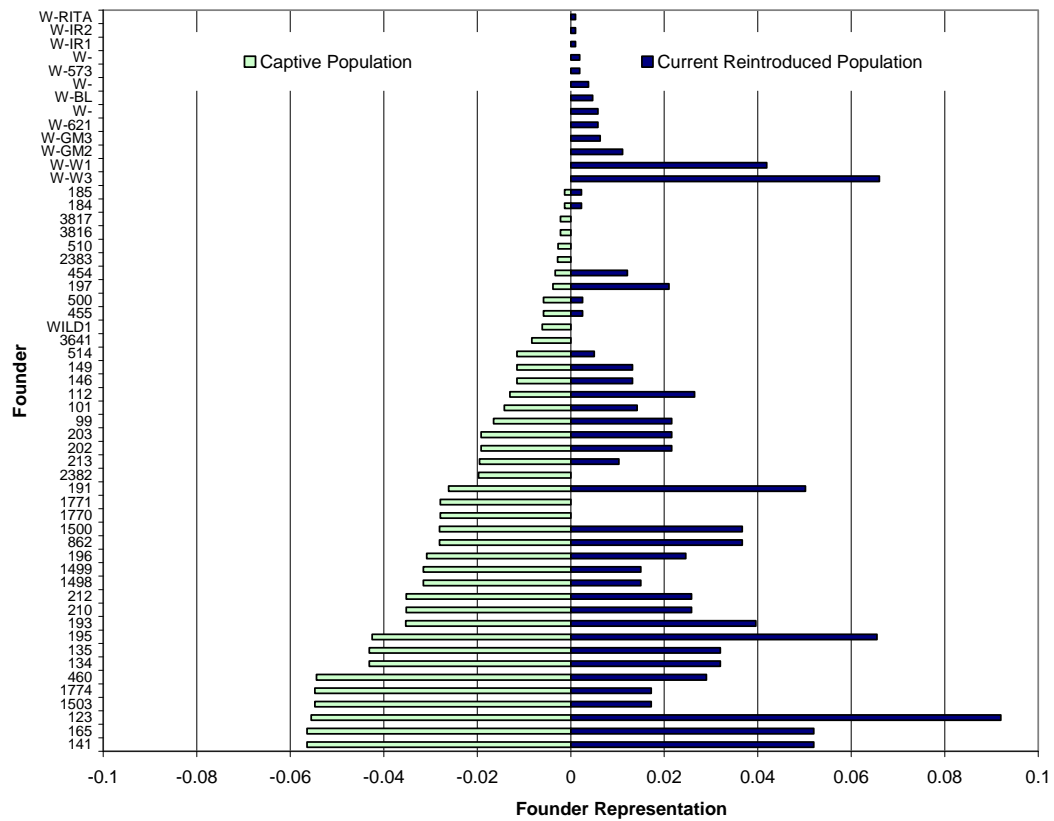


Figure 1.5: Representation of the founders in both the captive (light blue) and the current reintroduced population (dark blue). Each bar represents the proportion of the gene pool that are derived from each founder. There are 13 wild founders not represented in the captive population and 9 captive founders not represented in reintroduced population.

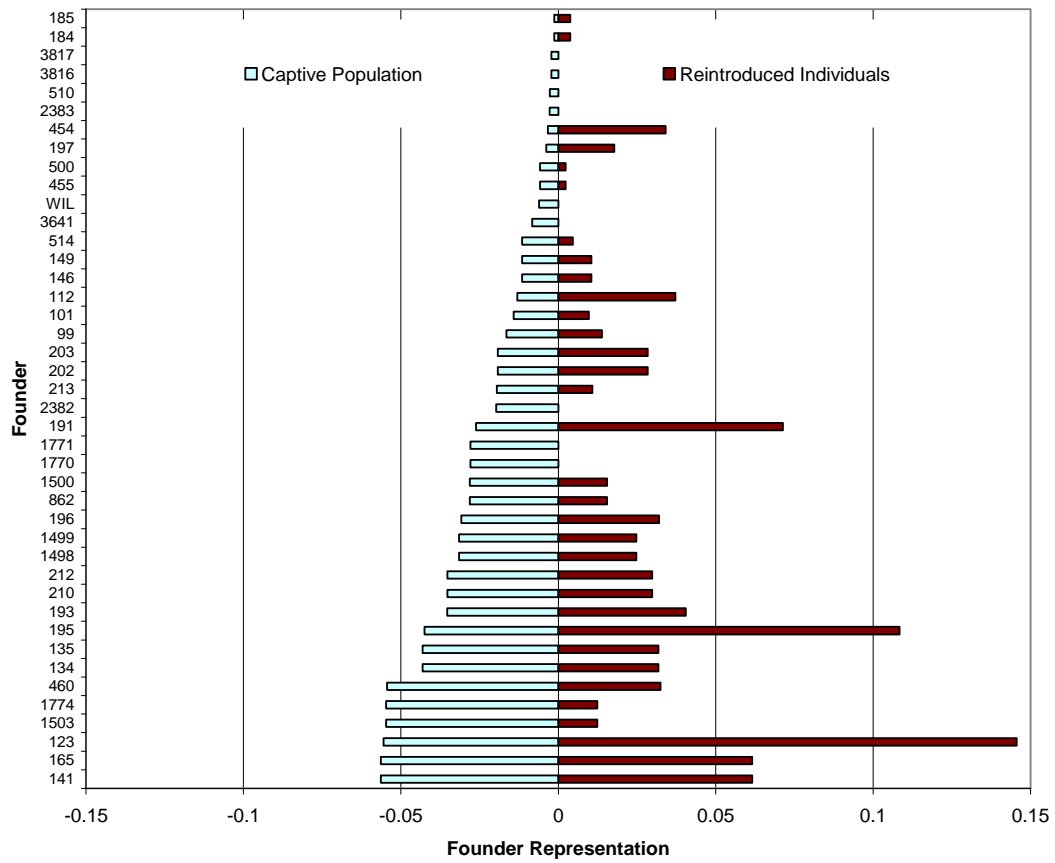


Figure 1.6: Representation of the founders in the captive population (light blue) and the original reintroduced individuals (dark red). There are 9 captive founders not represented in the population of animals that were reintroduced back to Brazil.

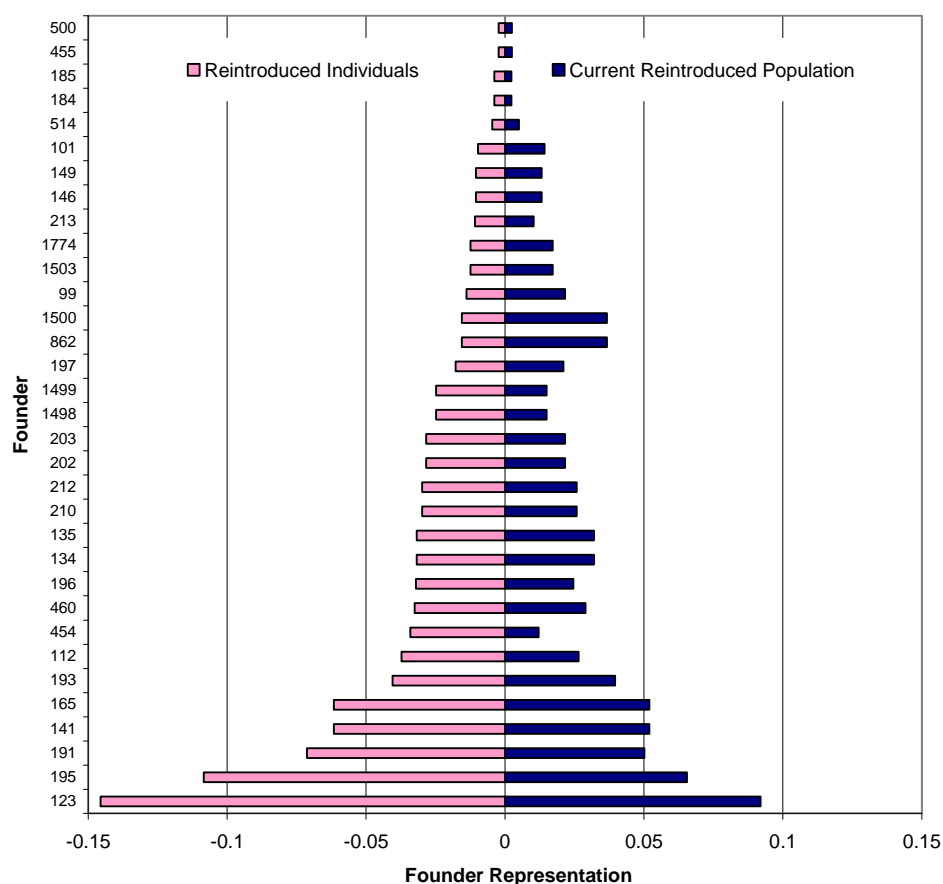


Figure 1.7: Representation of founders in original reintroduced individuals (dark red) and the current reintroduced population (dark blue). The founders represented in the original reintroduced animals are still represented in the current reintroduced population.

Current inbreeding coefficients (F) for the population range from 0 to 0.3158 with the average inbreeding at 0.0497 (0.0607 without UNK), so on average, matings are more distant than first-cousins ($F < 0.0625$) (Figure 1.8). Annual mean inbreeding coefficients increased most rapidly in the population from 1993 to 2000 (Figure 1.9). Starting in 2000, inbreeding leveled out and only increased slightly at a rate of 0.3% on average per year (Figure 1.10.).

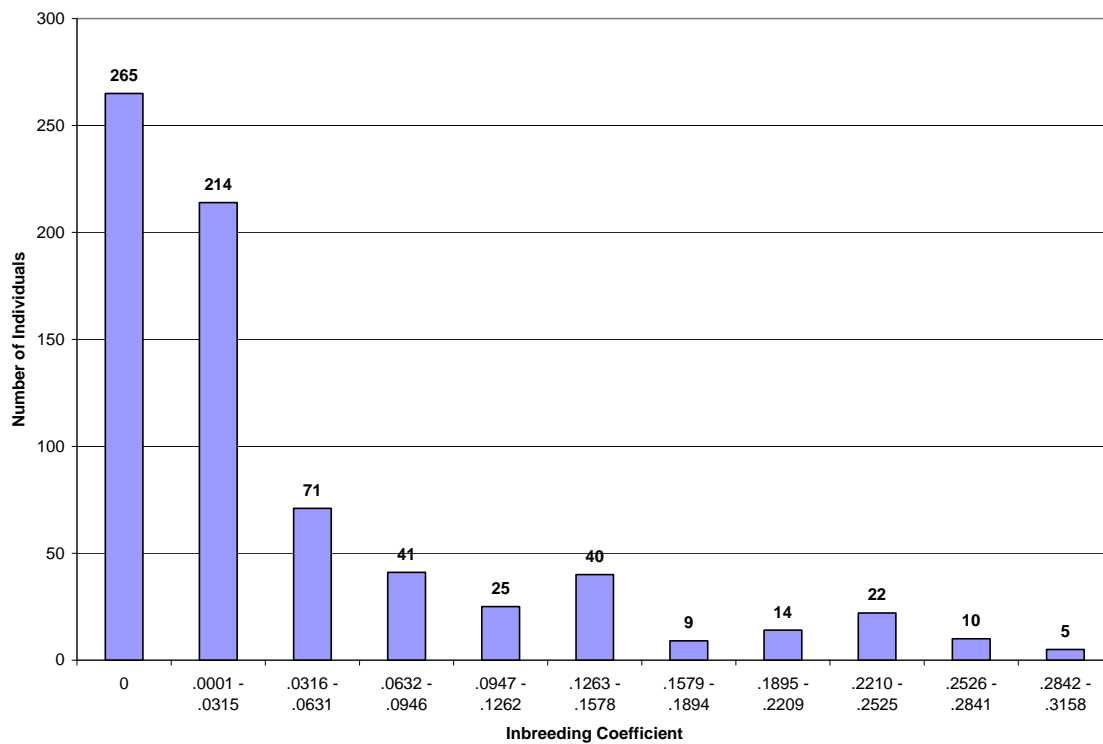


Figure 1.8: Distribution of inbreeding coefficients. One-third of the population has inbreeding coefficients less than 0.0315.

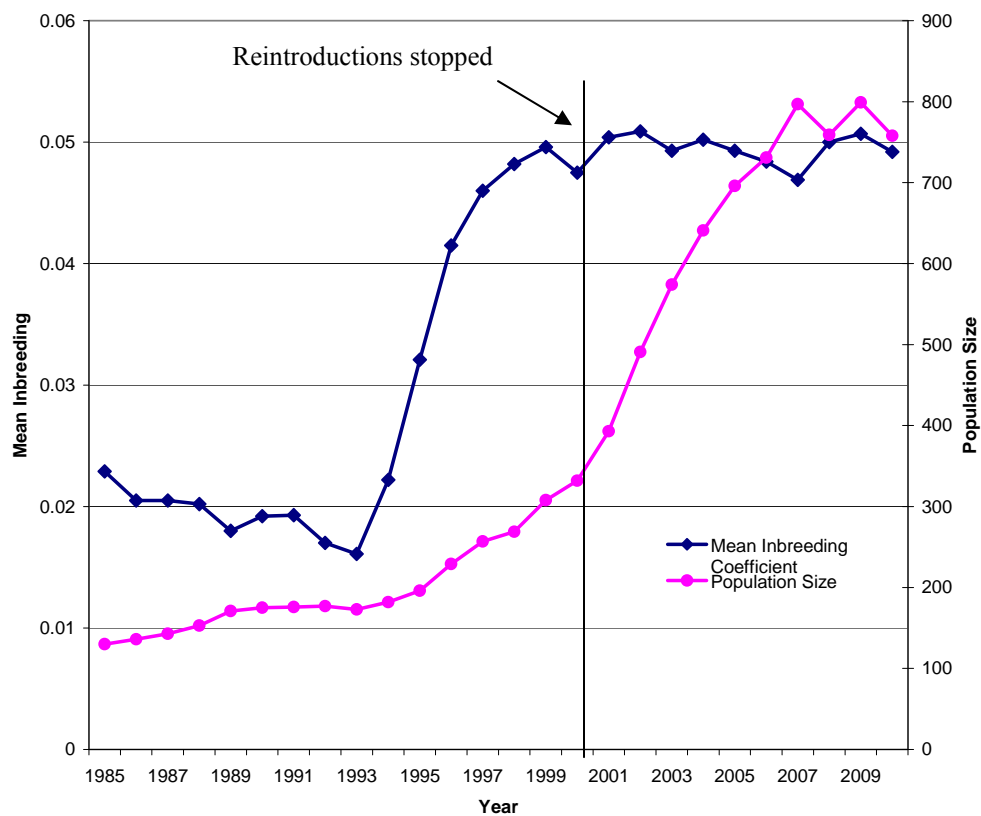


Figure 1.9: Change of inbreeding coefficients over time. After reintroductions ended in 2000, inbreeding increased by a rate of 0.3% on average per year.

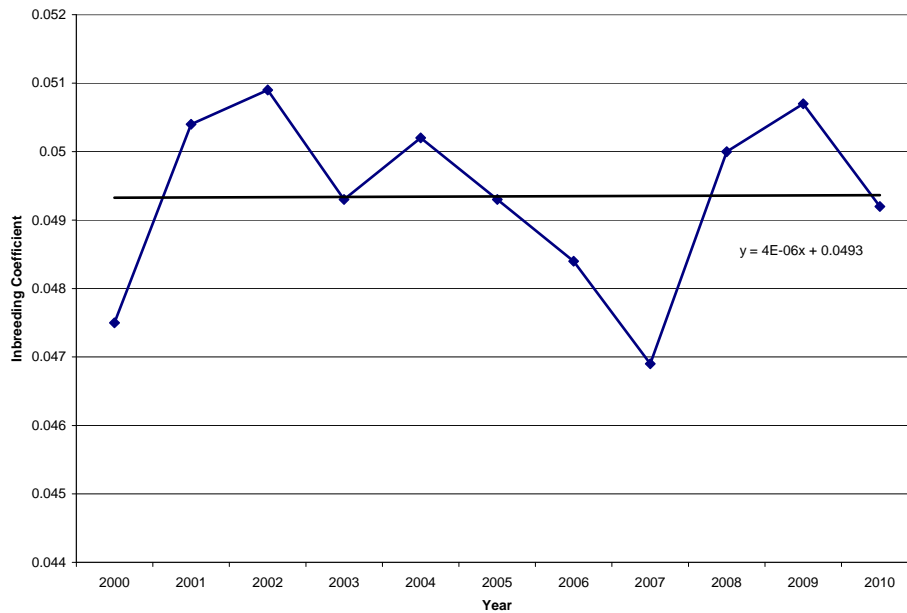


Figure 1.10: Mean inbreeding from 2000 to current. Rate of increase is less than a third a percent on average per year.

The reintroduced population has retained 96.59% of the genetic diversity relative to the source population (the population from which it was derived), well above the recommended goal of retaining 90% of the original heterozygosity (Fahrig and Paloheimo 1988, Henein and Merriam 1990). Over time, and as the reintroduced population grew, the captive and reintroduced populations became more genetically differentiated despite additional reintroductions (Figure 1.11).

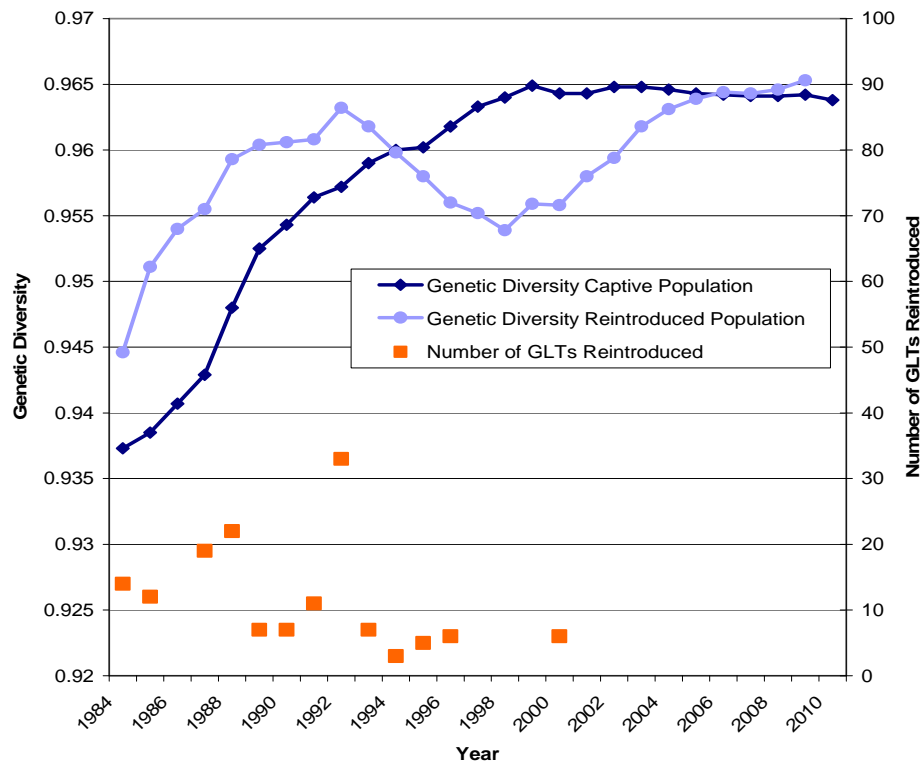


Figure 1.11: Levels of gene diversity in the captive and reintroduced populations relative to the gene diversity of the founders to the captive population (H_t/H_0). The numbers of animals reintroduced each year in shown at the bottom (orange squares), the last reintroduction was in 2000.

Metapopulation Analysis

The three reintroduced populations within the metapopulation were each analyzed separately (Figure 1.2).

Even though different animals were reintroduced in each population, the captive founders are relatively well represented in each fragment. Imbaú can be traced back to 35

founders, Rio Vermelho to 32 founders, and Dourada to 36 founders. Only Rio Vermelho is missing captive founders (ID# 1774, 1503, 1498, 1499).

Table 1.1: Management units with corresponding values for genetic diversity (GD) and mean inbreeding coefficients (F) both in counting the unknown animals as founders and not. Average mean kinship (MK) values are calculated with unknowns counted as founders. Population sizes (N) should be considered estimates.

Management Unit	No. Reintroduced	No. Founders	GD (w/o Unk)	F (w/o Unk)	Average MK	N
<i>RV</i>	44	32	92.79% (91.20%)	0.0466 (0.0603)	0.0721	222
<i>Imbau</i>	17	35	91.34% (89.70%)	0.0381 (0.0456)	0.0866	138
<i>Dourada</i>	65	36	95.49% (92.86%)	0.0625 (0.0968)	0.0451	285

Inbreeding is highest in the Dourada population at 0.0625 and lowest in the Imbaú population at 0.0381 (Table 1.1). All three subpopulations have maintained genetic diversity above 90% with Dourada maintaining over 95% (Table 1.1).

Mean inbreeding coefficients for each MU have increased over-time, especially from 1993 to 2000 when the populations were growing most rapidly (Figure 1.12). Since 2000, inbreeding has leveled out in the all three MUs comparable to the general reintroduced population trend (Figure 1.9)

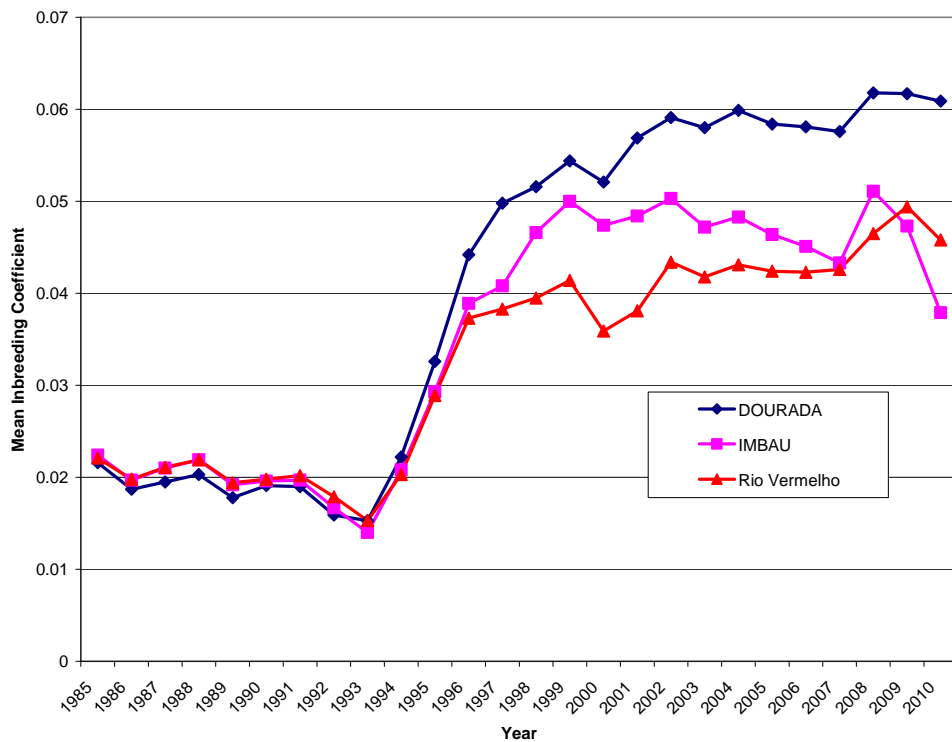


Figure 1.12: Change in mean inbreeding coefficients over time for each of the three management units.

Founder representation for the captive founders is mostly similar between the three populations. A large difference is observed with a few founders, including founder number 460 where Imbaú has a 0.13 representation and a less than 0.005 representation in RV and Dourada, in founder numbers 862 and 1500 representation is just over 0.06 in RV, but only 0.01 for Imbaú (Figure 1.13).

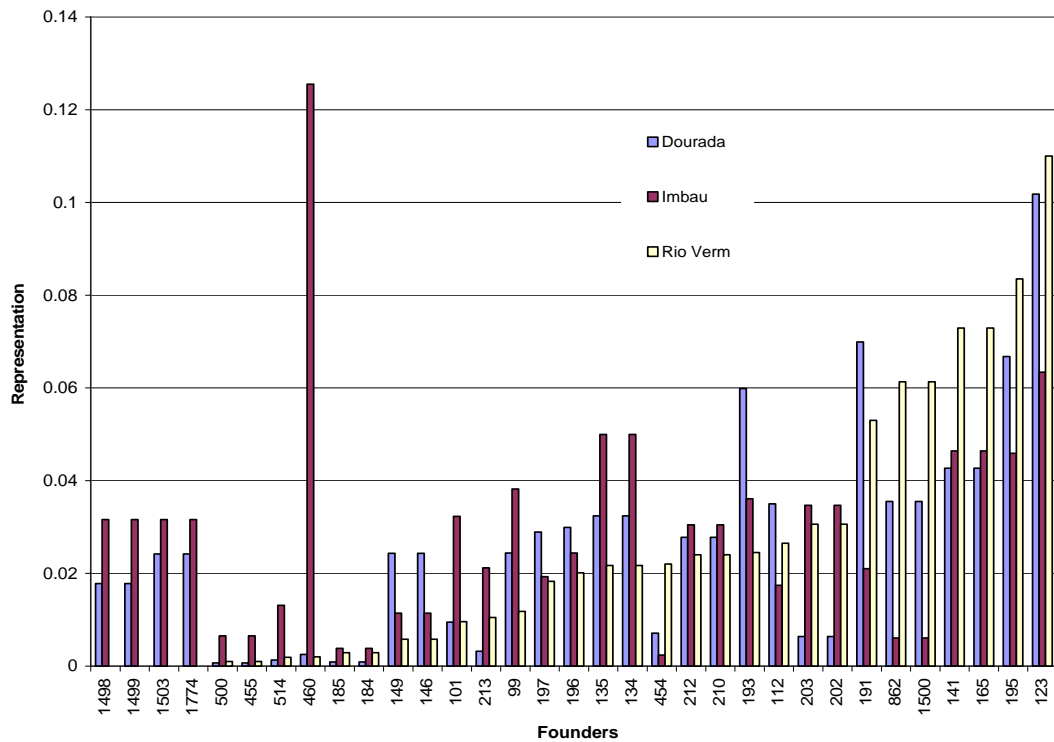


Figure 1.13: For each of the three management units, the proportion of genes in the living population that are derived from that founders.

The gene flow between the management units was also examined by tracking the founder alleles. All three units share representation from other units (Figure 1.14). The Dourada gene pool is dominated largely by the animals that were reintroduced there and their descendants, 15% of the representation is from outside Dourada. Representation is more evenly distributed at Rio Vermelho. Dourada and Rio Vermelho have representation from all three MUs, Imbaú has representation from Rio Dourada but is lacking representation from Imbaú. Any founders coming in from outside one of the three MUs were classified as “Other”. This category included wild founders as well as a few small populations of

reintroduced GLTs that are not in a management unit. This Other category is best represented in Rio Vermelho, 16%.

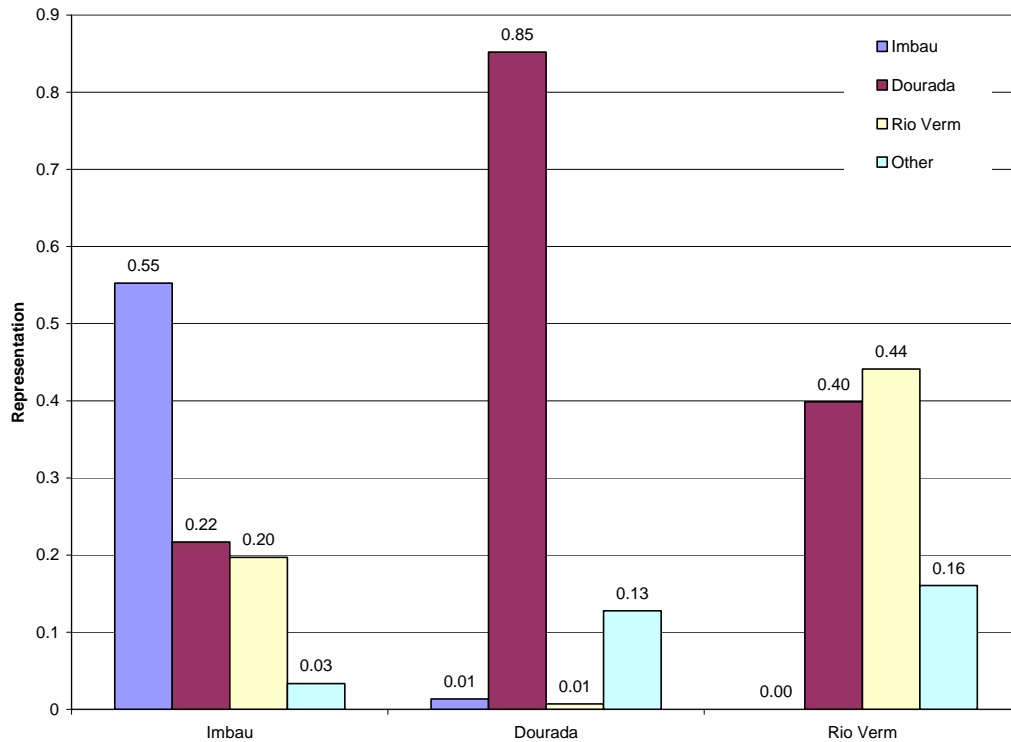


Figure 1.14: Representation of reintroduced founders in each of the management units

Genetic Management

Using MK any captive individuals that could be reintroduced to improve the genetic diversity of both the captive and reintroduced populations were identified.

Reintroductions that benefit both populations have a high MK in the captive population (over-represented) and low MK (under-represented) in the reintroduced population.

Since gene diversity is maximized when allele frequencies are equal, if overly represented individuals were removed from the captive population, heterozygosity can actually increase.

In this analysis, the change in genetic diversity in the captive population if it were removed against the change in the reintroduced population's genetic diversity due to the addition of that individual was plotted for each individual (Figure 1.15). Individuals in quadrant A represent reintroductions that would benefit both the captive and reintroduced populations. These are over represented animals in the captive population, but have few relatives in the reintroduced population. Reintroducing individuals from quadrant B would be harmful to the captive population, but beneficial to the reintroduced population. These are animals that are genetically valuable in the captive population and also under-represented in the reintroduced population. Individuals in quadrant C represent individuals that if reintroduced would benefit the captive population, but be harmful to the reintroduced population. These individuals are over represented in captivity and in the reintroduced population. Reintroducing individuals in quadrant D would be harmful to both the captive population and the reintroduced population. These individuals are valuable in the captive population and over represented in the reintroduced population. All of the 353 viable reintroduction candidates would have a positive effect on the genetic diversity of the reintroduced population if reintroduced and 191 reintroductions would be beneficial for both populations. There were no reintroductions that would be detrimental for both populations.

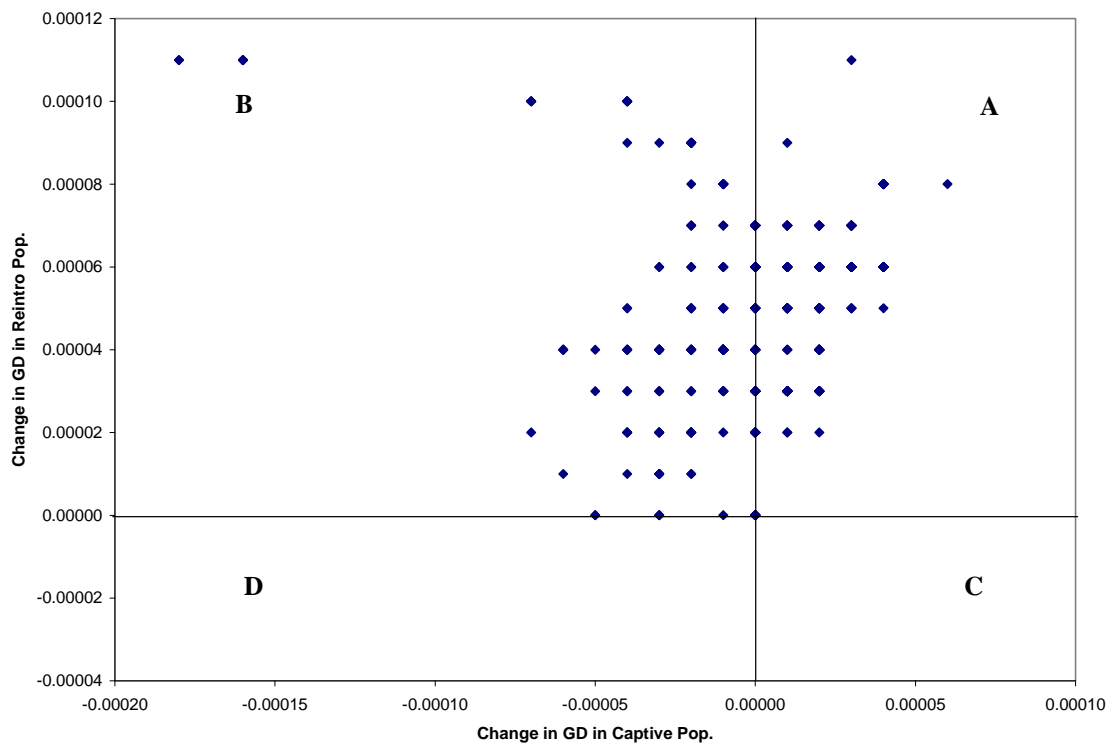


Figure 1.15: Change in genetic diversity with future reintroductions. Each point corresponds to an individual in the captive population and represents the change in genetic diversity in the captive and reintroduced populations if that captive individual were reintroduced.

The transfer of captive animals to the reintroduced population was modeled to determine the exact affect these transfers would have on the change in genetic diversity. Animals were selected that had the greatest averaged benefit for both populations. Because these populations are both relatively large, moving small numbers of animals have very little impact on the genetic diversity of either population. Both populations benefited from the transfer of animals to the reintroduced population until 300 animals had been transferred

(in groups of 10), at which point the genetic diversity in the captive population began to decline rapidly (Figure 1.16).

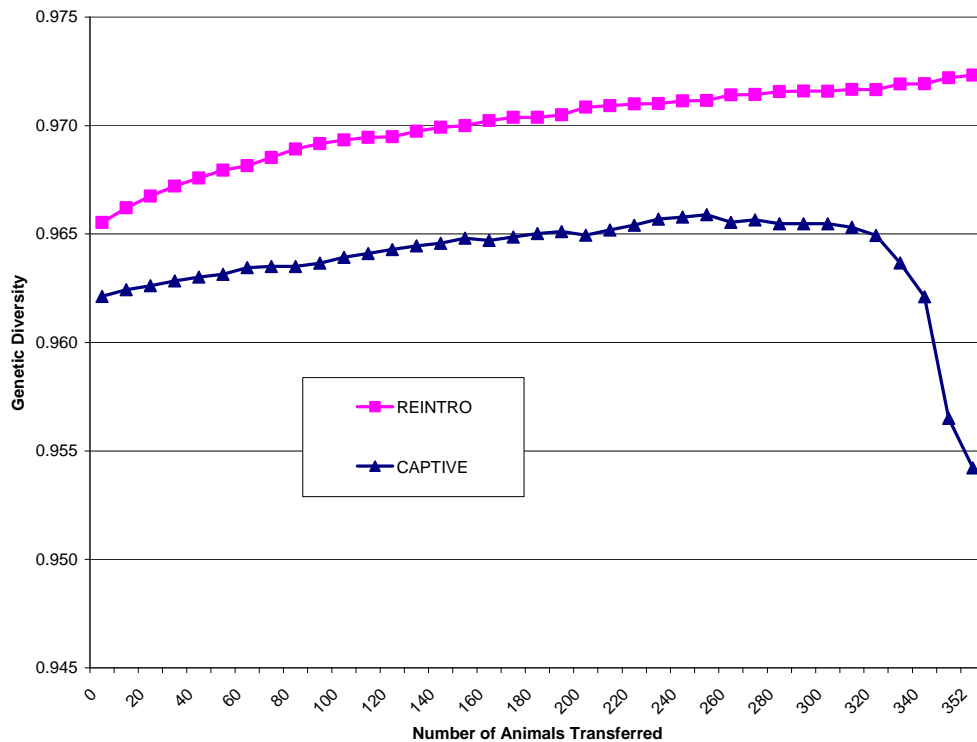


Figure 1.16: The effect of moving animals from the captive population to the reintroduced population on genetic diversity. Both populations benefited in terms of genetic diversity when animals were transferred to the reintroduced population. After 300 animals had been transferred, the genetic diversity of the captive population began to decline rapidly with further transfers.

The change in genetic diversity if individuals were translocated between management units was also examined. For each management unit, translocations could help increase genetic diversity and in only two of the cases did translocations have a negative effect on

the receiving population (Figures 1.17, 1.18, 1.19). Imbaú has the most to gain through translocations from both Rio Vermelho and Dourada with the greatest effect being a translocation from Rio Vermelho to Imbaú, improving the GD of Imbaú by 0.00143 and not negatively affecting the Rio Vermelho population.

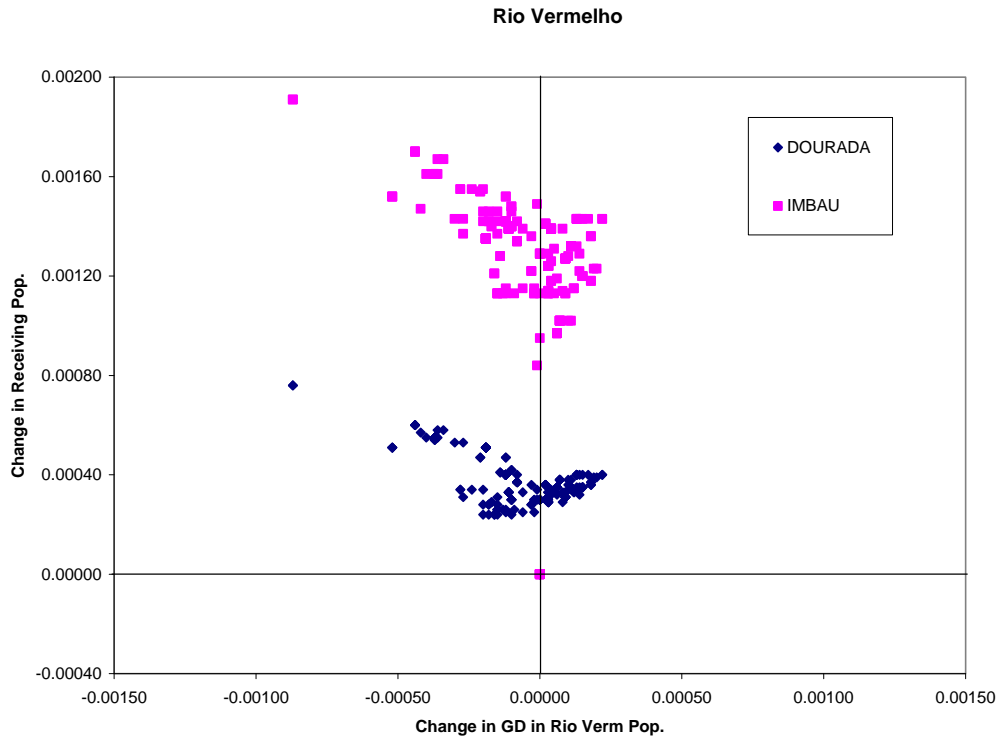


Figure 1.17: Genetic potential of future translocations from Rio Vermelho to both Imbaú (pink squares) and Dourada (blue diamonds). Each point corresponds to an individual in the Rio Vermelho population and represents the change in genetic diversity in the MUs if that Rio Vermelho individual were translocated.

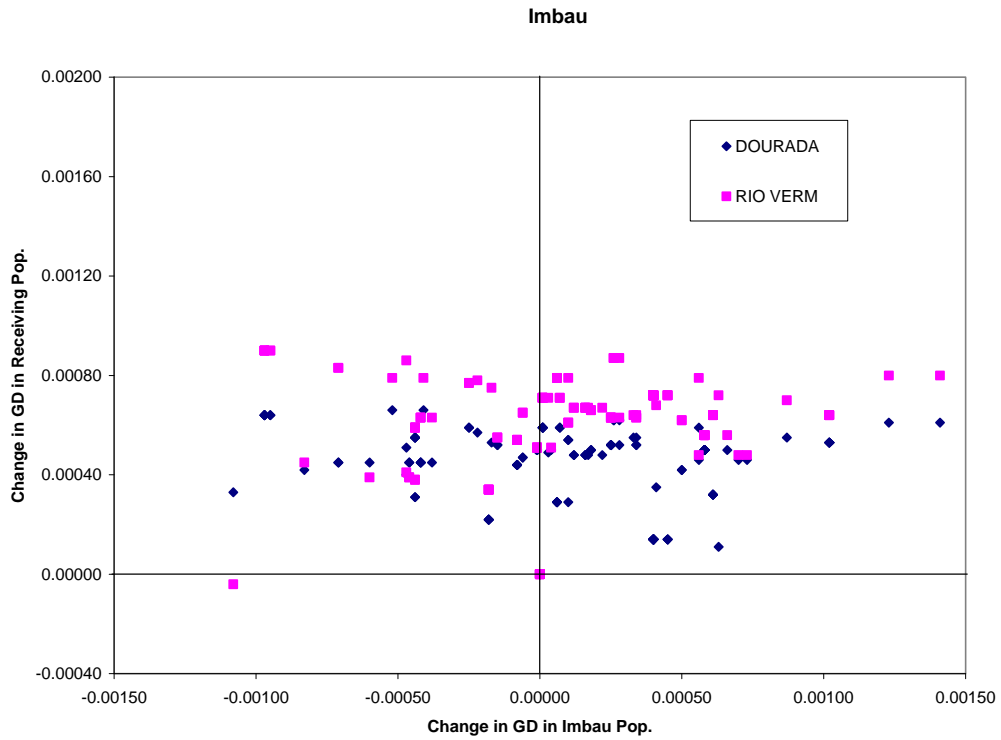


Figure 1.18: Genetic potential of future translocations from Imbau to both Rio Vermelho (pink squares) and Dourada (blue diamonds). Each point corresponds to an individual in the Imbau population and represents the change in genetic diversity in the MUs if that individual were translocated.

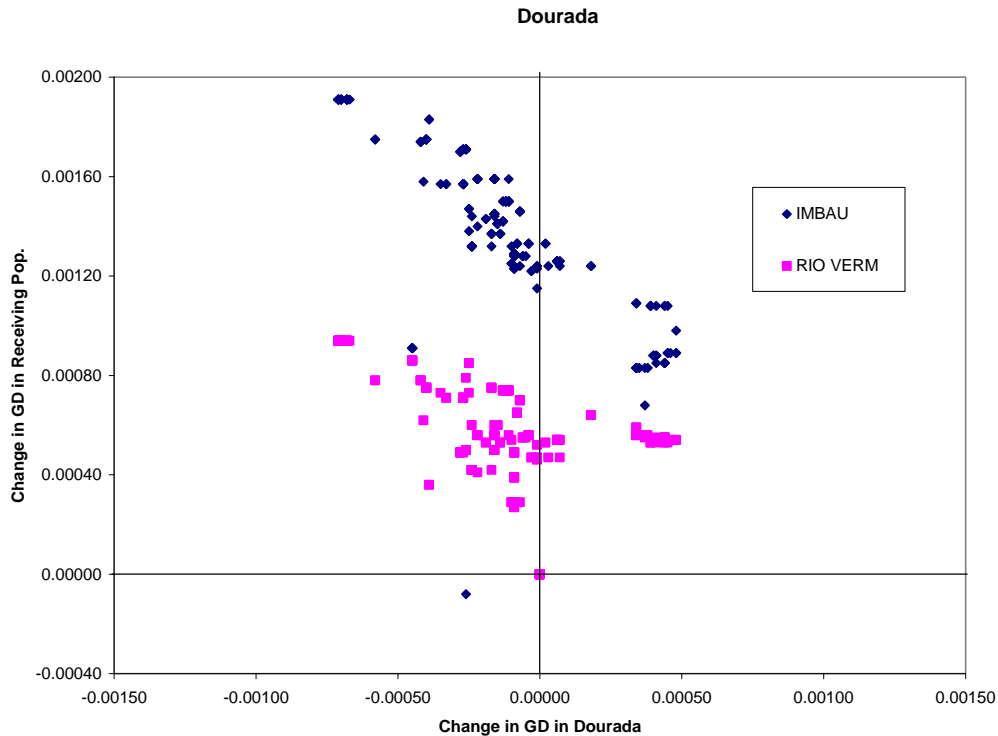


Figure 1.19: Genetic potential of future translocations from Dourada to both Rio Vermelho (pink squares) and Imbaú (blue diamonds). Each point corresponds to an individual in the Dourada population and represents the change in genetic diversity in the MUs if that individual were translocated.

Again, the effect future animal movements would have on the management units was modeled. This was done for Imbaú as it had the lowest starting genetic diversity (0.91334). Individuals were selected for translocations based on their benefit to Imbaú, but also chose animals whose removal did not have a negative impact on the originating population (Dourada or Rio Vermelho). After 20 animals were translocated from Dourada (in groups of 5), the genetic diversity of Imbaú increased to 0.92876 while the genetic diversity of Dourada showed only a slight decrease (0.95488 to 0.95480). After

the top 20 animals from the Rio Vermelho populations were translocated, the genetic diversity of the Imbaú population increased to 0.92730 (Figure 1.20). These translocations also raised the genetic diversity of the Rio Vermelho population from 0.92786 to 0.92922.

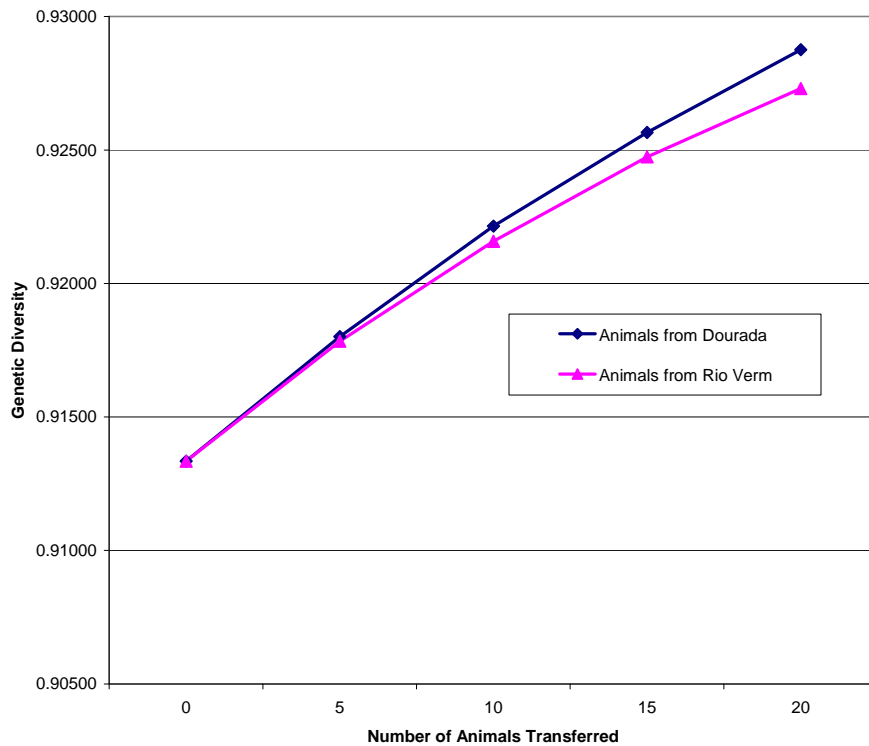


Figure 1.20: The effect of future translocations from Dourada and Rio Vermelho to Imbaú on genetic diversity. Translocations from both of these populations result in an increase in genetic diversity for Imbaú.

Discussion

Maintaining genetic health is important for long term population viability and is therefore frequently a goal of conservation programs. Evaluating genetic status is especially critical for small populations where the loss of genetic variation may put them at risk of extinction. Life history data collected from the extensively monitored population of golden lion tamarins was used to construct a pedigree and assess the genetic status of the reintroduced population.

Relative to the 46 captive founders, the reintroduced population has retained 96.53% of the source population's genetic diversity. This is well above the 90% recommended level and is the likely result of the careful selection of individuals for reintroduction. Using MK, animals were selected based on their potential genetic contribution to the reintroduced population (Ballou 1992). Management recommendations based on MK values has been shown to be an effective way to maintain genetic diversity and is frequently used in managing captive populations (Ballou and Lacy 1995, Ballou and Foose 1996). Similar techniques have been used in managing reintroduction programs for other endangered species such as the black footed ferret (*Mustela nigripes*), California condor (*Gymnogyps californianus*), and Assateague Island horses (*Equus caballus*). Through the use of genetic management, the loss of genetic diversity has been minimized for all of these recovering species. The status of the reintroduced population of golden lion tamarins compares favorably with these examples. The GLT reintroduced population benefits from a much larger founding population, 46 founders as compared

with the 17 founders for the California condors (Ralls et al. 2000) and a mere seven founders for the black footed ferret population (Russell et al. 1994, Wisely et al. 2003). The GLT population is much larger in size as well, over twice as large as these other species. This larger population and larger number of founders will contribute to the retention of genetic diversity overtime (Frankham et al. 2010).

Another factor that may contribute to this high level of maintained genetic diversity in the GLT reintroduced population is the relatively equal founder distribution. Equalization of founder representation is an effective way to maintain genetic diversity (Lacy 1989, Haig et al. 1990, Frankham et al. 2010). Equal founder representation could be explained by several different factors. First, even though many of the reintroductions took place on smaller forest fragments on private lands, many of them are connected to other smaller fragments and no tamarins were present at the time of reintroduction. This allowed for dispersing reintroduced animals to easily find vacant areas to establish breeding territories. This increase in breeding opportunities is likely to contribute to the equal founder representation. Second, each reintroduced individual may represent several captive founders such that multiple descendents were likely introduced. This would have also aided in the equalization of founder representation.

In looking at the transfer of genetic diversity from the captive to the reintroduced population based on founder representation, there were only 9 captive founders that were not represented in the reintroduced population (excluding those that came in to the

population after the program ended or have not yet reproduced in captivity).

Remarkably, the 33 shared captive founders between the captive and reintroduced individuals are still represented today; there has been no founder loss since the program began 25 years ago. This is likely due to the fact that animals that were reintroduced had duplicated founder representation as mentioned early. The reintroduced population is only in its fourth generation; therefore some disparity between the founder representation after several more generations is expected which could affect the genetic diversity as well as founder loss. However, this study demonstrates that selecting animals for reintroduction based on MK and when possible, selecting animals that represent multiple founders and ensure redundant representation of founders, is an effective way to capture the captive population's genetic diversity.

Over time, the genetic diversity of the reintroduced population has increased steadily with the exception of the small dip in the late 1990-early 2000s when reintroductions tapered off. As the reintroduction population increased in size, reintroduction had less of an impact on genetic diversity. In the larger population, the genetic characteristics are determined more by the mating behavior of the animals rather than by the selection of reintroduced animals. However, the recent increase in genetic diversity is likely due to the influx of wild tamarins. With the increasing population, tamarins are using more habitat and coming closer to wild populations. This immigration of new genes in the populations enhances the genetic diversity of the once closed reintroduced population.

The mean inbreeding in the current population is 4.97%, well under the relatedness of cousins; a majority of the population has inbreeding coefficients below 3.15%. The five animals with the highest inbreeding coefficients (0.3158) are all siblings and are the result of two consecutive inbreeding events between parent and offspring (first father - daughter mating, then mother - son mating). The greatest increase in inbreeding in this population is observed during the greatest population growth rate and inbreeding has only slightly increased at a rate of 0.3% on average per year since reintroductions ended in 2000. This is somewhat surprising as it was assumed there is limited gene flow between populations which leads to higher inbreeding (Frankham et al. 2010). If this population remains small and gene flow is restricted, it is likely inbreeding would increase.

The metapopulation analysis revealed some interesting results. It was expected that given the isolation of the three management units, the animals that were released in those units and their descendents would have stayed in those units. This was relatively true for Dourada, the oldest of the management units, where the representation of Dourada founders was 85%. It was less clear in Imbaú with 55% Imbaú representation and Rio Vermelho with 44% RV representation. It would be extremely difficult for animals to have dispersed the distances between these three MUs. In many cases they would need to cross a high traffic highway and travel around 15 kilometers. Throughout the duration of the reintroduction program however, there were cases where animals were translocated to different areas to ease density pressures. Rio Vermelho is a large forest that was vacant of tamarins when reintroduced started and this would have been an appropriate

translocation site for animals from the Dourada population. This could explain the large representation of Dourada founders at Rio Vermelho. More research is needed to determine the level of connectivity (i.e. gene flow) between the management units and forest fragments in general.

The Dourada population is the oldest of the reintroduction management units. It has a larger number of animals reintroduced, it has retained a higher level of genetic diversity (95.49%), and has the lowest average mean kinship, meaning that the population on average is less related than either Imbaú or Rio Vermelho. However, Dourada also has the highest mean inbreeding coefficient. This is likely due to a few animals that are breeding with their close relatives but are not closely related to the rest of the MU population.

Management Implications

Each of the management units is maintaining over 90% genetic diversity and can be considered significant in terms of their contribution to the conservation of golden lion tamarins. It is unlikely that these MUs independently could maintain this level of genetic diversity over time and in the future, the proportion of heterozygosity retained would decline. A possible treatment to reduce the deterioration of genetic diversity is to consider future reintroductions and/or translocations between management units.

Analysis of the reintroduced and captive population revealed that future reintroductions could increase the genetic diversity of the reintroduced population. There were 9 founders from the captive population that were not represented in the reintroduced population. Genetic management using mean kinships is a viable technique to select for possible reintroduction candidates. Using this method it was possible to selectively remove animals that are over represented in the captive population, but underrepresented in the reintroduced population. There were no captive animals that if reintroduced, would have been detrimental to the genetic diversity of the reintroduced population, but there were reintroductions that were detrimental to the captive population (Figure. 1.16). Each reintroduction in itself would have a very small impact on the populations' genetic diversity and it was not until over 300 captive animals had been transferred that the genetic diversity in the captive population would begin to decline (Figure 1.17). While the reintroduction of this many animals is not realistic, these results demonstrate that the captive population, which has been carefully managed to maintain genetic diversity, still serves as a valuable reservoir for future reintroductions if needed. At this point however, the forests that are monitored by the field teams are at capacity and reintroduction may not be logistically possible. New forests would need to be added to the program either through program expansion or reforestation.

Translocation of select individuals from one management unit to another could help increase genetic diversity of each management unit. While the goal of the GLT Association is to have these management units connect via forest corridors (AMLD

2009b), the translocation of animals now could help maintain, and even enhance the unit's genetic diversity. This is especially true for Imbaú which has the lowest level of genetic diversity (91.34%) out of the three management units and also has the smallest population size (138). As the smallest population, Imbaú would benefit by receiving animals from either Rio Vermelho or Dourada. It was demonstrated that the translocation of 20 individuals could raise the genetic diversity of the Imbaú population by nearly 2%. This is the first study known that has used MK values and the effect on GD to recommend translocation movements between in situ populations.

As the population of golden lion tamarins gets larger, it will become increasingly difficult to obtain reliable pedigree information. However, this study provides an example of how pedigree analysis can be a powerful tool for assessing the genetic status of small populations. Pedigree analysis provides information on genomic-wide levels of diversity that molecular data cannot yet provide. For populations of reintroduced species that are derived from pedigreed captive populations, it is advisable to continue these pedigrees through reintroduction to allow for similar evaluation to be used in developing management strategies to optimize the conservation of genetic diversity.

The overall genetic status of the reintroduced GLT population is favorable, however this population is small and fragmented and therefore still at risk. Further reintroductions could enhance the genetic diversity and carefully selected translocations could help increase the genetic diversity of the management units. However these are short term

solutions to a long term problem. Ultimately an increased population size could help ensure the maintenance of genetic diversity and increased migration rates could help reduce inbreeding level. Both of these measures would require an increase in habitat to connect or enlarge the fragmented population.

CHAPTER 2

Understanding Movement in a Fragmented Population of Golden Lion Tamarins

Introduction

Habitat fragmentation is one of the most pervasive threats affecting wildlife populations around the world. Fragments are often small and in many cases isolated, increasing a population's risk of extinction. Demographic variation, such as fluctuation in birth or death rates, can cause a small population's numbers to plunge so low that recovery is impossible (Drake and Lodge 2004). Due to lack of gene flow, small, isolated populations eventually suffer from low genetic diversity, inbreeding and inbreeding depression (Frankham et al. 2010). These threats, however, can be reduced if there is some movement of animals, and gene flow, between populations (Hanski and Gilpin 1997). Unfortunately, fragmentation often results in habitats surrounded by a matrix that discourages movement. Thus, conservation planning for endangered species in these situations includes developing metapopulation management strategies which encourage movement between populations (Beier and Noss 1998). Therefore, understanding the limits and the factors related to successful movement is then critical for creating successful metapopulation management plans.

Successful movement (gene flow) is a key component to achieving conservation goals for genetic diversity and population persistence. Organism movements, including natal dispersal, inter-patch movement, immigration and emigration can affect individual fitness, population dynamics, genetics, and species distribution (Bowler and Benton 2005). Movements in fragmented landscapes are of particular concern where long-term viability is often dependent on them (Frankham et al. 2010). Several variables are likely to affect movements in these landscapes such as the size of the fragments (Hill et al. 1996), distance between the fragments (Hill et al. 1996), and population density in the fragment (Aars and Ims 2000, Andreassen and Ims 2001). Understanding the influence these variables have on movement patterns and frequencies will lead to a better insight of the metapopulation structure and dynamics as the characteristics and persistence of metapopulations are strongly dependent on movement patterns between patches (Gilpin and Hanski 1991). For instance, migration can act to reduce extinction in patches with reduced populations through re-colonization of vacant patches (Hanski and Gilpin 1991). Additionally, the more migration that occurs, the more the population behaves (genetically) as a contiguous population (Frankham et al. 2010). While movement is less common in classic metapopulations, it is common in patchy populations characterized by several occupied patches (Harrison 1991), which can help prevent extinction and lead to a panmictic population (Gilpin and Hanski 1991). According to Hastings (1993), immigration rates of at least 10% per generation were enough to synchronize a population. Even one immigrant per generation is enough to keep populations from becoming totally differentiated (Frankham et al. 2010).

The movement of organisms through a landscape influences population viability, especially when populations are fragmented, but understanding the factors that affect movement and determining movement patterns can be challenging. Movement is a function of both the behavior of the organism (functional component) and the heterogeneity of the landscape that influence the organism's movement (structural component). Both of these components of movement are addressed in the concept of landscape connectivity as introduced by Merriam (1984). Landscape connectivity is the degree to which the landscape facilitates or impedes movement among patches (Tischendorf and Fahrig 2000). Structural connectivity refers to the habitat contiguity, whereas functional connectivity refers to the organism's movement patterns in the landscape, or their behavioral responses to landscape elements. To fully understand landscape connectivity, it is necessary to quantify these components.

Functional connectivity is difficult to measure; to measure directly it requires movement data which can be challenging and often impractical to obtain. Tischendorf and Fahrig (2000) suggest that measuring movement rates on as little as 1% of the landscape is sufficient for an assessment of landscape connectivity, but even so, very few studies have succeeded in this. Nearly all the studies that have measured landscape connectivity use a model approach where models are based on probability of movement (Fahrig and Paloheimo 1988, Henein and Merriam 1990), dispersal success (Schippers et al. 1996, Schumaker 1996), and search time, which is the number of movement steps individuals require to find a habitat patch (Doak et al. 1992). Genetic data measuring gene flow can

be used to quantify functional connectivity indirectly, however this restricts the analysis to animals that have reproduced once they have moved (Crooks and Sanjayan 2006). Structural connectivity is easier to measure, using landscape analysis as opposed to movement data, and is therefore most frequently used when discussing issues of connectivity. The frequent assumption is that structural connectivity matches functional connectivity, however there are several scenarios where this would not be the case. For example, an organism may use the matrix to move between fragments that are not structurally connected. Alternatively, two patches may be connected structurally with a corridor, but unless the organism is using the corridor, the patches remain functionally isolated. Clarifying the difference in the level of functional and structural connectivity is important when developing conservation strategies for any species.

The highly fragmented population of golden lion tamarins (*Leontopithecus rosalia*: GLT), an endangered primate endemic to the Atlantic Coastal Forest of Brazil, provides an ideal situation for studying how a fragmented landscape affects movement patterns in primates and identifying the level of connectivity. With less than 7% of the original forest remaining, the population now stands at approximately 1,600 individuals divided into 7 isolated populations of varying size (Wuethrich 2007, AMLD 2009a). In most cases, the habitat that surrounds the forest islands is pasture or cropland, likely inhibiting dispersal between populations. Both sexes of GLTs typically disperse from their natal groups when they reach sexual maturity, around 18 months (Baker and Dietz 1996). However, because the populations are isolated, dispersers have limited options and many

tamarins likely die trying to disperse (Dietz, personal communication). How many succeed is not known since little is known about how tamarins, or arboreal animals in general, disperse in a highly fragmented landscape (Palomares et al. 2000, Anderson et al. 2007).

The purpose of this study is to identify the factors that affect the movement of golden lion tamarins across their landscape and to develop a model to predict movement.

Specifically, distance, fragment size, population size, density of GLTs in these fragments, and type of structural connectivity were examined as the key factors most likely to play a significant role in movement. Additionally, the functional connectivity of the monitored population, based on tamarin movements in monitored populations, was evaluated to determine if it matches the structural connectivity.

Methods

Study Site and Population

The current golden lion tamarin population is confined to 8 municipalities in Rio de Janeiro state all within the Sao Joao watershed. There are over 25 private land reserves where golden lion tamarins have been reintroduced (AMLD 2009a). These Private Natural Heritage Reserves (RPPNs) and the tamarins that inhabit these small forests are a result of the reintroduction program which operated from 1984 until 2000 (Figure 2.1).

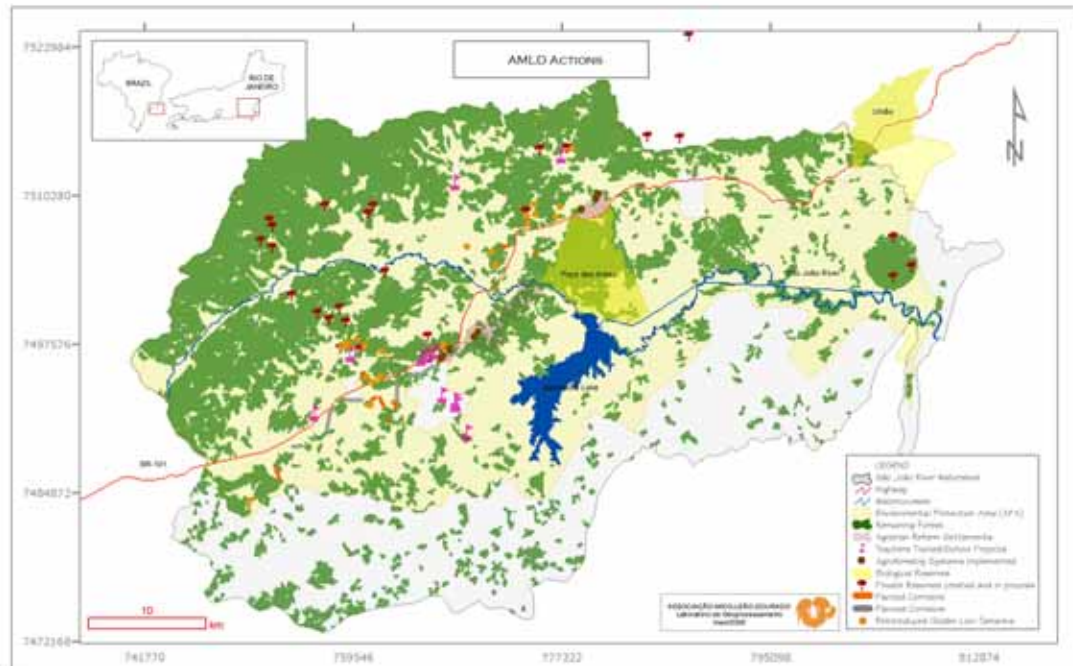


Figure 2.1: Map of GLT occurrence area. Image from AMLD 2009a.

A total of 146 captive-born and 7 confiscated golden lion tamarins have been released (Beck and Martins 2003). From these reintroduced animals, the population has grown and is currently estimated between 550 and 750, making up more than one-third of the entire wild population which is estimated at 1,600 tamarins (Beck and Martins 2003, AMLD 2009a). The current reintroduced population is made up of over 98% wild-born tamarins, descendents of captive-born animals.

At a metapopulation workshop held in 2009, the population of GLTs was classified into 7 different metapopulation management units (AMLD 2009b). These management units (MU) were defined based on distance between fragments and suitability for golden lion tamarins. In some cases, the MUs are composed of smaller fragments, but all fragments are within 100 meters of each other, a distance easily crossed by GLTs. Three of these MUs are composed of reintroduced GLTs and their descendents (Rio Vermelho, Imbaú, Dourada), two are composed of wild GLTs in the biological reserves (Poço das Antas and União) and two MUs contain wild populations that historically have not been monitored or managed (Figure 2.2).

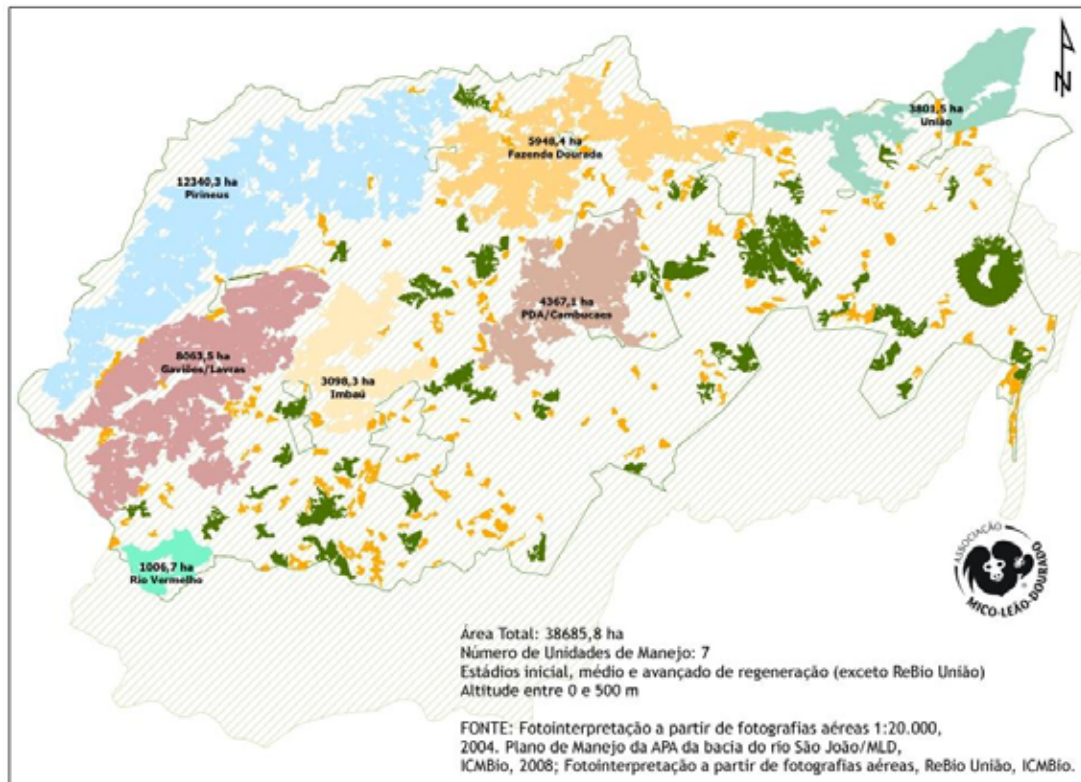


Figure 2.2: Map with GLT metapopulation management units (MUs). The size of each MU is shown in hectares. Image from AMLD 2009b

The population of GLTs has been extensively monitored for the last 25 years (Baker and Dietz 1996, Dietz et al. 1997, Kleiman and Rylands 2002). A large percentage of the groups living in these areas have been monitored and captured every six months to determine group composition and for the placement of radio telemetry collars, permanent tattoos, and temporary dye markings (Baker and Dietz 1996). These historical records provide continuous data on group composition, births, deaths, and migrants to and from the study groups. Using these records, any individual that changed location (i.e. animal moved to another group) was noted as a possible animal movement. All possible

movements were compared against the animals that had been translocated by the field team, and those translocations were excluded from analysis. Data from these successful movements were then examined to determine which factors may have contributed to their success.

The population was analyzed at several different levels. At the smallest level were movements between family groups. The next level of analysis was movement between neighborhoods where neighborhoods were defined by grouping any territories that were adjacent. Neighborhoods were created using ArcMap 9.3 software (Environmental Systems Research Institute, 2009) by placing buffers equal to the estimated diameter of the home range size for a golden lion tamarin (380 meters) around all the group territory centroids. Any adjacent groups were then categorized in the same neighborhood and were joined in ArcMap. The next level of analysis is that of fragments. Fragments were defined as patches of forests that were disconnected with other patches of forest. Connectivity was determined using spatial images from Google Earth (Google 2010). These fragments were also created in ArcMap. The final population level analyzed is functional units, where groups are identified by animal movement and functional connectivity. Groups with observed animal movements between them were categorized in the same functional unit.

Regression Analysis

Linear regression analyses were used to examine the relationship between the frequency of movements and several variables that could affect movement. Specifically, distance, size of the fragments tamarins were moving to/from, and population density at the time of movement in both the receiving and donor population were examined. Distance was measured as the Euclidian distance between the centroid of the group's estimated territory; therefore these distances would be the shortest possible path between two centroids. Distance calculations were done using ArcMap 9.3 software. Fragment size was calculated using a geometric tool that calculates the area of polygons in ArcMap 9.3 software. Densities were calculated as the number of GLTs per hectare where the number of GLTs was calculated based on the census records. All regressions were done in Excel 2007.

Logistic Regression Model

Logistic regression analysis was used to create a model for predicting movement between neighborhoods. For this analysis, pair-wise comparisons between all neighborhoods were created to characterize the possible moves based on several parameters (Table 2.1).

Table 2.1: Parameter used in logistic regression model.

Parameter	Classification	Measured	Description
LnDist	Continuous data	Used ArcMap 9.3 to measure the Euclidean distance between the centroids of the neighborhoods	Natural log of the Euclidean distance (m) between the neighborhoods
SizeFrom	Continuous data	Used ArcMap 9.3 to calculate the area of the neighborhoods	Size of the area (ha) the GLT was moving from
SizeTo	Continuous data	Used ArcMap 9.3 to calculate the area of the neighborhoods	Size of the area (ha) the GLT was moving to
Connected	0 = not connected, 1 = connected	Used Google Earth to determine if there was contiguous forest between neighborhoods	Determination of connectivity between all neighborhoods
Neighbor	0 = not a neighbor, 1 = neighbor	Used ArcMap 9.3 to determine neighbors	Determination of which neighborhoods were adjacent
DistC	0-3 (see table 2.2)	Used Google Earth to determine characteristic of distance	Characteristic of the distance between neighborhoods, in this case the path of least resistance was chosen
SDistC	0-3 (see table 2.2)	Used Google Earth to determine characteristic of distance	Characteristic of the shortest distance between neighborhoods
Moved	0 = stayed, 1 = moved	Used mark-recapture data	Movement between neighborhoods

Each pair (i.e. neighborhood 1 to neighborhood 2) was classified based on the variables of Euclidean distance between the neighborhoods, neighborhood size both for the donor neighborhood (SizeFrom) and the recipient neighborhood (SizeTo), whether the neighborhoods were connected, if they were neighbors, the characteristic of the distance between the neighborhoods (DistC), and the characteristic of the shortest distance

between the two neighborhoods (SDistC). Distance characteristics are defined in Table 2.2.

Table 2.2: Description of distance characteristics.

Value	Description of distance characteristics
0	No connectivity, no forest within 100 meters
1	Poor, Patchy connection or very thin connections, separated by 2 or more poorly connected fragments
2	Sub-optimal, separated by small road (<15 meters) or connected by more than one connection
3	Optimum connectivity, contiguous forest

Once all neighborhood pairs had been classified with these variables, movement data for each pair (0= no movement between neighborhood, 1= at least one individual movement between this pair of neighborhoods) was added as the dependent variable. Using SAS, version 9.2 software (SAS Institute 2009), univariate logistic regressions (Proc Logistic, SAS Institute 2009) was run to determine which of the variables to consider including in a multiple logistic regression. Variables that have a p-value < 0.25 were then considered for inclusion in the multivariate analysis since using the traditional p-value < 0.05 for selection criterion has been shown to fail to identify important variables (Hosmer and Lemeshow 2000). Once the variables were initially screened using the univariate analyses, stepwise methods were used to determine which variable should be retained in the full model to predict movement. Variables are eliminated based on statistical criteria. Both forward selection and backward selection procedures were run where the models are

built in a sequential fashion. The Akaike Information Criterion (AIC) was used as well as Wald statistic to measure goodness of fit to determine which model was a better predictor (Hosmer and Lemeshow 2000).

Functional Connectivity

Functional connectivity considers the behavioral responses of an organism to various landscape elements and is a good indicator of the level of movement in a landscape (Tischendorf and Fahrig 2000). In this study, functional connectivity was determined by measuring movement between groups. Any groups that had movement between them were classified as a functional unit. These groups were then merged using ArcMap 9.3 software to map the functional units and the functional connectivity. The functional connectivity was then compared against the structural connectivity previously measured (AMLD 2009b).

Cluster Analysis

Another method for examining the level of connectivity is through cluster analysis; in this case groups were clustered based on the number of movements between them. A dissimilarity matrix was created using information on the number of recorded moves between each group. Matrices were created for group in the Rio Vermelho area, the Imbaú area, and the Dourada area. Separate matrices were created for these group combinations because there was no recorded movement between any of these areas. For each pair of groups in the matrix, the dissimilarity between the pair was recorded as

1/(No. movements between these two groups). If there was no movement recorded between groups, a dissimilarity value of 20 was used, a number great enough to separate those groups without any movement from those with movement. Cluster analysis was performed using the program Proc CLUSTER in SAS, version 9.2 (SAS Institute 2009). The CLUSTER procedure in SAS is based on agglomerative hierarchical clustering method to group observations. In the cluster analysis, each observation begins in a cluster by itself. The next closest clusters are then merged to form a second cluster that replaces the first two. This process continues until only one cluster is left. Here the clusters were made based on the number of movements between groups and the population was divided into three subpopulations to aid in the viewing of clusters.

Results

Frequency of Movements

A total of 287 movements were documented from mark-recapture data with 239 unique individuals that moved. Most animals (82.4%) moved only once, 15.9% moved twice, 1.2% moved three times, and only one animal (0.4%) moved 4 times (Figure 2.3).

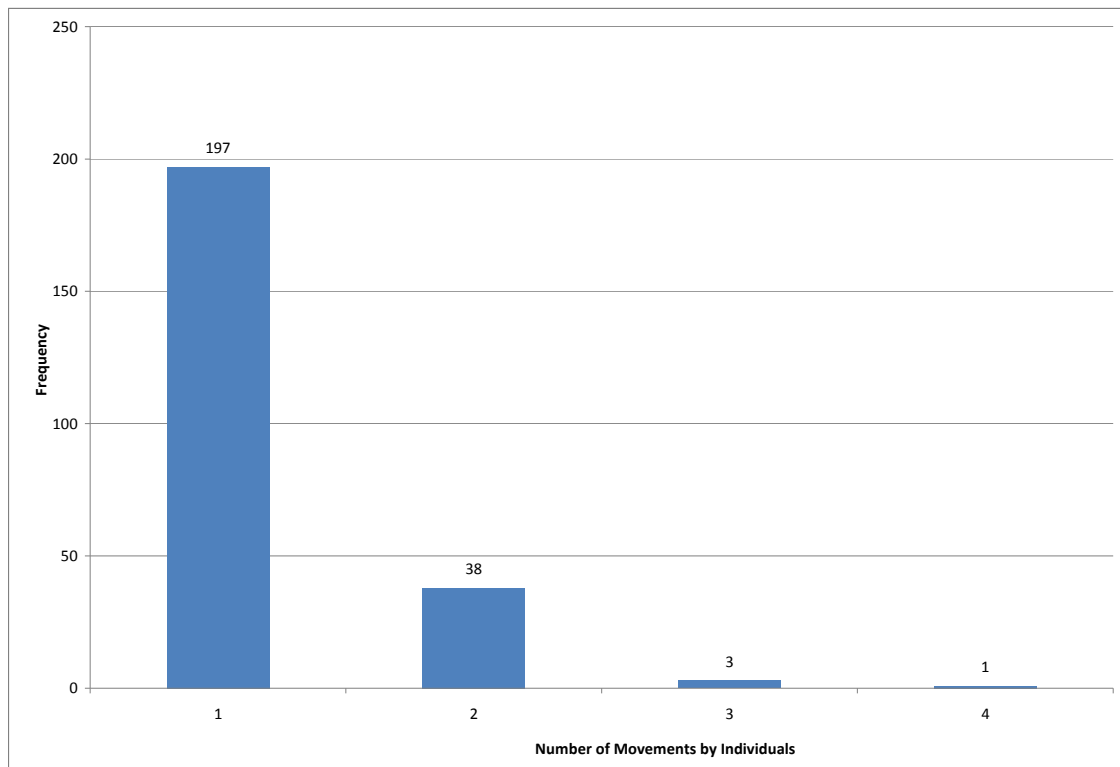


Figure 2.3: Frequency of animal movements. Most animals move only one time.

Distance

The average distance moved was 847 meters. Movements were more frequent at shorter distances with the most animals (20%) moving a distance range between 401-600 meters (Figure 2.4). Relatively few animals move more than 2000 meters, and the greatest distance traveled was just over 6600 meters. Distance and movements are inversely proportional ($p = 0.0002$); that is, as the distance increased, the number of movements observed decreased (Figure 2.5).

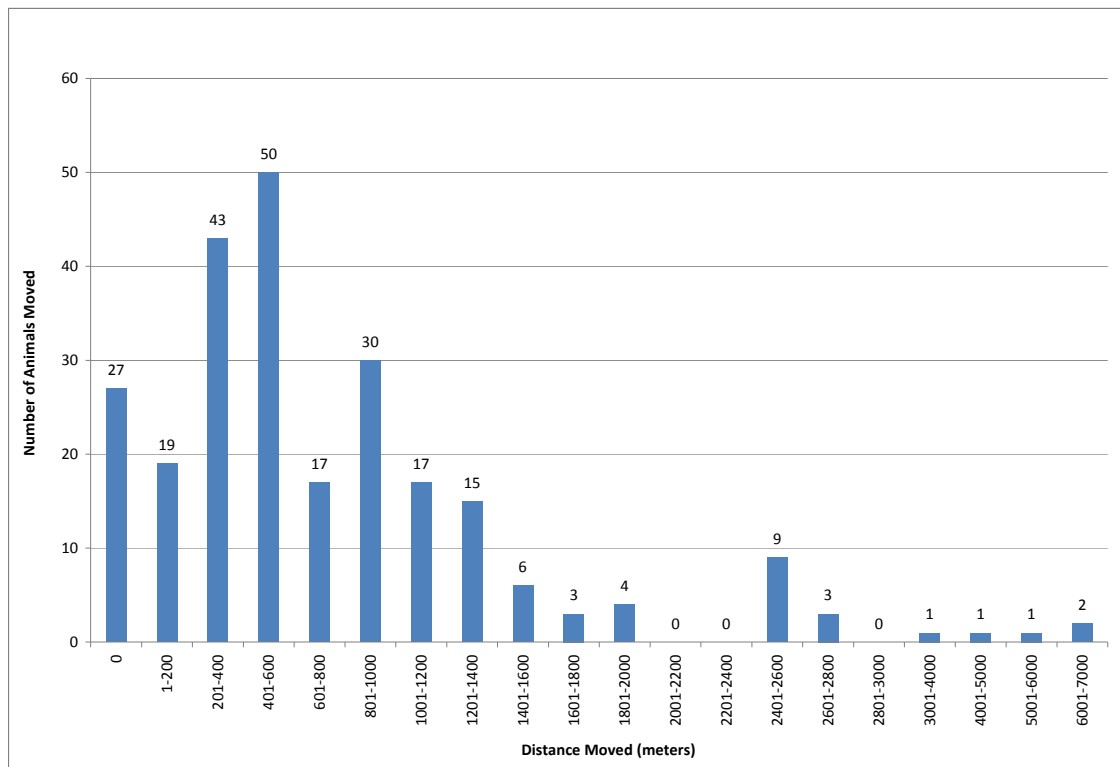


Figure 2.4: Frequency of distance moved. Most of the movements occurred when distances were less than 1,600 meters.

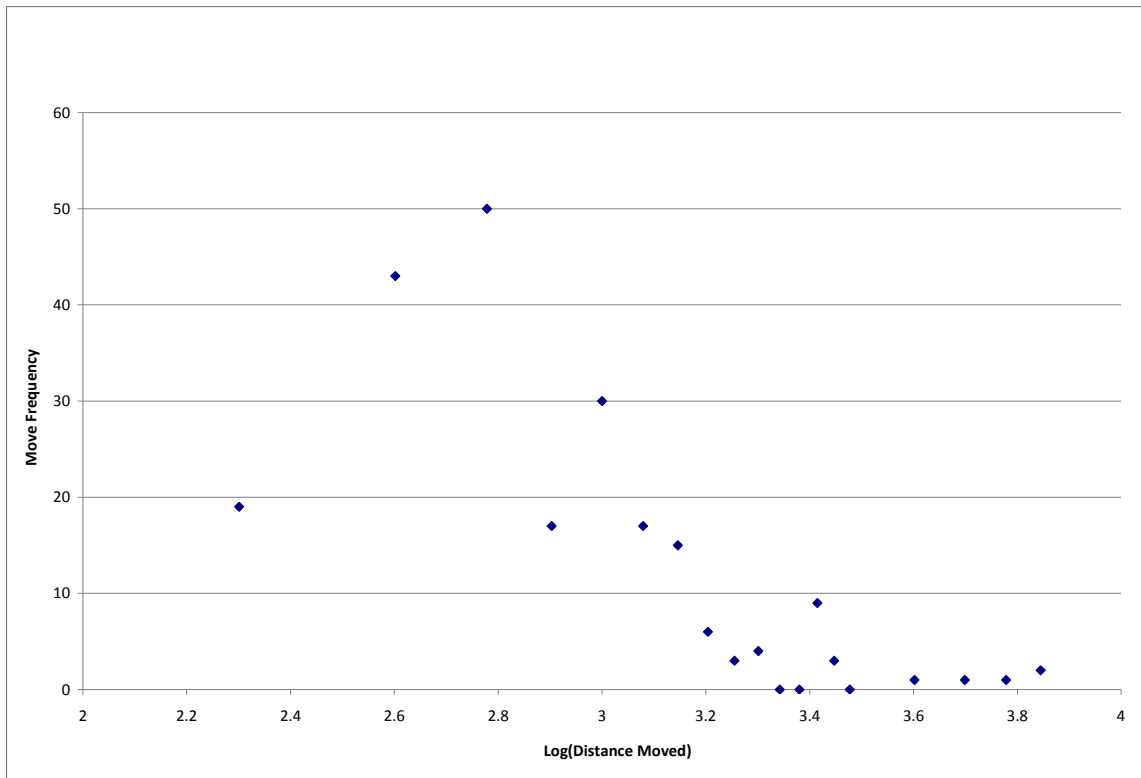


Figure 2.5: The relationship of distance and movement. Distance is inversely proportional to the number of movements ($p = .0002$).

Fragment Size

Fragment size and its relation to movements both to and from fragments was examined.

There is much variation in the data and the data suggest that there is no relationship between the frequency of moves and the size of the fragment the GLT moved to or the size of the fragment the GLT moved from (Figure 2.6).

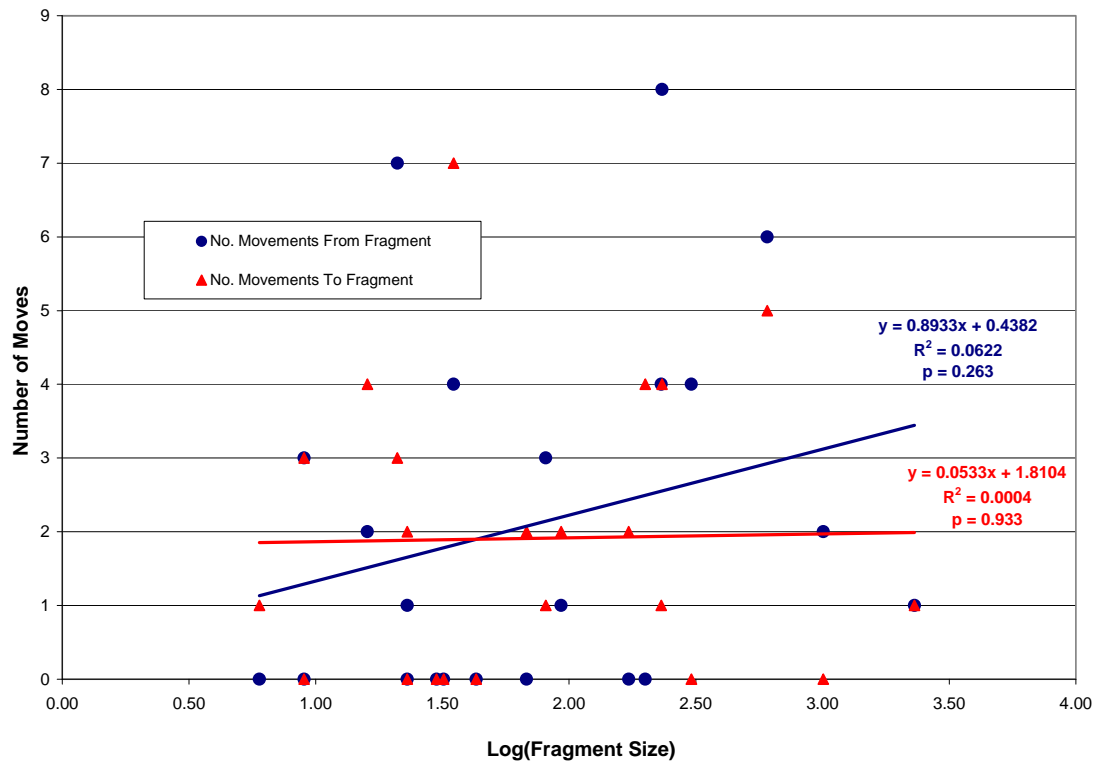


Figure 2.6; The relationship of the number of moves to fragments (red triangles) and from fragments (blue circles) with corresponding regression lines. Neither movement to or from fragments correlate with fragment size ($p = 0.933$, $p = 0.263$, respectively).

Movements within fragments were also documented. Unlike movements to and from fragments, movements within fragments did correlate with fragment size ($p = 0.0003$).

As the fragment size increased, the number of movements within the fragment also increased (Figure 2.7). One of the larger fragments in the population, Rio Vermelho, is illustrated in the figure, but was not included in the regression analysis as it was an obvious outlier; it has a disproportionately large number of moves for the fragment size which could be due to conflicting factors such as increased monitoring in this area.

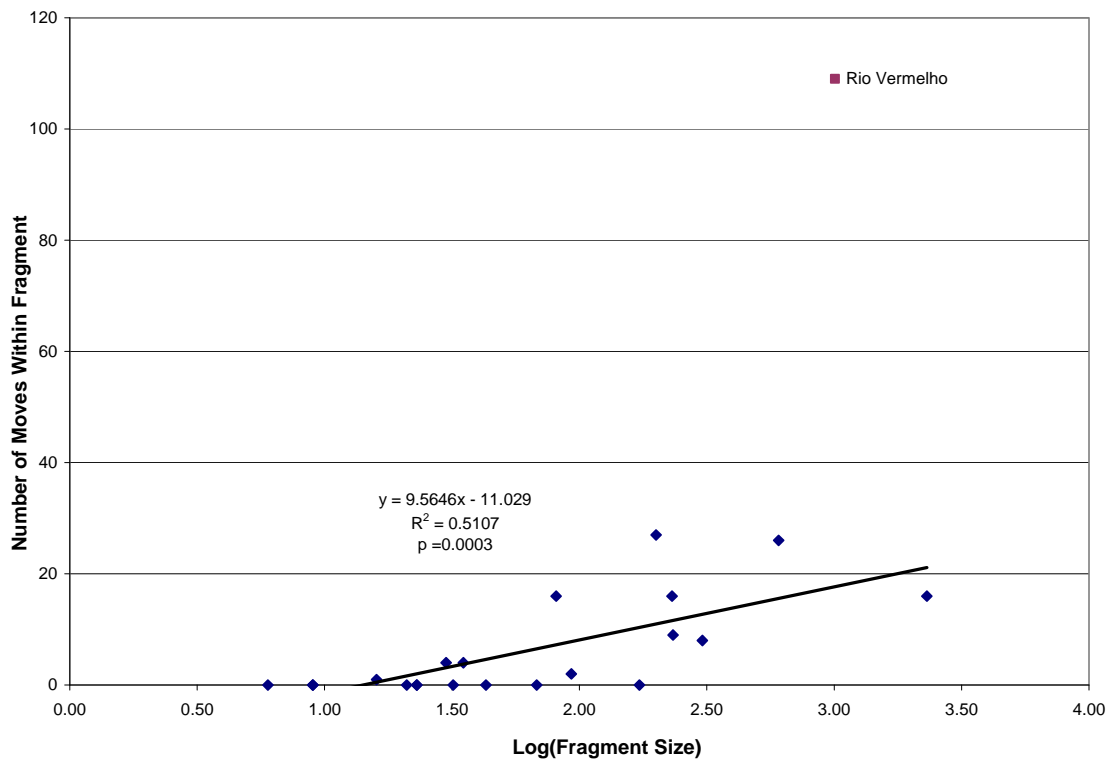


Figure 2.7: The number of movements within a fragment in relation to the fragment's size. Fragment size and the number of movements within a fragment are directly related ($p = 0.0003$).

Population Size

Analyzing both at the fragment level and the smaller neighborhood level, population size is inversely related to the number of movements (Figure 2.8 and Figure 2.9). There is a significant negative relationship for both movement to and from the fragment or neighborhood. Values are very similar for both directions of movement (to and from) since in many cases the moves were within the same fragment or neighborhood.

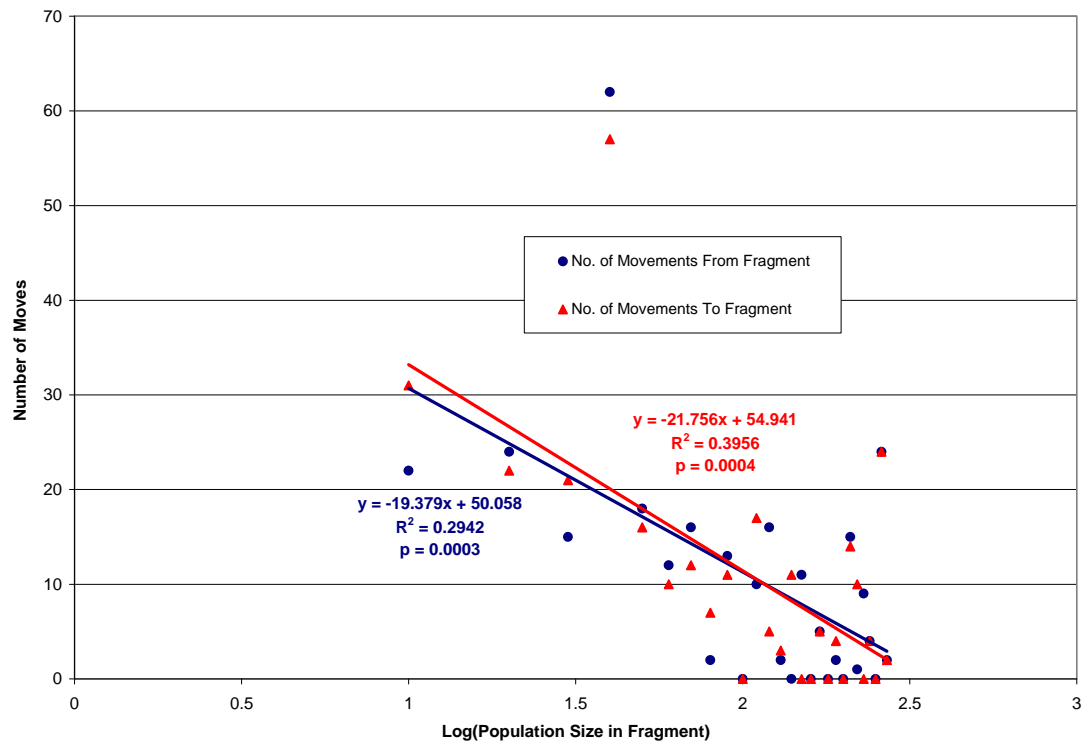


Figure 2.8: The number of movements from and to fragments in relation to the population size. Population size and the number of movements both to and from a fragment are inversely related ($p = 0.0004$ and 0.0003 , respectively).

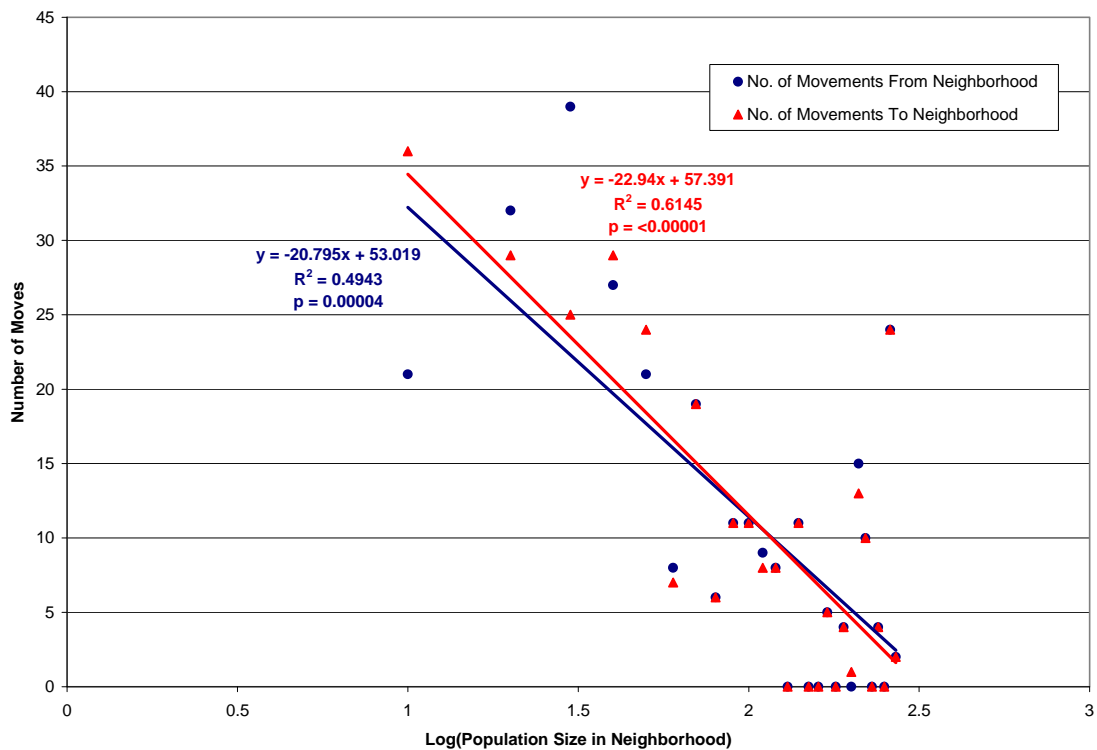


Figure 2.9: The number of movements from and to neighborhoods in relation to the population size. Population size and the number of movements both to and from a neighborhood are inversely related ($p = 0.00004$ and <0.00001 , respectively).

Density

A range of population densities exist for golden lion tamarins (Kleiman and Rylands 2002). In the Poço das Antas Biological Reserve, studies over the last two decades indicate an average density of 0.12 GLT per hectare. Population densities were examined at in both the fragments and neighborhoods the GLTs were moving to and from; density averages and ranges are reported in Table 2.3.

Table 2.3: Population density at both the fragment and neighborhood levels. There is no statistical difference between the from and to densities in either fragments or neighborhoods.

	Population Densities (GLT/Hectare)		
	Mean	Standard Error	Range
Fragments			
<i>From</i>	0.1889	0.0079	0.0042 - 0.7932
<i>To</i>	0.1737	0.0065	0.0006 - 0.5231
Neighborhoods			
<i>From</i>	0.2175	0.0059	0.0311 - 0.3886
<i>To</i>	0.2100	0.0063	0.0090 - 0.5746

Like population size, population densities were similar in the “to” and “from” groups since frequently, the movement occurred within the same fragment/neighborhood. The number of movements to and from both fragments and neighborhoods are not significantly related (Figures 2.10 and 2.11). Analyses of the data indicate no relation between the number and moves and the density of the population.

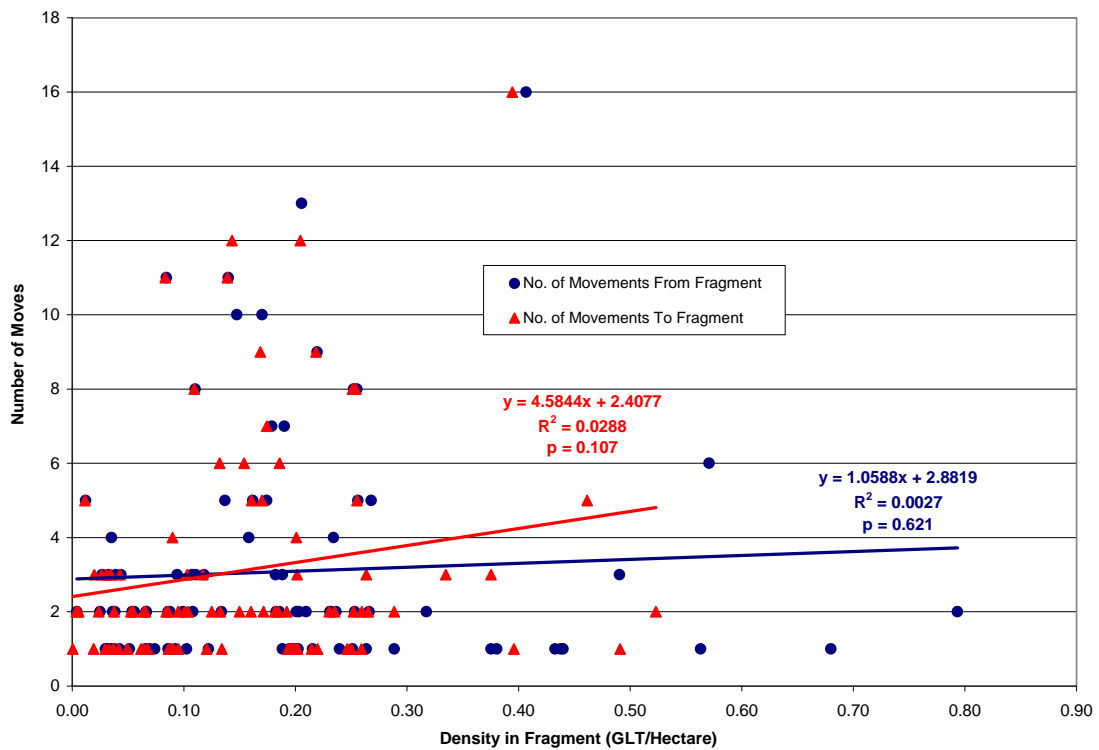


Figure 2.10: The number of movements from and to fragments in relation to the population density. Population density and the number of movements both to and from a fragment are not related.

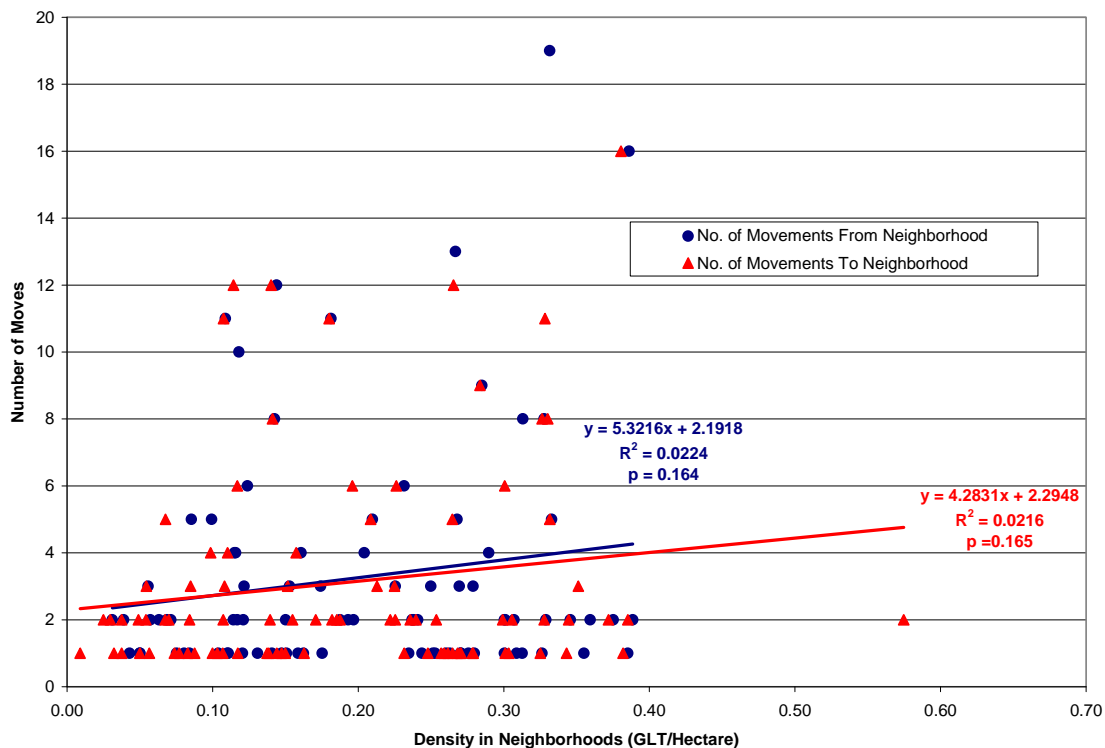


Figure 2.11: The number of movements from and to neighborhoods in relation to the population density. Population density and the number of movements both to and from a neighborhood are not significantly related.

Predicting Movement Between Neighborhoods: Logistic Regression Model

Of the seven variables considered in this analysis, all but the size of the neighborhood that the tamarins were moving to (SizeTo) were found to be significant at a level of 0.25; therefore this variable was removed from future consideration. During the reviews of the multivariate logistic regression, the DistC variable was collapsed into a binary variable; the original codes of 0 and 1 were collapsed into one group (coded 0) and original codes 2 and 3 were collapsed into another group (coded 1). The stepwise analysis with the

remaining 6 variables presented two possible models for predicting movement between neighborhoods. Model A used the natural log of the distance (LnDist), the neighborhood size the tamarin was leaving (SizeFrom), and whether or not the neighborhoods were neighbors to determine the probability of movement (P(M)):

$$P(M) = e^x / (1 + e^x) \text{ where}$$

$$x = \beta_0 + \beta_1(\text{LnDist}) + \beta_2(\text{SizeFrom}) + \beta_3(\text{Neighbors}),$$

and β_0 = the intercept and β_1, β_2 , and β_3 are the coefficients for those parameters as listed in Table 2.4.

Model B also included the natural log of the distance (LnDist) and size (SizeFrom), but used the characteristic of the distance (CDist; categorized as 1 for contiguous forest, 0 for all other characteristics) to predict movement:

$$x = \beta_0 + \beta_1(\text{LnDist}) + \beta_2(\text{SizeFrom}) + \beta_3(\text{CDist}),$$

where β_0 = the intercept and β_1, β_2 , and β_3 are the coefficients for those parameters as listed in Table 2.4.

Table 2.4: Logistic regression model parameters

	Parameter	Coefficient	Standard Error	<i>p</i> value	AIC Value	Wald Statistic
Model A	Intercept	-13.0627	4.3504	0.0027	91.7	$p < 0.001$
	LnDist	2.0433	0.5894	0.0005		
	SizeFrom	-0.6287	0.4167	0.1313		
	Neighbor	0.6265	0.3588	0.0808		
Model B	Intercept	-13.9064	4.1108	0.0007	87.8	$p < 0.0001$
	LnDist	2.1617	0.5514	<0.0001		
	SizeFrom	-0.7169	0.4084	0.0792		
	Cdist	0.7964	0.3183	0.0123		

Model A had an AIC value = 91.7, while model B had a AIC value = 87.8 and thus with the lesser value is a more powerful model. Therefore, the probability of movement ($P(M)$) between neighborhoods can best be described by the equation:

$$P(M) = e^x / (1 + e^x) \text{ where}$$

$$x = 13.9064 - 2.1617(\text{LnDist}) + 0.7169 (\text{SizeFrom}) - 0.7964 (\text{CDist})$$

As seen in Table 2.4, SizeFrom has a p value of 0.0792 which is not statistically significant at the 95% confidence interval. However, when this parameter was removed from the model, the AIC value increased to 88.556. Therefore, despite the higher value, this parameter contributes to a more powerful model and was kept in the full model.

The predicted probabilities of movements ($P(M)$) for different SizeFrom and LnDist values are shown in figure 2.10. The probability of movement was modeled at three set distances: a short distance of 500 meters, a medium distance of 5000 meters, and a far distance of 10,000 meters. Both neighborhoods connected with contiguous forest ($CDist = 1$) and those not connected ($CDist = 0$) were modeled for comparison.

When distance is set to short, probability of movement is fairly high and it increases as the size of the neighborhood the tamarin is moving from increases (Figure 2.12a). $P(M)$ is slightly higher when distance is characterized as contiguous forests.

When the distance is set to either medium or far, the probability of movement decreases as compared to the short distance (Figures 2.12b and 2.12c). $P(M)$ increases slightly as the size of the neighborhood the tamarin is moving from increases, but $P(M)$ never goes above 0.1.

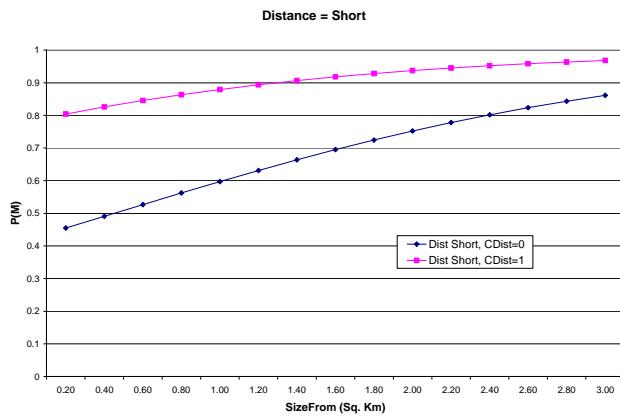


Figure 2.12a

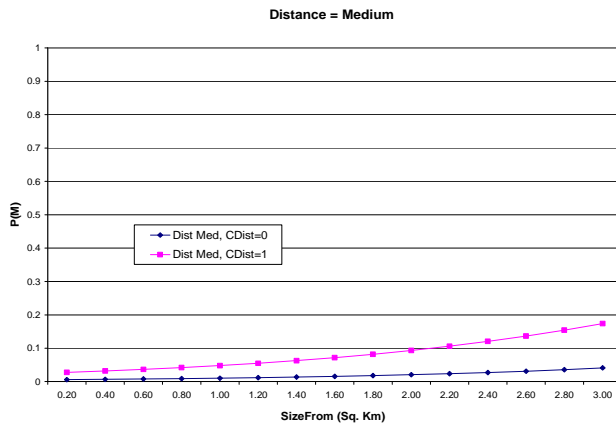


Figure 2.12b

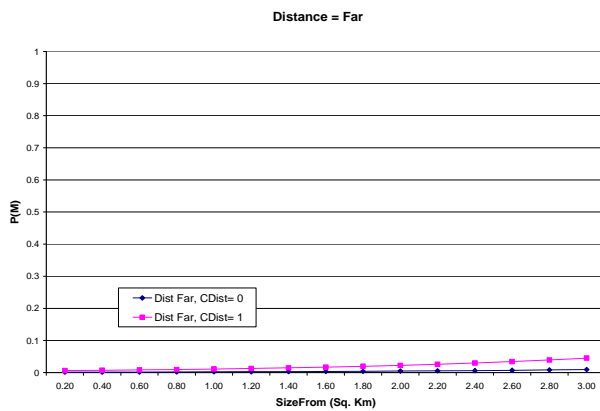


Figure 2.12c

Figure 2.12: Logistic regression model- distance is fixed to short (2.12a), medium (2.12b), and far (2.12c). Both contiguous connections (pink squares) and noncontiguous connections (blue diamonds) are modeled. As size increases, the probability of an individual moving also increases. However, at medium and far distances, movement is not likely.

The size of the neighborhood the tamarins were coming from (SizeFrom) was set constant at three different levels: small was set at 0.5 sq. km, medium set at 0.9 sq.km, and large set at 1.5 sq. km. The outcome was similar whether the size was small (Figure 2.13a), medium (Figure 2.13b), or large (Figure 2.13c). As the distance between the neighborhoods increased, the probability of movement decreased rapidly in all three sizes. The probability of an individual moving from a neighborhood regardless if that neighborhood was small, medium, or large, approached zero around 3000 meters ($\ln(\text{Distance}) = 8$). The result was similar both for distances characterized by contiguous forest connection (CDist = 1) and for those not (CDist = 0).

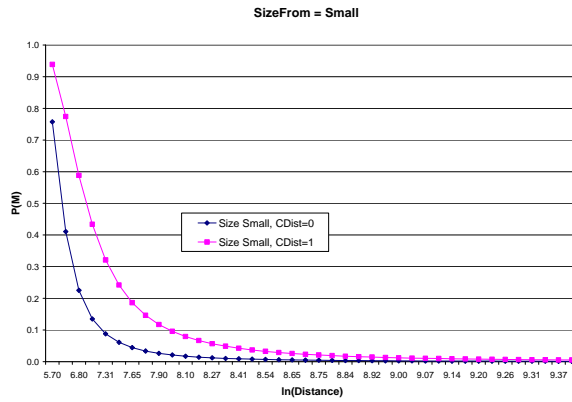


Figure 2.13a

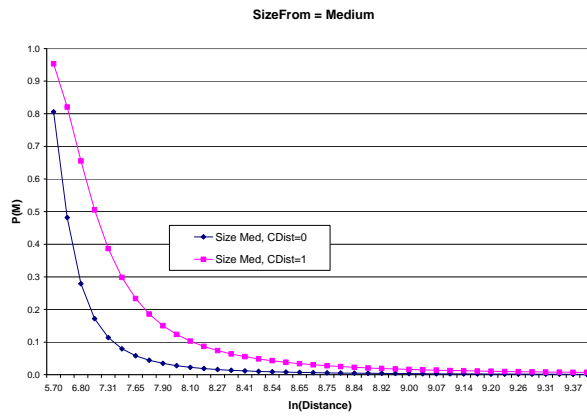


Figure 2.13b

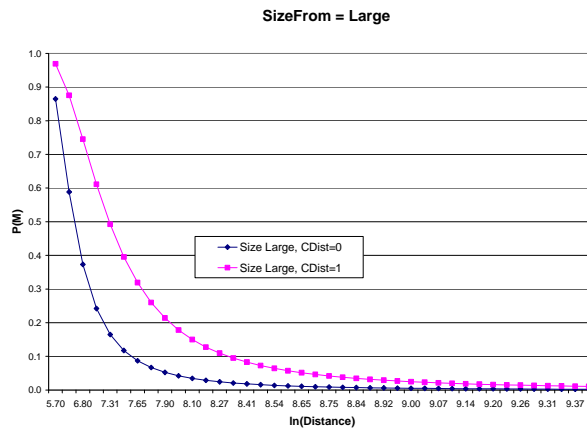


Figure 2.13c

Figure 2.13: Logistic regression model- size is fixed to small (2.13a), medium (2.13b), and large (2.13c). Both contiguous connections (pink squares) and noncontiguous connections (blue diamonds) are modeled. As distance increases, the probability of an individual moving dramatically drops until about 3000 meters at which point the probability of movement approaches zero.

Connectivity

In order to understand the functional connectivity of the population, all groups were classified into functional units based on whether or not they have shared animals or had moves between them. Figure 2.14 shows the functional units, demonstrating how the population is actually connected. Under this classification based on movement between the groups that are part of this study, there are 8 functional units. Movement between these groups has not been observed.

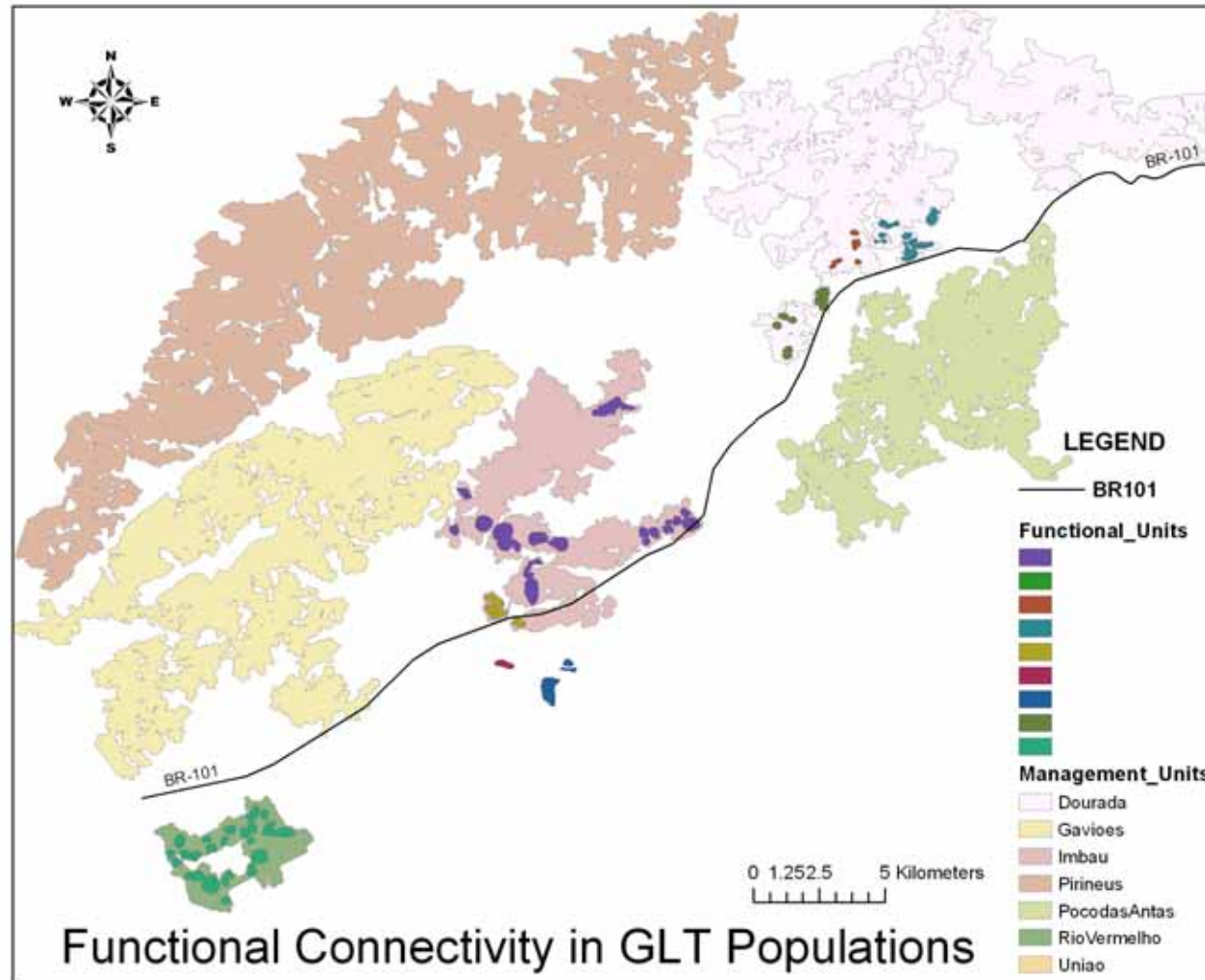


Figure 2.14: Map of GLT functional units. There are 8 different functional units classified based on group movements.

Cluster Analysis

In order to review the strength of connection between the groups, cluster analysis was used to hierarchically cluster the groups based on number of movements between them. Due to the low number of movements relative to the number of groups, it is difficult to observe clear definitions of clusters. The entire population was analyzed as three separate subpopulations (Rio Vermelho, Imbaú, and Dourada) since there was no movement documented between those subpopulations. In each subpopulation, a hypothetical group (labeled as XXXX) was added and used as an outgroup to calibrate the nodes representing no movement between groups. This group had no movement between any of the groups and should always have remained isolated and in its own cluster.

Rio Vermelho (Figure 2.15) appears to be best divided into four clusters, although four clusters explain only 35% of the variance. At least 11 clusters are needed to account for 70% of the variance.

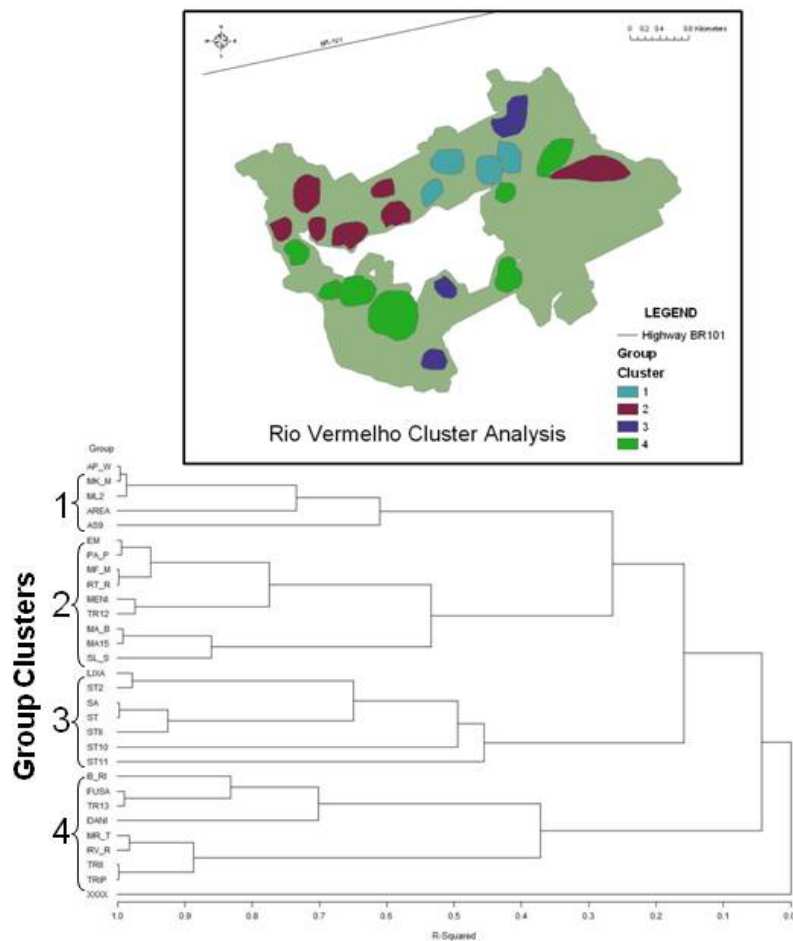


Figure 2.15: Cluster analysis for management unit Rio Vermelho with corresponding map. Rio Vermelho can roughly be divided into 4 different clusters with loose linkages between them. Those four clusters are highlighted on the map.

The Imbaú population can be divided into 7 clusters to account for about 50% of the variation (Figure 2.16). There are two clusters that appear to be relatively isolated-- the cluster with groups JG and JG2 and the cluster with groups AL2 and Andre.

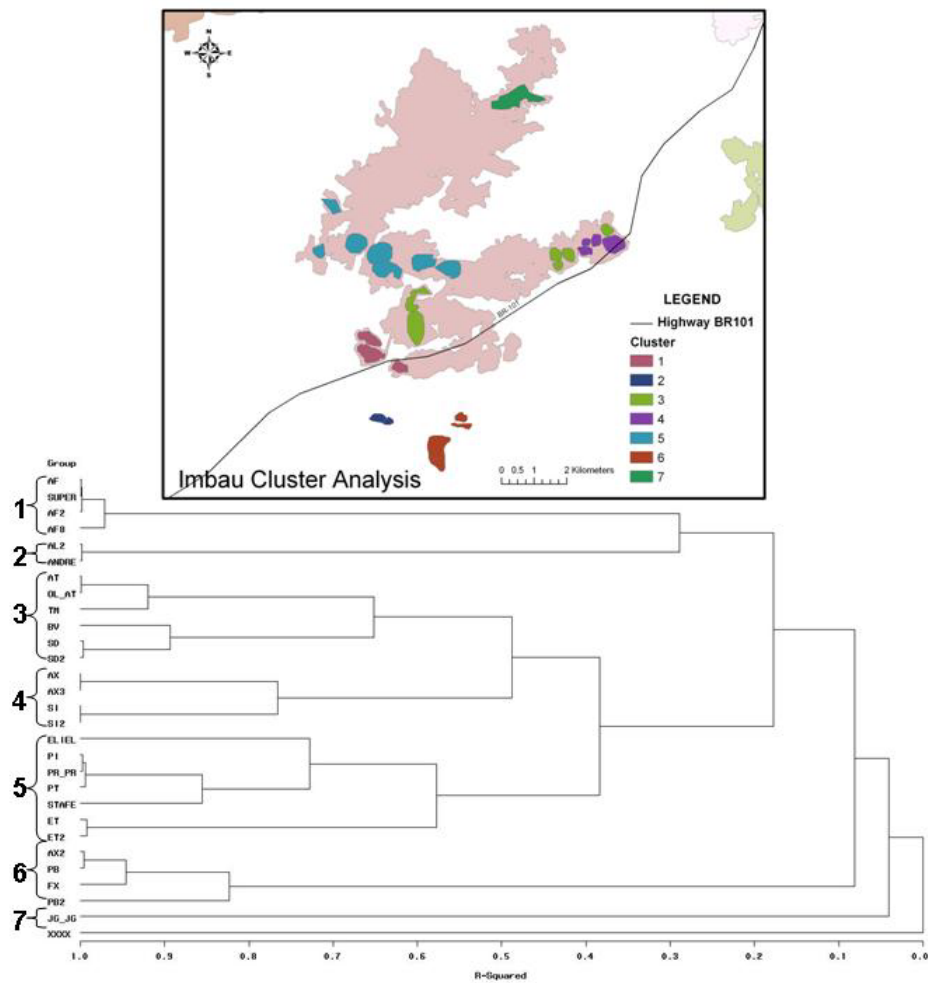


Figure 2.16: Cluster analysis for management unit Imbaú. Imbaú can be divided into 7 different clusters with the first six having linkages between them. The seventh cluster (groups JG and JG2) is relatively isolated from this subpopulation.

The Dourada population can be divided into 4 clusters accounting for only about one-third of the variation (Figure 2.17). Clustering into 7 groups accounts for approximately 50% of the variation.

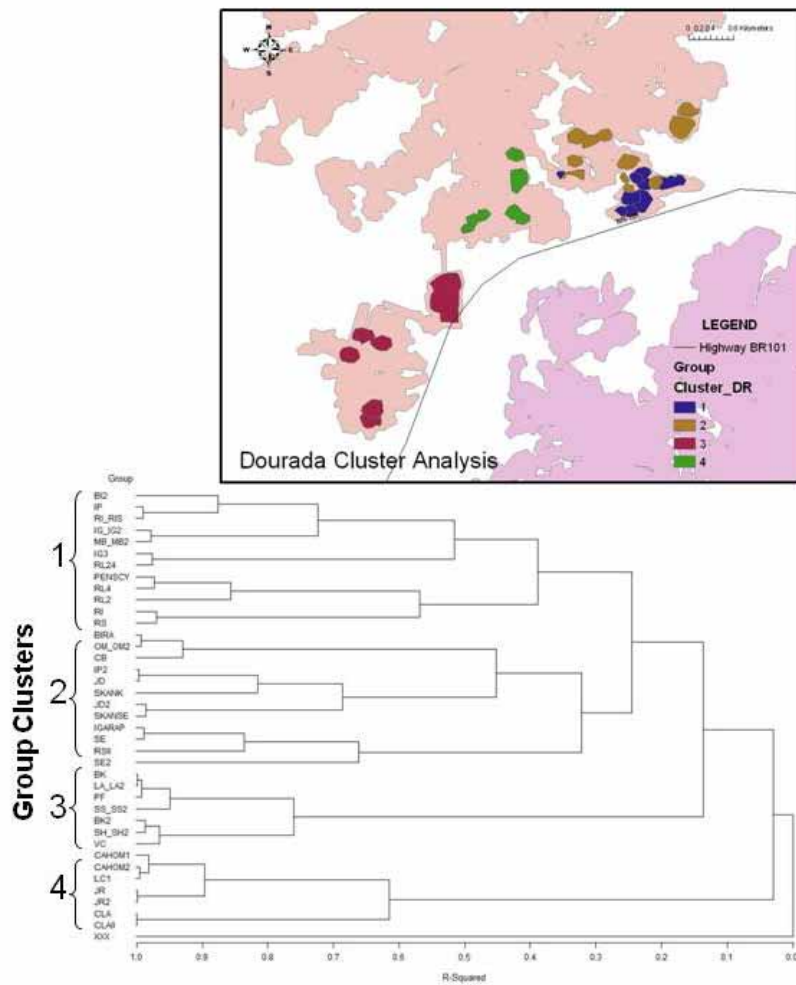


Figure 2.17: Cluster analysis for management unit Dourada with corresponding map. Dourada can be divided into 4 different clusters with loose linkages between them. Those four clusters are shown on map.

Discussion

Connectivity is critical for long-term viability of small populations, yet obtaining data to examine a population's level of functional connectivity is a challenge. This study examines the connectivity at various levels in the fragmented population of golden lion

tamarins and specifically determines which factors affect movement in the population. This information is then used to create a model by which future movements could be predicted. This study also determines the functional connectivity in this population of GLTs as compared to the structural connectivity. The results of this study form the scientific basis for a long-term metapopulation management plan to increase population viability.

From mark-recapture data, 287 movements between groups of golden lion tamarins were documented and the great majority of these (82.4%) were a single unique animal movement (Figure 2.3). Movement is often assumed to be a behavior that is associated with higher rates of mortality, possibly due to higher predation risk and the physiological costs of moving (Sutherland et al. 2000, Doherty and Grubb 2002), therefore minimizing these movements would be advantageous to the animal. Movement data for this study are limited to the amount of trapping done during the study in the areas monitored, so it is likely that the number of movements documented here is an under-representation of the number of movements that actually occurred.

The frequency of documented movements was used to look at several factors which could possibly affect these movements: distance, fragment size, neighborhood size, and population size and density at both the fragment and neighborhood level. Of all these factors, distance, population size, and movement within fragments had a significant relationship with the number of movements. Distance most clearly plays an important

role in the frequency of movements; most of the movements occurred at distances less than 1,600 meters (Figure 2.4) and the inverse relationship of move frequency and distance is highly significant (Figure 2.5; $p = 0.0002$). Distance is a common limit to movements and is supported by other empirical evidence (e.g. Hill et al. 1996, Serrano and Tella 2003). This is expected following the predictions based in Island Biogeography Theory (IBT) developed by MacArthur and Wilson (1967) and Metapopulation Theory (Hanski and Gilpin 1991). Given the fragmentation of many landscapes forming what are essentially islands, IBT has played a prominent role in the conservation of endangered species and their habitats. Golden lion tamarin habitat is highly fragmented and, although it is generally assumed that GLTs are willing to cross some open terrain while dispersing, movement rates are likely affected by distance as predicted by IBT. Under this theory, it is expected that as distance increases, movements would decrease. The data support this, suggesting that IBT is an important predictor of GLT movements in this landscape.

Fragment size (area) is frequently cited to have a negative relationship with emigration rates (Bowler and Benton 2005). In theory, a smaller fragment would have a greater edge to size ratio, increasing the likelihood that an individual would encounter an edge and possibly leave that fragment. In terms of immigration, as a fragment gets larger, the probability of an individual finding that fragment increases, so immigration rates should be higher in larger fragments. In their study on butterflies, Hill et al. (1996) found that a greater proportion of individuals emigrated from and immigrated into small fragments as

compared with larger fragments. This study, however, found no relationship between the size of the fragment or neighborhood the tamarins were moving to or from and the frequency of movements. This could be due in part to an aversion of the tamarins to enter inhospitable habitat; they may not be any more likely to leave a fragment even when they have increased encounters with the edge in a smaller fragment. The number of movements within the fragment and the size of those fragments were however significantly related (Figure 2.7; $p = 0.004$) so as the size of the fragments increased, there were more movements within those fragments. This complements the results pertaining to population size; as population size increased, the frequency of movements also increased. In larger populations, movement is more likely.

For golden lion tamarins, the number of breeding opportunities in a population is inversely related to population density. When population density is high (turnover is low), there are few breeding opportunities; when the population density is low, there are more breeding opportunities. At high densities, the older breeding females frequently remain in the population and allow their older daughter to stay and breed, leaving very few opportunities for new immigrants to join the group (Baker and Dietz 1996).

Dispersing golden lion tamarins are less likely to find a breeding opportunity in high density areas. Knowing the population density of the GLT populations allows us to determine if breeding opportunities are relatively abundant or scarce. Interestingly, density did not affect the number of movements in the study population, indicating that in this fragmented landscape, breeding opportunities may not be a primary factor for

frequency of movement especially when compared against distance. Several studies have observed an increase in emigration with an increase in density as increased density can reduce individual fitness and increase within patch competition (Aars and Ims 2000, Bowler and Benton 2005). One possible explanation for why this is not observed in GLTs could be that the restrictions of fragmentation make it difficult for tamarins to emigrate and they are more likely to attempt to stay in their current fragment or even try to return to their natal group. This was observed by a study done by Sales Coelho (2008) in the GLT population living in Rio Vermelho.

Creating a model for movement in the population of golden lion tamarins can be a valuable tool for conservation planning. Several variables were considered to be possible factors in predicting movement, but the resulting model indicated that distance, the size of the neighborhood the tamarins were moving from, and the characteristic of the distance as described in Table 2.2 are the variables needed to model movement. Earlier, when size and the frequency of movements were examined, no relationship with the size of the neighborhood was found, while here it was a significant variable. This can likely be explained due to difference in analysis method used. The first set of analysis was completed by looking at the frequency of movements, while in this logistic regression analysis, all moves were examined and were evaluated based on the 7 variables. Distance appears to have the greatest weight in the model. When distance is set to a medium or far distance, the probability of movement is less than 10% regardless of the neighborhood size (Figure 2.12). In all cases, the probability of movement was always higher when the

distance was characterized by a contiguous forest as opposed to less-than-optimum pathways (Figures 2.12 and 2.13). So although some of the forest fragments are connected by thin or patch connections, they may not be suitable for tamarin movement. This is further supported below when looking at the functional connectivity of the population.

While this model was significant and predicted very accurately when a tamarin would not move, it did not predict very accurately when the tamarin would move. The model could be improved by changing the population level from movement between neighborhoods to a smaller population level, such as movement between groups, increasing the sample size. Additional variables that could affect movement could be researched as well.

Connectivity is a two-fold parameter: structural connectivity refers to the landscape structure, whereas functional connectivity refers to the response of the animals to those landscape structures (Tischendorf and Fahrig 2000). These two can be synonymous when movement is restricted to preferred habitat and individuals do not move outside this habitat and move freely within the habitat (Tischendorf and Fahrig 2000). This study compared the previously defined structural connectivity that consisted of 7 management units as defined based on landscape images (AMLD 2009b), with the functional connectivity as defined by individual movement. The assumptions made under structural connectivity were that within management units there would be movement between groups, while between management units there is no movement (AMLD 2009b). This

study confirmed that between these large management units there is no movement, but interestingly, within management units, movement was also limited in 2 of the 3 management units examined. Imbaú has at least 2 different functional units that are not exchanging genes and Dourada has 3 different functional units again with no movement between them. These functional units that lack movement are, in most cases, connected by forest, but these connections are in some areas thin and could create bottlenecks between the groups. It is possible that these bottlenecks are prohibiting movement, but more research needs to be conducted in these particular areas. This study confirms the importance of measuring functional connectivity to obtain a full understanding of landscape connectivity; structural connectivity may not be a good indication of the true level of connectivity affecting population viability.

The cluster analysis was unique in this set of analyses in that it looked at the frequency of movements to group the clusters. The analysis revealed that in each subpopulation, several clusters were needed to adequately account for the variance. This is largely due to the fact that there are not very many movements occurring relative to the number of groups. While this analysis would be more effective if there were more moves observed to add to the strength of the clusters, it did reveal a few groups that are isolated. In particular, the Imbaú area has three clusters that are isolated; JG/JG2, AL2/Andre, and AX2, PB/PB2, FX. These groups are physically isolated from the rest of the population and this analysis further supports that when groups are geographically isolated, movement becomes increasing difficult and rare. Interestingly, when looking at the

spatial arrangement of the clusters, they are more or less geographically clumped in both Imbaú and Dourada, but this was not so for Rio Vermelho. Rio Vermelho is a relatively contiguous area so movement is likely to be easier in this habitat compared with the more fragmented areas of Dourada and Imbaú.

In this study, functional connectivity was analyzed on two levels: cluster analysis to look at the strength of the connectivity between groups and a second level of classifying functional units based on any movement that occurred between groups. When viewed together, these analyses provide a comprehensive view of functional connectivity for this population. In both Imbaú and Dourada, the functional connectivity and breakdown of clusters are very similar further demonstrating the limited movement within these areas.

Management Implications

This study provides information critical for creating a science-based metapopulation management plan for golden lion tamarins. When considering the movements in this fragmented population of golden lion tamarins, distance is perhaps the most important factor that will affect movement. Those tamarins that are moving travel an average distance of just over 800 meters. This has important implications for this landscape where distance between populations is several kilometers in an often inhospitable habitat. Additionally, the functional units are limited to small areas and even within the management units, there is limited movement. This could have consequences for the long-term genetic health of the population; restricted gene flow could lead to an increased

risk of inbreeding and a loss of genetic variation over time (Frankham et al. 2010). Translocations between the functional units could help to minimize these risks. The existing limited movement also indicates that the level of forest connectivity needs to be examined when considering movements. Connections that are less than optimal such as small strips of forest (corridors) or patchy connections may not be suitable to support movement between the fragments. Corridors may be a component of connectivity, but only if they promote movement among habitat fragments. More research needs to be done in this area to determine the effectiveness of these and other types of connections.

There are several methods available to measure landscape connectivity. Landscapes are not inherently connected; therefore the level of landscape connectivity must be evaluated from the organismal perspective. Empirical data involving animal movements provide the most direct measurement of connectivity but are often difficult to obtain (Tischendorf and Fahrig 2000, Calabrese and Fagan 2004). This study provides an example of how direct measurements using mark-recapture data can be used to assess the level of connectivity in a population; few species have this level of empirical data available to accomplish this. Multiple factors could potentially contribute to the probability of movement in a fragmented landscape, and in this case, distance is a primary factor in predicting movement. This study also demonstrates the importance of examining functional connectivity. In this population of GLTs, examining structural connectivity alone overestimated the actual amount of connectivity present in the population. The

long term viability of the golden lion tamarin population will likely depend on the ability to ensure high quality structural connectivity that support movements.

CHAPTER 3

Modeling Population Viability of Golden Lion Tamarins

Introduction

Understanding the threats that face endangered populations is critical for creating long-term management strategies. When populations are small, they are particularly vulnerable to extinction through demographic stochasticity and the loss of genetic variation, threats that may be completely unrelated to reasons the population became small in the first place. These threats can result in a small population becoming even smaller and entering what is termed the extinction vortex. First coined by Gilpin and Soulé (1986), the extinction vortex is a feedback loop that describes the possible fate of small populations. In efforts to prevent the extinction vortex, management strategies are developed that attempt to mitigate or reduce these threats to small populations and increase long-term population viability.

Population viability analysis (PVA) is a method of analyzing both the deterministic and stochastic threats on a population and predicting the probability of extinction into the future. This can be an extremely valuable tool to investigate a population's response to potential management strategies. PVA has been used extensively with hundreds of

species (Menges 2000) and the Conservation Breeding Specialist Group (CBSG) of the International Union for the Conservation of Nature (IUCN) has used this analysis to assess population viability for over 150 species (Frankham et al. 2010). While there has been some criticism of the accuracy of PVAs (Coulson et al. 2001, Reed et al. 2002), particularly in terms of the sensitivity of the risk of extinction when parameters are estimated, evaluations of PVA models indicate that they provide reliable predictions of a population's future. Brook et al. (2000) examined 21 species retrospectively to compare the predictions made by the PVA and the trends that were actually observed in the current population. They found that PVA models performed quite well at predicting the probability of extinction.

PVA provides perhaps the best tool conservationists currently have to evaluate the future of endangered populations. Like any model however, the limit of the PVA is in the accuracy and availability of data (Reed et al. 2002). Population models require substantial life history data and for many species, this is unavailable. This may limit the accuracy of the PVA. However, PVA is not intended to deliver absolute answers to questions pertaining to population viability, but rather to provide quantitative comparisons of population performance under different scenarios, for example different management options that may assist practitioners in making management decisions. The results of the model are relative to the information known at the time the model was completed.

The golden lion tamarin (*Leontopithecus rosalia*: GLT) is an endangered primate endemic to the Atlantic Coastal Forest of Brazil, one of 34 biodiversity Hotspots (Myers et al. 2000). Historically, this species was threatened by the pet trade and habitat loss which whittled the population down to an estimated 200 animals in the 1970s (Kleiman and Rylands 2002). Extensive deforestation has reduced GLT habitat to just 2% of its original area, restricting GLT populations to just 8 municipalities in Rio de Janeiro state (AMLD 2009a). Extensive conservation efforts have led to an increase in the population of golden lion tamarins, which now stands at approximately 1,600 individuals in the managed population divided into at least 7 isolated populations of varying size (Wuethrich 2007, AMLD 2009a). In most cases, the habitat that surrounds the forest islands is pasture or cropland, likely inhibiting dispersal between populations. These small isolated populations may be quite vulnerable to extinction. Understanding this vulnerability and the potential risks of extinction are critical for creating management strategies that promote population persistence.

Since 1990, priorities for research and conservation for golden lion tamarins have been set by a series of Population and Habitat Viability Assessment workshops conducted by CBSG. These research and conservation action priorities have been endorsed by ICMBio, the Brazilian governmental authority for wildlife conservation. The third, and most recent Population and Habitat Viability Analysis Workshop for Lion Tamarins was held in 2005, where the need for a metapopulation management plan was identified as a top priority in order to effectively conserve golden lion tamarins (Holst et al. 2006).

With an increase in fragmented populations, metapopulation biology has become increasingly important in developing long-term conservation strategies. A metapopulation structure, where an overall population is composed of a number of smaller populations with some level of migration between them, can help reduce genetic and demographic deterioration (Hanski and Gilpin 1991). Metapopulations that are limited to a small number of populations face a real possibility of all subpopulations going extinct simultaneously, resulting in the extinction of the metapopulation (Nisbet and Gurney 1982). In terms of genetics, metapopulations that have low rates of extinction and high levels of migration behave like one large contiguous population (Frankham et al. 2010). Even a small number of migrants can have a large impact on genetic variation. Population genetics theory shows that even one migrant per generation is enough to reduce differentiation between subpopulations (Frankham et al. 2010).

In 2009, a metapopulation management workshop was held for GLTs to begin the development of a metapopulation management plan (AMLD 2009b). The result of this workshop was the re-classification of the tamarin population into seven different management units (MU). These seven units are the seven largest fragments of habitat evaluated as suitable for GLTs (Figure 3.1). These fragments range in size and it is assumed that these units as a metapopulation will be enough to protect golden lion tamarin in perpetuity (AMLD 2009b). In Chapter 2 of this dissertation, it was determined that the functional connectivity within some of these management units may be compromised. In MUs that were composed of several fragments and were connected by

a less than optimal connection, movement may be restricted. Based on analysis of GLT movement from this dissertation, 11 functional units were identified as opposed to the 7 management units. The purpose of this study is to take this new information on population structure and use a PVA model to examine population viability. First, this study will examine the viability of the metapopulation and the value of each functional unit included in it. The most valuable units will then be combined to determine the minimum set of functional units needed to maintain a viable metapopulation.

Additionally, for any functional units that are not viable, strategies to improve their status will be modeled. Included in this will be determining what is needed in terms of natural dispersal and/or translocations to maintain the targeted 90% genetic diversity for 100 years for all of the functional units. If this is possible, this analysis will go one step further to determine if the functional units collectively can maintain the same level of genetic diversity as the metapopulation modeled as a panmictic population.

Methods

Study Population

The current golden lion tamarin population is confined to 8 municipalities in Rio de Janeiro state all within the Sao João watershed. At a metapopulation workshop held in 2009, the population of GLTs was classified into 7 different metapopulation management units (AMLD 2009b). These management units (MU) were defined based on degree of isolation and suitability for golden lion tamarins. Fragments 50 hectares or larger and within 100 meters of each other were categorized in the same MU as it was believed that

GLTs can easily cross a distance of 100 meters. Therefore, in some cases, the MU is composed of several fragments that are separated by a distance of less than 100 meters. Three of these units hold populations that are composed of the descendents of reintroduced GLTs (Rio Vermelho, Imbaú, Dourada), two are composed of “wild” (i.e. naturally occurring) GLTs in the biological reserves (Poço das Antas and União), and two MUs (Pirineus and Gaviões) that are wild populations that have not historically been monitored or managed (Figure 3.1). There are a few small populations of GLTs outside of these MUs. For the purposes of this study, these tamarins were excluded from analysis as most of these are groups of tamarins that have not been monitored for over 20 years and their current status is unknown.

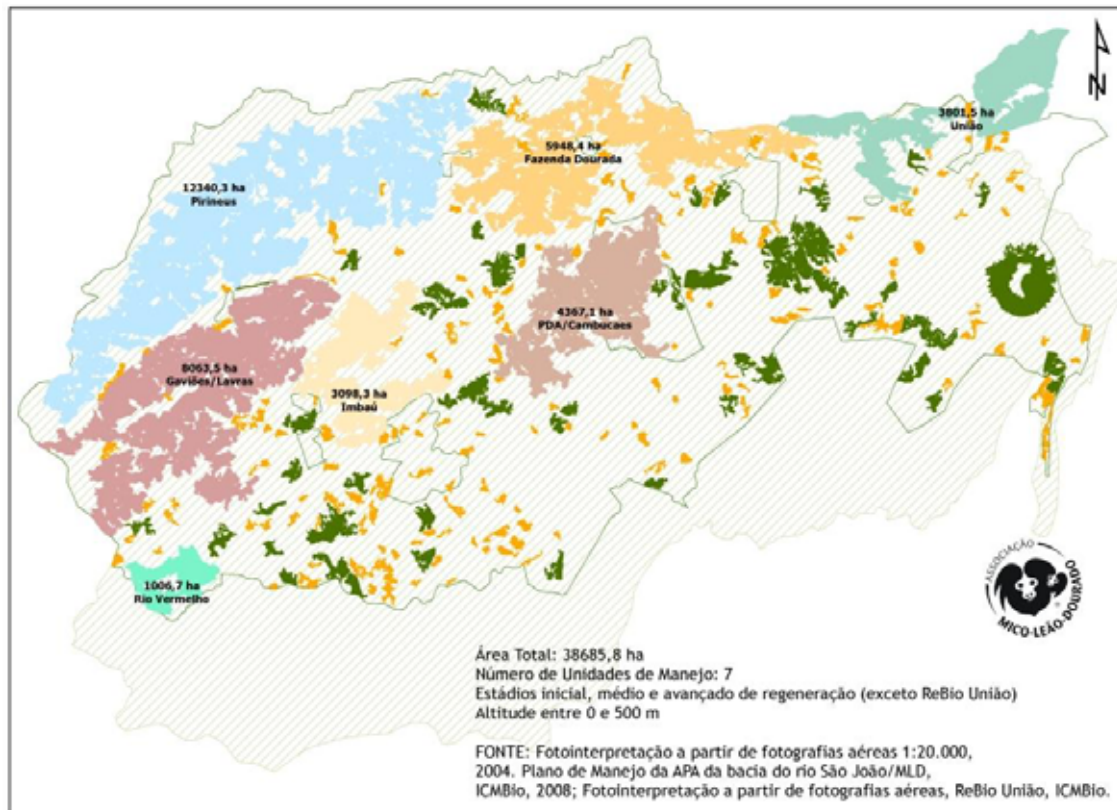


Figure 3.1: Map with GLT metapopulation management units (MUs). The size of each MU is shown in hectares. Image from AMLD 2009b.

In Chapter 2 of this dissertation, the study population was categorized into 11 functional units based on documented movement that occurred between groups (Figure 3.2).

Groups that exchanged animals (even one) were classified in the same functional unit.

These functional units are also used here for this population viability analysis.

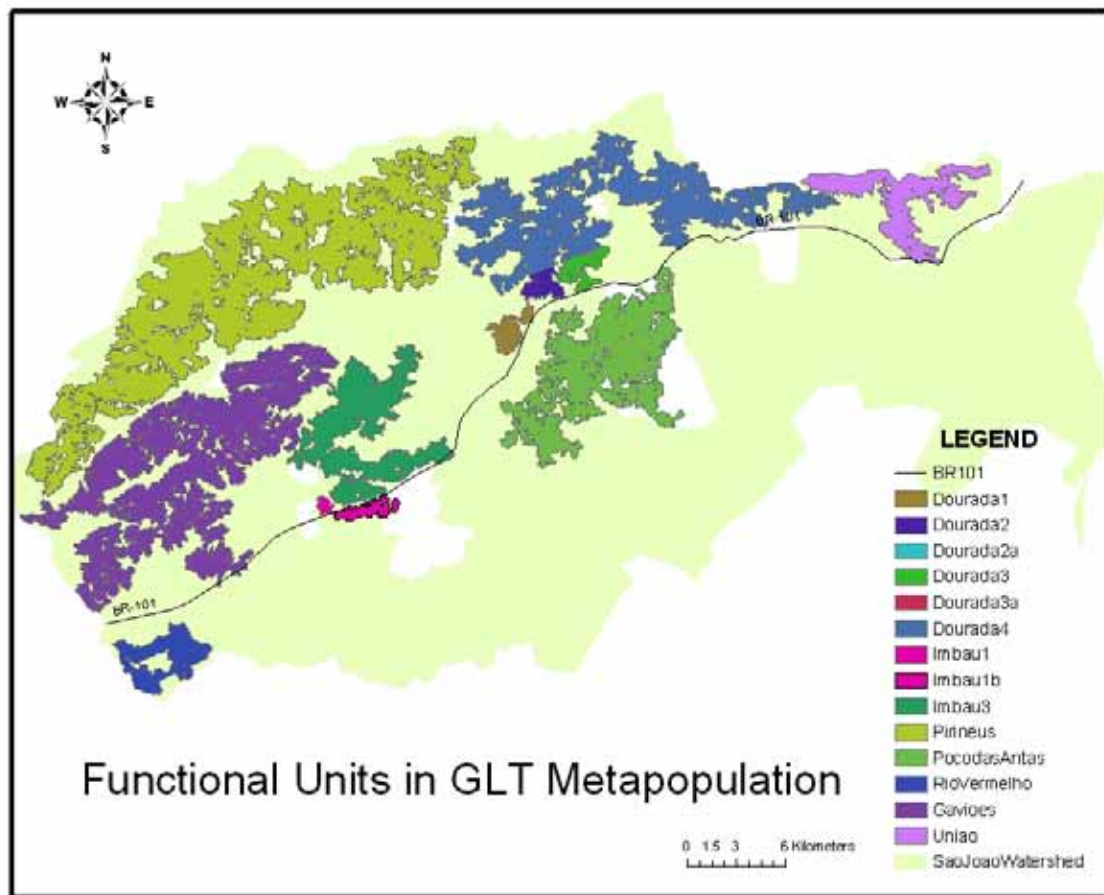


Figure 3.2: Map showing 11 GLT Functional Units.

Population Viability Analysis

VORTEX version 9.99 (Lacy 1993, Lacy et al. 2003), a simulation software program was used to assess long-term viability of the metapopulation of golden lion tamarins under a variety of scenarios. *VORTEX* is an individual based modeling program that follows the fate of each animal in the population based on user-defined parameters (Miller and Lacy 2003). It is a Monte Carlo simulation of both the deterministic and stochastic events on

the population. When the program begins, individuals are created to form the starting population. The program then steps through, on an annual basis, the life cycle events such as births, deaths, dispersal, and catastrophes, that occur at probabilities defined by the user based on species specific data. For many parameters, *VORTEX* also allows the user to enter variation (as a standard deviation) for the parameter. For each year and each iteration, values chosen for those parameters are randomly selected from a normal or binomial distribution with means and standard deviation that have been specified by the user. This is how *VORTEX* incorporates stochastic annual environmental variation into the predictions, with each iteration of the model yielding a different result depending on which values the parameter take on for each year and iteration. Therefore, by running several iterations, *VORTEX* provides a probability outcome and the range of possibilities for the fate of the population. The output is described in detail in Miller and Lacy (2003), but the values used in this study are listed and defined below.

- Stoc-r: The mean stochastic growth rate experienced in simulations with standard deviation (SD) across iterations
- PE: The probability of extinction, calculated as the proportion of iterations that went extinct
- Genetic Diversity: The mean percent expected heterozygosity remaining in the extant population with standard deviation across iterations
- N (at 100 years): The mean population size for those extant populations at 100 years

VORTEX Model Parameters

The biological data used for the *VORTEX* model were primarily derived from population data resulting from the extensive field study in the Poço das Antas Biological Reserve. Close monitoring of this population has provided over 20 years of life history and group composition data (Baker and Dietz 1996, Dietz et al. 1997, Kleiman and Rylands 2002). These data have been entered into a computerized database, SPARKS (Single Population Animal Records Keeping System, version 1.52; International Species Information System, Eagan, MN). Using this database, estimates were made for the parameters in *VORTEX*. Many of these values were also used in the 2005 Population and Habitat Viability Assessment (PHVA). The baseline input is outlined in Table 3.1 and further described below.

Table 3.1: Baseline data used in *VORTEX*

<i>VORTEX</i> Parameter	Input
Number of iterations	500
Number of years	100
Extinction definition	1 sex remains
Inbreeding depression	Yes
Lethal equivalents (LE)	4.07
LE subject to purging	50%
<i>Reproductive Systems</i> (Long-term Monogamy)	
Age of first offspring- males	4
Age of first offspring- females	4
Maximum age of reproduction	16
Maximum number of progeny per year	5
Frequency of 1 offspring	21%
Frequency of 2 offspring	58%
Frequency of 3 offspring	8%
Frequency of 4 offspring	12%
Frequency of 5 offspring	1%
Density-dependent reproduction	No
Percent adult females breeding	73% (Standard Dev. = 9.4%)
Percent adult males in breeding pool	100%
Sex ratio	1:1

Number of iterations and years: The model ran 500 independent iterations for each scenario modeled. Each iteration was modeled out to 100 years. The generation length for GLTs is about 7 years (Kleiman and Rylands 2002) so this was the equivalent of about 14 generations.

Breeding system: Golden lion tamarins are generally classified as long-term monogamists. Although there is some departure from this, for example Baker et al.

(1993) reports of multi-male groups where one or both males may be breeding, long-term monogamy is still the best descriptor of their breeding system, where typically a mated pair will remain together over multiple breeding seasons (Coimbra-Filho and Mittermeier 1973, Kleiman and Rylands 2002).

Age of first reproduction: *VORTEX* considers the age of first reproduction to be the age when an animal actually reproduces as opposed to the age it becomes sexually mature. While GLTs are sexually mature at 18 months (Dietz et al. 1994), it is at 4 years old when the breeding rates match those of fully breeding adults (Holst et al. 2006). This is true for both males and females.

Age of reproduction senescence: *VORTEX* assumes that animals can breed at a normal rate throughout their adult life. Once an animal reaches senescence, that animal is removed from the model. Based on the life table analysis in SPARKS, golden lion tamarins can reproduce as late as 16 (Ballou and Mickelberg 2008).

Offspring production: In the wild, GLTs can produce up to two litters per year, with the average litter size of 2.1. The recorded greatest number of offspring produced in a year is 5 offspring. The distribution of litter size is listed in Table 3.1.

Breeding pool: Based on the historical dataset, 73% of the females are considered potential breeders; the environmental variation is 9.4% (Holst et al. 2006). For males,

100% are considered available for breeding. When a breeding vacancy appears, a male from another group will fill it.

Mortality rates: *VORTEX* defines mortality as the annual rate of age-specific death from year x to $x+1$. For golden lion tamarins, mortality rates are affected by the mortality that occurs during dispersal, typically occurring between ages 2 and 4. At high densities, vacancies in groups are rare and mortality is likely to be high for those dispersing animals since they are unable to enter a group. Additionally, females are less likely to get into a group than males (Holst et al. 2006). Therefore, for this model, age and sex-specific mortality rates are calculated as density dependent. The following functions are based on the 2005 PHVA (Holst et al. 2006) and were used to model age and sex-specific mortality:

When $N < .5 K$ (K = carrying capacity), mortality was equal to M_O where the age and sex specific values for M_O are shown in Table 3.2.

When $N \geq .5 K$, mortality was modeled as an increasing linear function (see Figure 3.3), from M_O when $N = .5 K$, to a maximum of M_D when $N = K$. The age and sex specific values for M_D are also shown in Table 3.2.

As females were expected to have higher mortality during dispersal than males due to the difficulty of them integrating into a group, the functions used in *VORTEX* to

implement the different mortality rates, as functions of N/K , differed for males and females.

For Females: mortality = $MO + ((N > (K/2)) * ((MD - MO) / ((K/2) + 1)) * (N - ((K/2) + 1)))$

For Males: mortality = $MO + ((N > (K/2)) * (0.75 * (MD - MO) / ((K/2) + 1)) * (N - ((K/2) + 1)))$

These functions were not applied to the first age class since those mortality rates were not affected by dispersal and were significantly different than the other age classes.

Table 3.2: Mortality values. These are the values for M_O and M_D used in formula to model density dependent mortality rates.

Sex	Age (Years)	M_O	M_D	SD
Females	0	32.8%		0.087
	1	12.0%	19.6%	0.133
	2	12.8%	24.5%	0.076
	3	15.3%	21.0%	0
	Adult	8.3%	12.6%	0.067
Males	0	29.8%		0.07
	1	12.6%	15.9%	0.099
	2	15.1%	19.5%	0
	3	13.4%	15.3%	0.075
	Adult	8.9%	12.5%	0.082

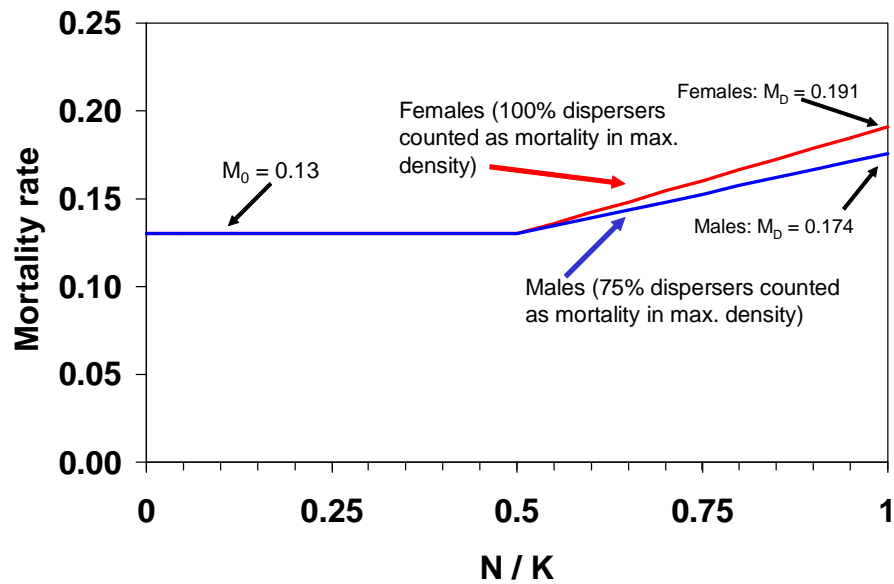


Figure 3.3: Example of the density- and sex- dependent mortality function used in modeling. Figure from Holst et al. 2006.

Inbreeding depression: *VORTEX* allows the user to include the detrimental effects of inbreeding depression in the model. This is done through a reduction in survival of offspring to their first year. For golden lion tamarins, lethal equivalents were estimated at the 1997 PHVA workshop as 4.07, 50% of these were lethal alleles subject to purging (Ballou et al. 1998). The same values were used for this model.

Catastrophes:

The population was modeled with two catastrophes, fire and trains.

Fires:

Fire data used in this model was based on the analysis completed for the 2005 PHVA (Holst et al. 2006). During that PHVA, the IBAMA GIS database on fire events was used to access the occurrence of fire from 1998-2004 in the GLT habitat range. Only three of the areas had records of fires during those years. The frequency of fire in those areas was calculated and the annual probability of fire was determined. Those data are listed in Table 3.3. The severity was recorded in *VORTEX* as a 0.5% reduction in survival for the populations affected.

Table 3.3: The annual probability of fire occurring in populations where fire had been documented.

Population	Annual probability of fire occurring
Poço das Antas	0.71
União	0.28
Rio Vermelho	0.14

Trains:

Two of the GLT populations have train tracks that run through their habitat: Poço das Antas (PDA) and União. Data from the 2005 PHVA were again used for train catastrophes in this model (Holst et al. 2006). Over the last 21 years, there had been 4

recorded deaths associated with the trains amounting to a 19% chance per year. GIS was used during the PHVA model to calculate the proportion of track that traveled through the two areas. The proportion of track that traveled through Poço das Antas is 15% so the chance of a train accident is 2.8% per year ($15\% \times 19\%$). In União, the proportion of track is 10% therefore there is a 1.9% chance per year. In PDA, the train tracks run in areas that are not directly adjacent to tamarin territories (i.e. there are open grassy areas between them) so the severity was for PDA was a 1% decrease in survival, while União has group territories located near the tracks so the severity of a 4% reduction in survival was used.

Population Size and Carrying Capacity:

Population size for Rio Vermelho, Imbaú 1 and 2, Dourada 1, 2, 3, and PDA was determined based on the most recent population census (AMLD 2009b). For the remaining populations, size was calculated based on average density estimates. Density values were derived from over 20 years of field data at PDA where the low occupancy density is 0.073 GLT/Hectare (Kleiman and Rylands 2002). Very little work has been done in Pirineus, Gaviões, and Dourada⁴. It is thought that the density is likely to be lower in the mountainous habitat of Pirineus and Gaviões than in PDA. Lower densities are also estimated in União (Kleiman and Rylands 2002, Kierulff and Rylands 2003); therefore, to be conservative, density estimates for these areas were assumed to be half of the low density estimates of PDA, and the population sizes that were calculated accordingly. Population sizes used in the model are listed in Table 3.4. For all

populations, carrying capacity was set as equal to the initial population size since the suitable habitat for GLTs is currently occupied.

Table 3.4: The population size of each population modeled.

Functional Unit	Est. # GLTs
Pirineus	450
Gavioes	294
Rio Vermelho	234
Imbau1	24
Imbau2	114
PDA	444
União	139
Dourada1	97
Dourada2	61
Dourada3	120
Dourada4	176

Dispersal

VORTEX is able to model dispersal between populations. Dispersal rates are entered as probabilities of dispersal in any given year. So a dispersal rate of 1% indicates that 1% of the population is expected to disperse in any given simulation year. Dispersal rates are specified below in the scenario descriptions.

Defining Viability:

A population is considered viable if the probability of extinction as calculated in *VORTEX* is 0% for the 100 years modeled. When modeling metapopulations, *VORTEX* reports the genetic diversity retained in each population (functional unit) in the

metapopulation and the average of these is reported as the WithinPop genetic diversity. *VORTEX* also reports the genetic diversity retained in a metapopulation as a whole. The genetic goal for this study is that 98% of the genetic diversity is retained at the metapopulation level and 90% retained at the population or functional unit level. This target of 90% is derived from the target used for captive populations (Ballou and Foose 1996). This is a proper model for these small in situ populations since it is a balance between preserving genetic diversity and also accepting a low level of inbreeding that maybe unavoidable in these small populations.

To evaluate the viability of the GLT metapopulation, six scenarios were modeled:

1. *Population Viability- Is the current population, composed of several functional units, viable?*
2. *Functional Unit Value- What is the value of each functional unit to metapopulation persistence?*
3. *What is the minimum set of functional units needed to maintain a viable metapopulation?*
4. *Functional Unit Rescue- What is needed, in terms of migration, to maintain those functional units that are at high risk of extinction?*
5. *Is it possible to maintain a metapopulation through dispersal where all the functional units are maintaining a minimum of 90% genetic diversity and the metapopulation as a whole is maintaining a minimum of 98% genetic diversity?*

6. *By increasing natural dispersal and translocations, is it possible to maintain the same level of genetic diversity within the functional units as with the population as one panmictic population?*

The specific methods for each of these scenarios are described below.

Scenario 1: Population Viability- Is the current population, composed of several functional units, viable?

The baseline parameters listed in Table 3.1 were used to model population viability for this scenario. Given the structural connectivity of the Dourada functional units, particularly between Dourada4 and 3 and Dourada4 and 2, dispersal rates were included in the baseline. Dispersal rates were estimated based on the number of unknown animals that appeared in the monitored populations (Dourada2 and 3) during the study period (20 years). Over this time, 31 unknown individuals were recorded in Dourada3 while in Dourada2, 4 unknown individuals were recorded. The rate of dispersal is then 0.8% between Dourada4 and 3 and 0.1% between Dourada4 and 2. It was assumed that dispersal at these rates was possible in both directions, between Dourada2 and 4 and between Dourada3 and 4. These are relatively low rates of dispersal. There was no other dispersal modeled in this scenario.

Scenario 2: Functional Unit Value- What is the value of each functional unit to metapopulation persistence?

For this scenario, all values remained the same as in the first scenario. However; functional units were removed one-by-one from the metapopulation to determine if it affected metapopulation viability in terms of increase in extinction risk or a decrease in retained genetic diversity.

Scenario 3: What is the minimum set of functional units needed to maintain a viable metapopulation?

The functional units with the highest retained genetic diversity and lowest probabilities of extinction are considered the most viable. Simulations were run starting with the most viable functional unit and then subsequently adding functional units based on highest level of genetic diversity and lowest PE. Units continued to be added to the model one at a time until the metapopulation had 0% probability of extinction and could maintain at least 98% genetic diversity.

Scenario 4: Functional Unit Rescue- What is needed, in terms of migration, to maintain those functional units that are at high risk of extinction?

This scenario use the same baseline model as in Scenario 1, but considered only those populations that were at any risk of extinction. To maintain the populations that were at risk of extinction, the level of dispersal from the nearest population was increased incrementally until the probability of extinction was 0 for all populations.

An alternative method was modeled by using translocations to maintain the population. Translocations were modeled in *VORTEX* using harvests and supplementations. *VORTEX* has an option to take animals that are harvested (i.e. removed from a population) and use these for translocations with a user-defined percentage surviving translocation. For this model, 95% of the translocations were assumed to survive. This differs from dispersal in that the mortality rate is higher during dispersal; 25% die during dispersal whereas 5% die during translocations. For this scenario, the number of translocations was increased incrementally to determine the lowest level of translocation needed to maintain all populations with a zero chance of extinction. The proportion of retained genetic diversity was also considered in this scenario. In order to be considered rescued, the population needed to be viable as defined above (have a 0% probability of extinction as well as maintain at least 90% genetic diversity).

Scenario 5: Is it possible to maintain a metapopulation through dispersal where all the functional units are maintaining a minimum of 90% genetic diversity and the metapopulation as a whole is maintaining a minimum of 98% genetic diversity?

Starting with the baseline model, dispersal between neighboring functional units was added incrementally to determine how much dispersal was needed to reach the genetic target of 98% retained genetic diversity for the metapopulation and 90% for the functional units. Dispersal was modeled at 1%, 2%, and 5% between functional units where connections could logistically be made. Table 3.5 is the dispersal matrix used indicating which units had dispersal modeled between them.

Table 3.5: Dispersal rate matrix for functional units. A value of 1 indicated that dispersal was included between these functional units (cell is shaded), 0 indicates no dispersal was modeled. Rio Vermelho is not included as it had no dispersal with any units.

		Recipient Units									
		Pirineus	Gaviões	PDA	União	Imb1	Imb2	Dour1	Dour2	Dour3	Dour4
Source Units	Pirineus		1	0	0	0	0	0	0	0	1
	Gaviões	1		0	0	0	1	0	0	0	0
	PDA	0	0		0	0	0	0	1	1	0
	União	0	0	0		0	0	0	0	0	0
	Imb1	0	0	0	0		1	0	0	0	0
	Imb2	0	1	0	0	1		0	0	0	0
	Dour1	0	0	0	0	0	0		1	0	0
	Dour2	0	0	1	0	0	0	1		1	1
	Dour3	0	0	1	0	0	0	0	1		1
	Dour4	1	0	0	1	0	0	0	1	1	

Scenario 6: By increasing natural dispersal and translocations, is it possible to maintain the same level of genetic diversity within the functional units as with the population as one panmictic population?

For this scenario, both dispersal and translocation were used to attempt to raise the WithinPop (the average of all the functional units) genetic diversity to either 98% (the overall metapopulations target goal) or even better, raise it to 99% which is the level retained in the overall metapopulation

The amount of dispersal was increased incrementally (1%, 2%, 5%, 7%, 8%, 9%, 10%, 12%, 15%) between populations where connections could logistically be made (see Table 3.5) until the highest amount of genetic diversity was retained without compromising the functional units. There is a higher level of mortality associated with dispersal, so high levels of dispersal can negatively affect the population size. A dispersal level that

maximized genetic diversity without significantly decreasing the population size was selected and used as a baseline to which translocations were added to further increase genetic diversity.

As with dispersal, several levels of translocation were tested to examine the effect on WithinPop genetic diversity. Animals were harvested at equal rates from all functional units except for Imbaú1 which was too small to support harvest and Poço das Antas, which was harvested more to compensate for animals not harvested from Imbaú1. Functional units were supplemented equally except at medium-high and high levels where Pirineus and Imbaú1 received fewer animals given their population sizes. Both harvests and supplementations were done every 5 years starting with year 1, all the way until year 100. Equal numbers of sexes were translocated, all at age 3. Table 3.6 lists the numbers of animals translocated for each scenario. Three additional simulations were run using the high level of translocation (460 animals) and increasing the frequency of translocations from every 5 years to 3, 2, and 1 year intervals.

Table 3.6: The number of animals translocated between each functional unit at each translocation level. All the translocations occurred every 5 years for those levels listed below.

Functional Unit	Low		Medium		Medium-High		High	
	Harvest ♂:♀	Suppl. ♂:♀	Harvest ♂:♀	Suppl. ♂:♀	Harvest ♂:♀	Suppl. ♂:♀	Harvest ♂:♀	Suppl. ♂:♀
Pirineus	1:1	1:1	5:5	5:5	10:10	5:5	20:20	20:20
Gavioes	1:1	1:1	5:5	5:5	10:10	10:10	20:20	20:20
RioVerm	1:1	1:1	5:5	5:5	10:10	10:10	20:20	20:20
PDA	2:2	1:1	10:10	5:5	15:15	10:10	30:30	20:20
Uniao	1:1	1:1	5:5	5:5	10:10	10:10	20:20	20:20
Imbau1	0	1:1	0	5:5	0	10:10	0	10:10
Imbau2	1:1	1:1	5:5	5:5	10:10	10:10	20:20	20:20
Dour1	1:1	1:1	5:5	5:5	10:10	10:10	20:20	20:20
Dour2	1:1	1:1	5:5	5:5	10:10	10:10	20:20	20:20
Dour3	1:1	1:1	5:5	5:5	10:10	10:10	20:20	20:20
Dour4	1:1	1:1	5:5	5:5	10:10	10:10	20:20	20:20
Total No. Translocated	22		120		230		460	

Results

Deterministic Output

The deterministic output was used to determine if the model was producing results that seemed realistic for the golden lion tamarin population. The deterministic characteristics reflect the population dynamics without stochastic variation such as inbreeding depression or migration. The values produced by the model are shown in Table 3.7. The population has the potential to grow 13.8 % per year and the exponential rate of increase (r) is 0.129. The generation length and age structure are representative of the information available on golden lion tamarin biology. As these values are within the range of what is expected and observed for GLT populations (Ballou et al. 1998, Holst et al. 2006), this

model is producing reasonable results and is adequately modeling population dynamics in the absences of random fluctuations.

Table 3.7: Deterministic results for baseline model.

Parameter	Results
Lambda	1.138
r	0.129
Generation length (years)	7.95 (males) 8.03 (females)

Scenario 1: Population Viability- Is the current population, composed of several functional units, viable?

In this study, population viability is defined at two levels. At the metapopulation level, the metapopulation must retain at least 98% genetic diversity and 0% probability of extinction to be considered viable. At the functional unit level, units must retain 90% genetic diversity and 0% probability of extinction. Based on these criteria, the metapopulation is viable for the 100 years modeled. The probability of extinction during this time is 0% for the metapopulation and only one functional unit, Imbaú1, has any risk of extinction (Table 3.8). This is the smallest of the populations (initial $N = 24$) and has a 30% chance of going extinct with a mean time to extinction of 66 years. Including Imbaú1, there are 5 functional units that are not able to maintain a minimum of 90% genetic diversity for 100 years (Table 3.8). The genetic diversity retained by the

metapopulation is 99% while the average retained genetic diversity of all the functional units (WithinPop) is only 87%, far less than the population as a whole.

Table 3.8: Baseline model output. The SD values given are standard deviations. Values are the average of the 500 simulations except for the initial N.

Functional Unit	N (initial)	stoc-r		PE	N (at 100 yrs)*	Genetic Diversity	
		Average	SD			Average	SD
Pirineus	450	0.065	0.117	0	430	0.9654	0.0048
Gaviões	294	0.063	0.119	0	278	0.9472	0.0093
Rio Vermelho	234	0.062	0.120	0	221	0.9351	0.0123
PDA	444	0.062	0.117	0	422	0.9646	0.0052
União	139	0.057	0.124	0	129	0.8923	0.0246
Imbau1	24	0.022	0.174	0.302	16	0.5023	0.1821
Imbau2	114	0.055	0.126	0	105	0.8706	0.0364
Dourada1	97	0.054	0.127	0	89	0.8527	0.0405
Dourada2	61	0.050	0.137	0	54	0.8164	0.0615
Dourada3	120	0.060	0.126	0	112	0.9226	0.0197
Dourada4	176	0.058	0.122	0	166	0.9302	0.015
WithinPop	NA	0.055	0.128	0.027	184	0.8727	0.0374
Metapop	2153	0.065	0.068	0	2022	0.9928	0.0005

* For functional units extant in year 100

Scenario 2: Functional Unit Value- What is the value of each functional unit to metapopulation persistence?

The metapopulation's viability was not affected by the removal of any one of the functional units; there was still a 0% probability of extinction and it maintained greater than 98% genetic diversity regardless of which population was removed. Imbaú1

continued to show a $PE > 0$ regardless of which other populations were removed; the average probability of extinction was 29% (range 26.8%-35%). However, in addition, Dourada2 had a 0.2% probability of extinction when Dourada4 was removed, but this was the only scenario where any unit in Dourada had a probability of extinction.

Across the different simulations where each functional unit was removed, genetic diversity changed very little. When Dourada3 was removed from the metapopulation, overall retained genetic diversity dropped from 93.02% to 91.63%. When Dourada4 was removed from the metapopulation, genetic diversity in Dourada2 dropped from 81.64% to 77% and genetic diversity in Dourada3 decreased from 92.26% to 87.26%.

Scenario 3: What is the minimum set of functional units needed to maintain a viable metapopulation?

Starting with the most viable functional unit, additional units were added sequentially until the metapopulation's retained genetic diversity reached at least 98%. Units were added based on their level of genetic diversity retained and PE, starting with the unit with the highest level of genetic diversity and lowest PE (Pirineus). The units were modeled as isolated, so there was no dispersal between them. Results from these simulations are shown in Figure 3.3, including the proportion genetic diversity retained with each additional unit and the population size at the end of the 100 years. With just 2 populations, Pirineus and Poço das Antas (PDA), 98% genetic diversity is retained in the

metapopulation (Figure 3.4). To reach 99% and match the level of genetic diversity held by the entire metapopulation with all 11 units, at least 4 populations are needed: Pirineus, PDA, Gaviões, and Rio Vermelho. Individually, each of these functional units retained more than 90% genetic diversity.

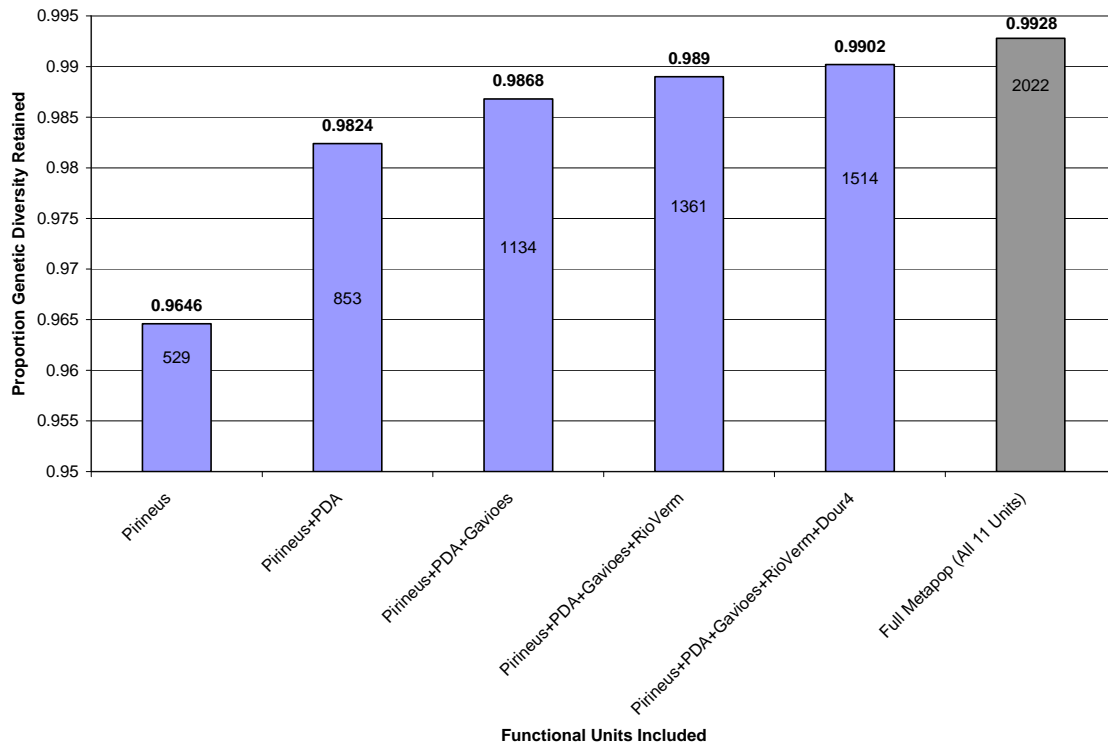


Figure 3.4: Proportion of genetic diversity retained with the minimum functional units needed for a viable metapopulation. Population size is noted inside the bar. The full metapopulation is also plotted (gray) as a reference for the maximum genetic diversity possible.

Scenario 4: Functional Unit Rescue- What is needed, in terms of migration, to maintain those functional units that are at high risk of extinction?

According to the baseline model, only Imbaú1 is at risk of extinction. This functional unit could be rescued through both translocation and increased dispersal. An increase in dispersal from Imbaú2 to Imbaú1, where 1.5% of the population moves every year, is enough to eliminate the risk of extinction (Table 3.9). Using translocations, Imbaú1 could be rescued by moving one male and one female from Poço das Antas to Imbaú1 every 5 years. Poço das Antas was selected as the donor population since it is one of the more viable populations and can support harvest. It is also one of the best monitored populations making translocation from this unit more feasible than from units that are not as well-studied.

To reach the genetic goal of retaining 90%, more translocations are needed. With 6 animal translocations (3 males and 3 females) from Poço das Antas (PDA) every 5 years, the retained genetic diversity increased to 91.43%.

Table 3.9: Values needed to rescue Imbau1.

	PE	GeneDiv (SD)	N	Mean TE (yrs)
Baseline	0.302	0.5023 (0.1821)	16	65.8
Dispersal 1.5% Imbau2 to Imbau1	0	0.8356 (0.0493)	22	68.3*
Translocation 1.1 from PDA to Imbau1, every 5 yrs	0	0.8534 (0.0455)	22	76.7*
2.2 from PDA to Imbau1, every 5 yrs	0	0.8976 (0.0276)	23	41.8*
3.3 from PDA to Imbau1, every 5 yrs	0	0.9143 (0.0201)	24	45*
Dispersal + Translocation 1.5% Dispersal Imbau2 to Imbau1 + 1.1 translocated from PDA	0	0.8916(0.0292)	23	62.3*

* In these cases, during at least one of the iterations (but not more than half), the population went extinct but was recolonized before the end of the simulation (100 years), so the PE = 0.

Scenario 5: Is it possible to maintain a viable metapopulation through dispersal where all the functional units are maintaining a minimum of 90% genetic diversity and the metapopulation as a whole is maintaining a minimum of 98% genetic diversity?

Without dispersal or translocation, the metapopulation as a whole is able to retain 99% of its genetic diversity. However five of the functional units were not able to maintain at least 90% of their genetic diversity (Table 3.8). To increase the retained genetic diversity within those units, dispersal was increased between the functional units nearest each other starting at 1% dispersal, then increasing to 2% and 5% to determine how much dispersal was needed to retain at least 90% genetic diversity. The dispersal matrix for the functional units is in Table 3.5.

By adding 1% dispersal, 3 of the 5 functional units increased to above 90% genetic diversity. With 2% dispersal between neighboring functional units, the retained genetic diversity of all the functional units was increased to > 90% (Table 3.10, Figure 3.5). Imbau1 and Dourada2 showed the greatest increase in genetic diversity, increasing from 50% and 82% to 90.6% and 97% respectively (Figure 3.5). At all levels of dispersal, the metapopulation retained over 98% genetic diversity.

Table 3.10: Level of dispersal needed to retain at least 90% genetic diversity in all functional units.

Functional Unit	Dispersal			
	Baseline (0%)	1%	2%	5%
Pirineus	0.9654	0.9755	0.9789	0.9821
Gaviões	0.9472	0.9722	0.9767	0.9804
Rio Vermelho	0.9351	0.9352	0.9348	0.9344
PDA	0.9646	0.9679	0.9704	0.9732
União	0.8923	0.9395	0.9566	0.9723
Imbau1	0.5023	0.8674	0.9083	0.9392
Imbau2	0.8706	0.9495	0.9631	0.9725
Dourada1	0.8527	0.8973	0.9191	0.9495
Dourada2	0.8164	0.9626	0.9693	0.9735
Dourada3	0.9226	0.9664	0.9724	0.9768
Dourada4	0.9302	0.9736	0.9795	0.9828
WithinPop	0.8727	0.9461	0.9572	0.9670
Metapop	0.9928	0.9921	0.9918	0.991

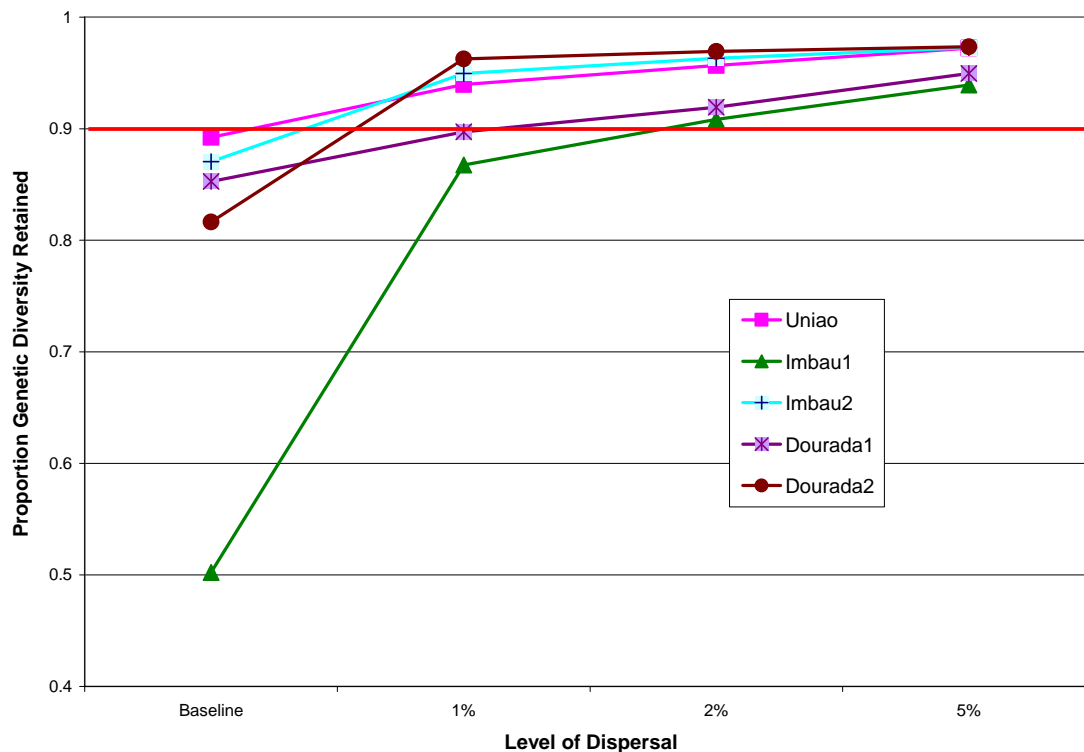


Figure 3.5: Proportion of genetic diversity retained for 5 functional units at increasing dispersal levels. Each line is a different functional unit, only those that were not able to maintain 90% GD in the baseline model are represented. The red line at 0.9 indicates the genetic target for functional units to be considered viable.

Scenario 6: By increasing natural dispersal and translocations, is it possible to maintain the same level of genetic diversity within the functional units as with the population as one panmictic population?

The metapopulation modeled as one panmictic population is able to retain 99% of its genetic diversity, while the average genetic diversity of the functional units (WithinPop) is far lower, only 87% (Table 3.8). When dispersal between the functional units was

added in Scenario 5, the WithinPop genetic diversity increased to 96.7% with 5% dispersal, but this is still below the level of the metapopulation (99%). This difference between the two values can be decreased through an even greater increase in migration between the functional units using both dispersal and translocation.

Dispersal

Several levels of dispersal between neighboring functional units were tested (1%, 2%, 5%, 7%, 8%, 9%, 10%, 12%, and 15%). The WithinPop genetic diversity peaked at 97.03% retained when dispersal was set at 10% and began to decline around 12% dispersal (Figure 3.6). Retained genetic diversity increases relatively rapidly from 87.27% at the baseline dispersal level up to 96.7% at the 5% dispersal level. After 5%, the amount of genetic diversity gained in any functional unit or WithinPop with additional dispersal is relatively small. As the level of dispersal increased, the metapopulation size decreased from 2022 to 1207 individuals at 15% dispersal. The metapopulation gradually decreases as the dispersal rate increases, but continues to retain at least 99% genetic diversity until the level of 8% dispersal.

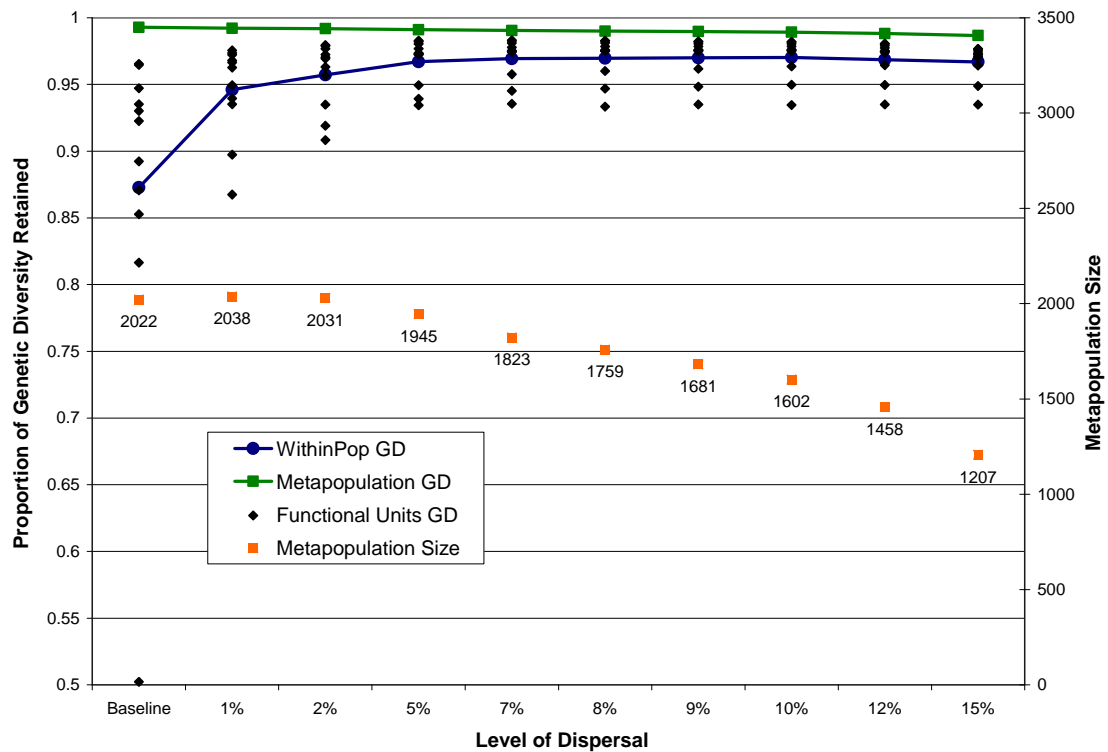


Figure 3.6: Level of dispersal needed to increase WithinPop genetic diversity. Percents of genetic diversity retained for both the metapopulation (green squares) and WithinPop (blue circles) are shown. Each functional unit's genetic diversity is plotted as well (black diamond). Metapopulation sizes are shown (orange squares) at the different levels of dispersal tested.

Translocations

Dispersal between neighboring populations itself was not able to increase genetic diversity within the populations to the level of the metapopulation. Translocation can be a valuable tool for enhancing genetic diversity (Griffith et al. 1989). Therefore, several rates of translocations were used to identify what level was needed to maximize the retained WithinPop genetic diversity. Translocation levels are defined in Table 3.6.

These levels of translocation were added to the 5% dispersal level since it had a high level of retained genetic diversity and this level also maintain a large metapopulation size.

The increase in WithinPop genetic diversity as compared with the metapopulation values which fluctuated between 98.89% and 99.74% is illustrated in Figure 3.7. The benefit of translocation was maximized when the level was “high” and translocations occurred every 2 years, so a total of 460 animals were moved every two years. With this level, the WithinPop genetic diversity was increased to 98.05%. This meets the target for population viability (98%), but it is still not as high as the level maintained by the metapopulation as a panmictic population (99%). These values are also listed in Table 3.11 as well as the genetic diversity of each of the populations.

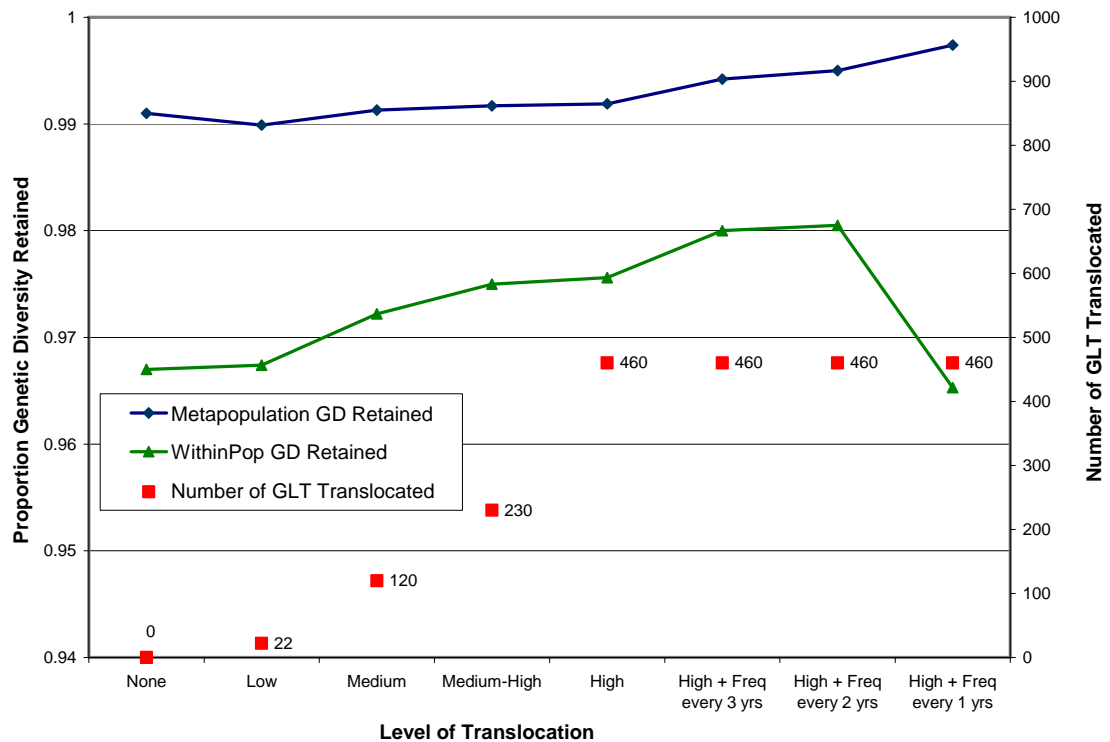


Figure 3.7: Increase in retained WithinPop genetic diversity at different levels and frequencies of translocation. Translocations occurred every 5 years unless otherwise noted.

Most functional units benefited from the translocations; as the number of animals moved increased, the amount of genetic diversity increased (Table 3.11). This was especially true for Imbau1, the smallest functional unit, which increased from 93.92 % to a maximum of 95.39% and Rio Vermelho which increased from 93.44% to 99.3% at the highest level and frequency of translocations. The genetic diversity in Dourada1 increased as well, from 94.95% until a maximum 96.86% at the level of medium-high translocations, but dropped to 84.29% at the highest level and frequency of translocation.

Dourada1 was the only functional unit to drop below the targeted 90% retained genetic diversity at any level of translocation.

Table 3.11: The effect of translocations on retained genetic diversity.

Functional Unit	Genetic Diversity Retained							
	5% Disp	Level of Translocation, including 5% dispersal						
		Low	Med	Med-High	High	High, every 3 yrs	High, every 2 yrs	High, every 1 yrs
Pirineus	0.9821	0.9750	0.9831	0.9837	0.9807	0.9883	0.9894	0.9927
Gaviões	0.9804	0.9759	0.9817	0.9824	0.9832	0.9886	0.9895	0.9935
Rio Verm	0.9344	0.9432	0.9520	0.9636	0.9799	0.9858	0.9876	0.9930
PDA	0.9732	0.9749	0.9752	0.9772	0.9842	0.9881	0.9898	0.9683
União	0.9723	0.9739	0.9774	0.9791	0.9818	0.9866	0.9873	0.9762
Imbau1	0.9392	0.9390	0.9474	0.9498	0.9444	0.9539	0.9511	0.9304
Imbau2	0.9725	0.9703	0.9762	0.9785	0.9760	0.9797	0.9807	0.9772
Dourada1	0.9495	0.9550	0.9627	0.9686	0.9510	0.9499	0.9487	0.8429
Dourada2	0.9735	0.9747	0.9754	0.9766	0.9794	0.9807	0.9825	0.9728
Dourada3	0.9768	0.9778	0.9785	0.9794	0.9832	0.9848	0.9863	0.9756
Dourada4	0.9828	0.9820	0.9849	0.9865	0.9878	0.9932	0.9929	0.9954
WithinPop	0.9670	0.9674	0.9722	0.9750	0.9756	0.9800	0.9805	0.9653
Metapop	0.9910	0.9899	0.9913	0.9917	0.9919	0.9942	0.9950	0.9974

Discussion

The results of the simulations run for the current metapopulation composed of 11 functional units indicate that the metapopulation is viable for the next 100 years. The population shows a favorable potential to grow, 13.8% per year. This growth rate is comparable to what has been observed in the captive population (Ballou and Mickelberg 2008), the reintroduced population (Beck and Martins 2003), and the growth of the population in União following the initial translocations in the 1990s (Kleiman and

Rylands 2002). At this growth rate, should additional habitat become available, the population could grow to fill it.

Each functional unit individually had no perceivable impact on metapopulation viability for the 100 years, the retained genetic diversity never dropped below 99% regardless of which functional unit was removed, and the probability of extinction remained the same. This reveals that no one unit is supporting the entire metapopulation but rather it is the collection of functional units that is helping maintain viability. The very minimum collection of functional units needed to maintain a viable metapopulation included just two units: Pirineus and Poço das Antas. Together they retained 98.24% of the genetic diversity, just over the 98% target for genetic diversity retention. These are the two largest functional units and their combined areas are estimated to support just under 1,000 individuals. Since there are few threats to the golden lion tamarins in the model, these units are able to remain viable as long as the population size is large enough. The 5 largest populations (Pirineus, Poço das Antas, Gaviões, Rio Verm, Dourada4) together over 99% of the current genetic diversity, which is the same level of genetic diversity retained by the metapopulation with all 11 functional units. However, to function as a metapopulation, these units would need to be structurally and functionally connected. This is possible for four of these units, but Rio Vermelho is geographically further isolated from the other units, making it logistically difficult to connect this unit with the others.

The Dourada units are the only units that are structurally connected and the baseline model included low levels of dispersal between Dourada2 and 4 and Dourada3 and 4 based on the appearance of unknown animals in these areas (Chapter 2). When Dourada4 was removed, the probability of extinction for Dourada2 increased to 0.2%. This rate is still very low, but it demonstrates that this small population is viable in part due to its connection with Dourada4.

Even though the metapopulation is able to retain 99% of genetic diversity, five of the functional units were not able to maintain 90% genetic diversity, the target for genetic diversity retention in each unit. The largest factor influencing this is likely to be population size; the five functional units not able to maintain 90% genetic are the five smallest units. This is particularly true for Imbaú1, which has only 24 individuals and a 30% probability of extinction. This is a surprisingly low level of extinction for such a small population, and again demonstrates that, given the life history of the GLT population, it can persist in these small populations provided there are no additional threats. The best way to maintain Imbaú1 is through linkages with its larger neighboring unit, Imbaú2, or through translocations. To meet the genetic goal of 90% retention, 6 individuals need to be translocated to Imbaú1 every 5 years. However, even with these measures in place, the population is just too small to remain truly viable. Even though the probability of extinction at the end of the simulations (100 years) was 0%, the unit still went extinct at least once in the 500 iterations, which is indicated by the mean time to extinction (MTE). If the unit went extinct during the iteration, as long as it was

recolonized before the end of the 100 years, it still maintains a 0% probability of extinction. Unfortunately, *VORTEX* does not provide output on the number of times a population goes extinct and is then recolonized, so this is unknown. It is probable that the only way this unit can be rescued without ever going extinct is if it is combined with Imbaú2 through structural and functional connectivity so that the population size can be increased.

Even though Imbaú1 was the only unit that had a probability of extinction, four other units were not able to maintain 90% genetic diversity. With these small population sizes, genetic drift becomes the driving force for evolution as opposed to natural selection (Frankham et al. 2010). The most feasible way to increase each unit's genetic diversity is through increased connectivity between neighboring units. At 1% dispersal between neighboring units, the genetic diversity increased greatly for those units with the lowest level of retained genetic diversity (Imbaú1 and Dourada2). With dispersal at 2%, all units maintained at least 90% gene diversity. This level of dispersal is slightly higher than what might be typical for golden lion tamarins, but is still possible for these units. With the current landscape structure however, dispersal is unlikely between most units. Connectivity needs to be improved, perhaps by creating forest corridors, to encourage dispersal which could help maintain higher levels of genetic diversity in those smaller functional units.

The model indicated that with 2% dispersal, the functional units and metapopulation were able to meet genetic goals and retain a 0% chance of extinction. This is a good indication of what is needed for GLT population persistence. If connections between functional units can be created to promote dispersal, this will greatly benefit the population. However, these functional units are still not able to maintain the same level of genetic diversity as the metapopulation as a whole. In efforts to maximize retained genetic diversity, Scenario 6 examined the strategies needed to possibly match the average functional unit genetic diversity (WithinPop) to what is maintained in the entire metapopulation when modeled as a panmictic population. Even at the highest level of 15%, dispersal alone was not enough to increase the WithinPop genetic diversity of 87% to the 99% maintained by the metapopulation, and these high levels of dispersal compromised population size. The added mortality that occurs during dispersal (25% mortality) meant that as a higher percentage of animals were moving, a quarter of those animals were dying, leading to a population decline and ultimately a gradual decline in the metapopulation genetic diversity as well. This decline in population size was more pronounced after the 5% dispersal level.

Another way to increase connectivity is through translocations. By adding translocations to a 5% dispersal rate, the WithinPop value increased to 98%. However, the level of translocation needed to reach this target is unrealistically high; 460 animals moved every 3 years. This demonstrates that even with moving many animals between units, it is still not as effective as having one panmictic population. In this study, there were no

circumstances of combined dispersal and translocations where the functional units could maintain as much genetic diversity as the panmictic metapopulation. This has important implications for the population of GLTs. Even with corridors to increase dispersal and potential managed translocations, genetic diversity will be compromised due to the fragmented structure of the population.

It is important to note that these levels of genetic diversity produced by the model are likely to be overestimates. *VORTEX* starts each simulation by creating populations with unrelated founders, and the genetic diversity retained at the end of the simulation is relative to those founders (Miller and Lacy 2003). For most of the functional units, the actual populations were started with far fewer founders than are modeled in *VORTEX* and some level of inbreeding is evident from pedigree examination (Chapter 1, Dietz et al. 2000). The mortality rates used in the model, however, are based on monitored populations and would include any increase in mortality due to inbreeding. This helps balance the potential overestimation of genetic diversity although does not remove it completely.

Management Implications

This analysis reinforces that when golden lion tamarins have protected habitat and relatively low threats, the metapopulation can be maintained. It also illustrates the importance of connectivity to maintain the small functional units with lower levels of genetic diversity. Whenever possible, functional units should be connected to encourage

gene flow between them. This is especially true for Imbaú1, which was the most vulnerable functional unit. Ensuring long-term survival and minimizing the loss of genetic diversity in Imbaú1 will require immigration of animals either through dispersal or through translocation. However, based on the model, translocation could perhaps provide the best solution for genetic diversity retention. As it now exists, this functional unit is a sink population and will depend on a source, (both Imbaú2 and Poço das Antas were modeled) to not go extinct. Cohesive connectivity both structurally and functionally to Imbaú2 would help decrease the risk of extinction and increase viability.

Surprisingly, only two functional units were needed to retain 98% of the genetic diversity, and 5 were needed to maintain 99%. These larger areas can support the larger populations that can maintain more genetic diversity than the smaller areas. Even though the model suggests they are not needed for genetic diversity, the smaller units are not without value. Most of the smaller units are composed of reintroduced or translocated animals that may have founder alleles that are not represented in the other units.

Removing them from the managed population would result in a loss of those unique alleles. Additionally, some of these smaller units (Imbaú1) are easily accessible making them quite valuable for ecotourism and educational outreach opportunities. Golden lion tamarins are viewed as ambassadors for the Atlantic Forest (Kleiman and Mallinson 1998, Kleiman and Rylands 2002), and continuing to protect and maintain these small units has positive implications for the protection of the forest as well as for other species living in these forest.

While the golden lion tamarin population is one of the best studied primates in the world, there still are information gaps that, if filled, could make this model more accurate in its predictions. For example, very little is known about the populations living in mountainous areas of Pirineus and Gaviões. More research is needed in these areas to accurately estimate population size and densities which are suspected to be different than those in other study areas given the habitat difference. Additionally, having more information on mortality rates during dispersal could help produce a more accurate model. It is likely that mortality rates during dispersal were underestimated in this study.

In this population viability analysis, genetic diversity was used as a measure of viability in addition to probability of extinction. Very few PVAs include genetics at all in the analysis; this may greatly underestimate the risk of extinction of these populations (Allendorf and Ryman 2002). This is especially true for small populations vulnerable to the loss of genetic variation through genetic drift and inbreeding. Allendorf and Ryman (2002) recommend a goal of retaining at least 95% genetic diversity for 100 years. Soulé (1986) suggests nothing lower than 90% for 200 years, meaning a population cannot accumulate more than 10% inbreeding in the population over the 200 years. Captive breeding programs set genetic goals at 90% retention for 100 years (Ballou and Foose 1996). Depending on the circumstances that surround a population, different targets for genetic diversity can be set. For example, an early Florida Panther population analysis established a goal to maintain 90% genetic diversity and have 95% survival for 100 years

(Ballou et al. 1989). Viability for the Red-cockaded Woodpecker was set at 90% retention for 200 years based on Soulé's recommendation (Haig et al. 1993). Analysis by Haig et al. (1993) showed that the population was not able to reach this target. For this study on golden lion tamarins, setting a metapopulation genetic target of 98% retention was based on previous analysis suggesting that this is a reasonable goal (Holst et al. 2006). Populations that are much smaller may not be able to meet this target. Therefore the target for the functional units in the GLT population was set lower, at 90% retention for 100 years.

Other measures exist for setting goals to maintain genetically viable populations such as using the effective population size (N_e). For short-term persistence, an effective size of 50 is the minimum that should be considered (Franklin 1980); this would be equivalent to an increase in inbreeding coefficient of 1% per generation. For long-term persistence and in order to maintain evolutionary potential (i.e. balance the loss of genetic variation due to genetic drift with the gain due to mutations), larger effective sizes are needed. The recommended effective size needed to maintain evolutionary potential ranges from 500 (Franklin 1980) to 5000 (Lande 1995). Many endangered species, including golden lion tamarins, may have much lower effective population sizes (Frankham et al. 2010). While populations with effective sizes less than 500 may not go extinct, it does subject the population to increasing vulnerability over time. Effective population sizes are estimated to be about 11% of the actual population size (Frankham 1995) which means the N_e for the wild population of GLTs may be only 220 individuals, far less than Franklin's

recommendation of 500 individuals. The captive population of GLTs has a N_e/N ratio of about 0.3 (Ballou and Mickelberg 2008). Using this ratio for the wild population increases the wild N_e to about 600 individuals, although this ratio is likely to be too high for the wild population. The N_e/N of the reintroduced population (data from Chapter 1, calculated by the software PMx) is calculated at 0.17. Based on this ratio, the wild population would have a N_e of about 360 individual, still under the recommended minimum level. Increasing the N_e for golden lion tamarins will require an increase in habitat for golden lion tamarins

Many studies base population viability on demographic rates and probability of extinction, excluding genetic factors. Given the importance of genetic diversity for long-term population persistence, it should be included in PVAs whenever possible. If this study would have used probability of extinction alone to define viability and had not included genetic goals, only one functional unit would have been identified as not viable as opposed to the five identified as not viable when genetic goals were included. This greatly overestimates viability.

Strategies to conserve endangered species need to be based on population viability theory and should include specific quantitative objectives (Foose et al. 1995). Population viability analysis (PVA) can be a powerful tool to investigate the long-term viability of populations to determine if these objectives can be met. This study is an important demonstration of how PVA can be used to assess quantitatively, the viability of a

population in terms of probabilities of extinction as well as specific genetic goals. Using the most current data available, the model can provide valuable information needed to assist in making management decisions that promote long-term population persistence.

SUMMARY WITH RECOMMENDATIONS

This section of the dissertation is intended to provide a summary of each of the data chapters, highlighting key information, especially that which is relevant to golden lion tamarin management. This section also contains recommendations based on the dissertation results.

Chapter 1

Using pedigree analysis to evaluate the genetic status, results indicate that the population of reintroduced GLTs is relatively favorable. The reintroduced population has maintained over 96% genetic diversity relative to the source population, the hypothetical population from which the founders were obtained. The current population also has a relatively a low mean inbreeding coefficient ($<5\%$), and most of the population has inbreeding coefficients less than 3.15%. Although select reintroductions could increase genetic diversity slightly in the reintroduced population, most of the captive founders are represented in the reintroduced population. Those that are not represented entered the captive population after the reintroductions ended in 2000.

Each of the three management units that are inhabited by reintroduced GLTs and are part of the large metapopulations are each maintaining around 90% genetic diversity. This is

the minimum recommended. One way to increase genetic diversity in these management units is to selectively translocate animals between them. Imbaú was the smallest management unit and benefited the most from the modeled translocations.

Beyond the golden lion tamarin population, this dissertation chapter demonstrates the power of using pedigrees to estimate genetic characteristics. While many populations may not have the level of data needed to construct a pedigree, when the information is available, this is a preferred method of analysis. It provides a genome-wide level of genetic diversity, which is valuable when making management recommendations to maximize genetic diversity. Managing populations based on the diversity at a few loci estimated by molecular analysis could lead to high diversity at those loci, but a loss of diversity at all others. As the GLT population increases however, getting reliable pedigree information will become increasingly difficult and future genetic assessments will likely have to include molecular analysis.

Chapter 2

This chapter examined several factors that could possibly affect golden lion tamarin movement in a fragmented landscape including area size, population size, density and distance. Distance had the most significant relationship with the frequency of movement, so as distance increased fewer movements were observed. The average distance traveled between groups was nearly 850 meters. Logistic regression analysis was used to create a model that described the probability of movement. The variables included in the model

were distance, the size of the area the tamarin was moving from, and the characteristic of the distance between the areas (well connected or not connected). In this case again, distance had the strongest effect on predicting the probability of movement. More research needs to be done, however, to improve this model; the model predicted very accurately when a tamarin would not move, but it did not predict very accurately when the tamarin would move. The model could be improved by changing the population level to look at movements between smaller units as well as evaluating additional variables that could affect movement.

Chapter 2 demonstrates the importance of evaluating functional connectivity, the measure of animal movement in a landscape. The GLT population had previously been categorized into 7 management units based on landscape contiguity, the structural connectivity. By using movement data in three of management units, functional connectivity was evaluated. Groups that had movement between them were classified in the same functional unit. Two of the three management units evaluated had limited movement within the management unit; that is, structural connectivity did not match functional connectivity. Dourada had 3 distinct functional units and Imbaú had two. These are the most heavily fragmented management units and movement between groups is likely much more difficult than in more contiguous management units. The results of this study indicate that these fragmented areas might require a different management strategy than the other areas. Increasing connectivity between functional units should be a critical component of management in these areas. This can be accomplished through

translocation or perhaps corridors. However, several of the functional units are currently connected by corridors. These corridors are relatively new, and evaluating their functionality is vital to understanding the dynamics in these populations. It may be that tamarins require higher quality connections or multiple connections are needed in these fragmented landscapes where movement might be restricted. One possibility is that the shape of these areas is restricting movement. The more linear the landscape, the more likely it is that a tamarin has to move directly through another group's territory, which may prohibit movement. More research needs to be done on these topics.

Chapter 3

The population viability analysis using *VORTEX* demonstrated that the golden lion tamarin metapopulation is viable for the 100 years modeled. When GLTs are given adequate habitat and have low threats, the population has a potential to increase, up to 13.8% per year. This potential to increase is likely the reason why the wild population has been able to recover from the population low of around 200 animals in the 1970s. Even though the metapopulation was viable, there were 5 function units that were not viable. These units are the smallest units and could be maintained as viable if dispersal could be increased between them. This supports the results from Chapter 1 and 2; units need to have improved connectivity to remain viable.

The analysis indicated that a viable metapopulation could be maintained with just the two largest populations. This demonstrates the importance of these large populations, but the

value of those other units should not be underestimated. Many of these other units support populations of reintroduced and translocated tamarins. These populations may have founder alleles that are not represented in other areas. Some of these smaller areas are used for ecotourism and can be used to help support the project financially as well as be used for education outreach opportunities. Additionally, GLTs in these other units can be used as an umbrella species to protect these valuable fragments of Atlantic Coastal forest.

This chapter also illustrates the importance of incorporating genetic diversity targets in viability goals. If viability would have only included the probability of extinction, only one population would not have been viable as opposed to the five that were not viable when including goals for genetic diversity retention. Population viability analyses that do not include genetic diversity goals run the risk of overestimating population viability.

The results of this dissertation indicate that the golden lion tamarin population is in relatively good status considering its population size. This is likely the result of the last 3 decades of intensive management. While the current status is good, the future for golden lion tamarins will rest on the ability to connect the current fragmented landscape and promote gene flow between populations. If these fragments remain isolated there will be a likely increase in inbreeding and decrease in genetic diversity, particularly in the smaller units. However, proper management, including translocations and increased connectivity, can promote long-term population viability.

Future Work and Recommendations:

- Translocations between management units would help increase genetic diversity in those units that are maintaining low levels of genetic diversity. Imbaú is the highest priority to receive translocated animals and will need translocations to remain viable.
- Further analysis needs to be completed to develop a model to describe the probability of movement. The first step would be to conduct the same analysis at a smaller population level. Looking at movements between groups, for example, could improve the model since there would be 287 moves as opposed to the 14 used to create this model. If the model is still not accurately predicting movement, the second step is to examine other possible variables such as fragment shape.
- Based on the functional connectivity analysis, the current management units need to be re-defined. Using the 7 metapopulation management units described based on structural connectivity most likely overestimates gene flow within the units. Using the 11 units as described in Chapter 2 is a more accurate approach.
- In some fragments (Dourada and Imbaú), small, thin connections do not appear to be supporting movement. Perhaps high quality connections are needed in these fragmented areas to support golden lion tamarin movement. The level of

connectivity needed to support movement needs to be researched further and more research is needed specifically on corridor use.

- While a majority of the populations has been monitored over the last 20 years, there are a few areas where little is known about there GLTs living there. Both Pirineus and Gaviões may contain a large number of GLTs. For this population viability analysis (Chapter 3), very conservative population size estimates were used. More research in these management units, particularly in terms of population density could provide information that would improve the model.
- Long-term population viability of the small functional units depends on increasing movement between units. Increasing connectivity between functional units is recommended to help support the populations living in those units. Translocations could be used as a short term solution to increase genetic diversity. In the long-term, increasing corridors between these smaller functional units could help increase viability.

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