

ABSTRACT

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GOLDEN LION TAMARIN,
LEONTOPITHECUS ROSALIA

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Animals move through their environment in response to resource, competitor, and predator distribution. In this dissertation I examine resource and space use in wild golden lion tamarins (GLTs, *Leontopithecus rosalia*). In chapter one I present the results of a field study exploring factors predicting sleeping site selection. GLTs preferentially slept in tree holes. Each group had a few frequently used sites typically found in large, living trees on hillsides near other large trees. Topography and small-scale forest and tree variables were better than habitat-level classifications in predicting sleeping site use. In my second chapter I evaluated home range calculation methods. Using 19 years of data for 15 groups of GLTs, I calculated a yearly home range for each group with the three most commonly used methods: minimum convex polygon (MCP), grid cell, and kernel density estimates. MCP produced the largest home range estimates, grid cell the smallest, and kernel estimates were intermediary. Kernel estimates were preferred because probability of use may be calculated for any

part of the home range, there is high concordance between observation spatial distribution and home range shape, and there is a lack of relationship between sample size and home range size. In my third chapter I tested three hypotheses explaining home range size in group-dwelling animals. First, I tested the dominant hypothesis, which states that home range size is determined by group energetic needs and, therefore, group size. The second and third hypotheses relate to numbers of adult females and males present in groups. More adults may increase ranging because of increased reproduction, search for breeding opportunities, or defense. I also examined how variation in predation affects population density and demography and, thus, mediates space use. I found support for all three hypotheses. Larger ranges were occupied by groups that were large, had two breeding females, and/or more potentially breeding males or adult natal males. Intense predation resulted in lower population densities, smaller groups, only one breeding female per group, and fewer adult natal males. Population density and predation had significant, negative impacts on home range size.

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LEONTOPITHECUS ROSALIA

By

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Preface

This dissertation contains an introduction section and three chapters. All chapters are presented in manuscript form, with abstract, introduction, methods, results, discussion, and acknowledgements, followed by tables, figure legends, and figures. A single bibliography is provided at the end. Chapter 1 was published in the *American Journal of Primatology* in 2007.

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Introduction

Animals move through their environment in response to ecological and social pressures. The pattern of spatial movement may provide information on the animal's critical daily needs, as well as give an indication of how changes in the environment (e.g. seasons, predator density, etc.) impact movement. Limited resources may constrain movement or may force individuals to travel further in order to meet basic requirements. Factors that may impact travel include habitat characteristics (Coimbra-Filho 1978; Garcia and Braza 1993), food distribution (Garber and Hannon 1993; Wrangham et al. 1993; Johnson et al. 2002), sleeping site distribution (Lima and Dill 1990; Day and Elwood 1999), encounters with predators (Heymann 1987; van Schaik and Mitrasetia 1990), and weather conditions (Schmid 1998; Suchi and Rothe 1999).

Each of these factors can have strong influence on ranging, with potentially additive effects of multiple factors. An increase in travel may be required to find sufficient food in poor quality habitat (Doran-Sheehy et al. 2004) or when food is patchily distributed (Rylands 1986; Chapman et al. 1995). The use of multiple centrally located sleeping sites may allow a decrease in daily travel, while enabling adequate food intake and minimizing search overlap on consecutive days (Chapman et al. 1989). The presence of predators has been associated with a decline in ranging in times of heavy predation (Borowski 1998; Norrdahl and Korpimäki 1998; Nie and Liu 2005), but also a lack of change in travel patterns (Wolff and Davis-Born 1997; Hubbs and Boonstra 1998; Jonsson et al. 2000). Animals typically decrease travel during heavy rain (Dawson 1979; Goldsmith 1999; Ganas and Robbins 2005) and

extend resting in the midday when temperatures are highest (Doolan and MacDonald 1996; Wauters 2000; Erkert and Kappeler 2004).

Members of the family Callitrichidae, such as the golden lion tamarin, are endangered, small-bodied primates that are considered energetically constrained because of their high energetic demands and small body size (Thompson et al. 1994; Caine 1998; Suchi and Rothe 1999). As an additional constraint on many callitrichids, groups maintain a larger home range in proportion to biomass than do most primates (Terborgh and Stern 1987; Raboy and Dietz 2004). Given these characteristics, movements through their environment should be controlled in order to maximize energy intake while minimizing energy expenditure.

In addition to these spatial characteristics, callitrichids are cooperative breeders with adult offspring assisting in carrying and provisioning infants (Bales et al. 2000). Many species of callitrichids also have a variable mating system, with field reports of monogamy, polygyny, polyandry, and even polygynandry (Terborgh and Goldizen 1985; Sussman and Garber 1987). In the golden lion tamarin, groups typically consist of a reproductive female, a dominant reproductive male and their offspring; however, some groups contain multiple reproductive females, and/or one or more unrelated males in the group who may be reproductively active (Baker et al. 1993). Natal females that reach sexual maturity in the group and stay until 3-4 years of age often reproduce, or may inherit the breeding position from an aging mother (Dietz and Baker 1993). This variability in mating system and high level of cooperation may reflect a combination of social, environmental, and reproductive pressures.

The goal of this dissertation was to explore the interplay of resource use, group composition, population dynamics, and spatial movement in the golden lion tamarin, *Leontopithecus rosalia* at Poço das Antas Biological Reserve, Brazil. My first chapter analyzes forest and tree characteristics surrounding preferred sleeping sites. Choice of sleeping site is thought to serve several functions: protection from parasites, predators, and disease (Aquino and Encarnación 1986; Caine et al. 1992; Anderson 1998; Anderson 2000); proximate early morning or late afternoon access to feeding resources (Chapman 1989; Chapman et al. 1989; von Hippel 1998); and shelter from inclement weather (Aquino and Encarnación 1986; Anderson 1998; Anderson 2000). Sleeping trees may be chosen based on physical characteristics of the forest surrounding the tree (Dawson 1979; Garcia and Braza 1993) and/or physical characteristics of the individual tree (Day and Elwood 1999; Anderson 2000). Each sleeping site function may predict a different suite of site characteristics.

Previous research on lion tamarins suggested that they are constrained by their need for naturally occurring tree cavities for sleeping (Coimbra-Filho 1978; Valladares-Padua and Prado 1996). This is of particular concern in an area such as Poço das Antas Reserve, where very little primary forest remains. While golden lion tamarins have been observed sleeping in sites other than tree holes, this may be the result of insufficient mature forest and a paucity of adequate tree holes (Dietz et al. 1997). The objective of this chapter was to describe the physical and spatial characteristics of golden lion tamarin sleeping sites, decide which factors distinguish frequently used sleeping sites from infrequently used sleeping sites and random sites, determine if the availability of mature forest limits tree hole use by lion tamarins, and

examine the functions of sleeping sites in light of their physical characteristics and locations.

In my second chapter, I explore common methods for calculating home-ranges. A home range is defined as the area occupied by an animal or animal group during a given time period (Burt 1943; Kernohan et al. 2001) and differs from a territory, which is actively defended against conspecifics (Burt 1943). The shape and size of an animal's home range may reflect selection pressures (Schoener 1981) and are influenced by abiotic, habitat, and social factors including season (Burt 1943), group biomass (Milton and May 1976; Dietz et al. 1997; Kelt and Van Vuren 2001), resource distribution (Law and Dickman 1998; Kelt and Van Vuren 2001; Raboy and Dietz 2004; Mitchell and Powell 2007), habitat composition (Kierulff et al. 2002), and energetic requirements (McNab 1963; Mace et al. 1983). In addition to biotic factors, methodological factors can play a large role in the final outcome of a home range analysis (Laver and Kelly 2008) and may lead to misinterpretations of ranging patterns.

The purpose of this second chapter is to provide guidance to field biologists in selecting the home range method appropriate to their objectives and in designing a data collection scheme that meets the needs of those goals. We use long-term data from our study population to compare home range sizes calculated using the three most commonly used methods, examine the impact of independent data points on final home range size, determine the role of methodology in final home range size and fragmentation, explore the impact of time of day and seasonality on home range

estimates, and give recommendations for study duration and the number of groups or individuals required to give an adequate picture of ranging for a population.

My final chapter examines factors that affect the variation in home range size across study groups and over years of study. Animals are thought to occupy the smallest home ranges adequate to provide energy sufficient for survival and reproduction (Maynard Smith 1974; Wilson 1975), a hypothesis supported by the relationship found between body size, energetic demands, and home range size (McNab 1963; Milton and May 1976; Mace et al. 1983). Extending this logic to use of space in social animals, as group size increases, travel should increase due to greater food requirements and heightened intra-group foraging competition (Clutton-Brock and Harvey 1977; Terborgh 1983; Chapman 1990; Wrangham et al. 1993). This ecological constraints model has been the predominant explanation of home range size for the last 20 years, with support for the hypothesis coming from many studies (Herrera and MacDonald 1989; Barton et al. 1992; Watts 1998; Gillespie and Chapman 2001; Dias and Strier 2003). Despite the dominance of the ecological constraints hypothesis, recent reports suggest that food availability and group size may be insufficient to predict travel patterns (Adams 2001; Struhsaker 2006). Space use may reflect the combined effects of several factors acting at different levels (Chapman and Chapman 2000), including breeding system (Clutton-Brock and Harvey 1977), social factors (Chapman and Pavelka 2005; Struhsaker 2006), and population density (Benson et al. 2006; Horiuchi 2006). We use 19 years of data collected at Poço das Antas Reserve, Brazil to test three non-mutually exclusive

hypotheses to explain variation in the home range size of golden lion tamarins: ecological constraints, male presence, and female presence.

Starting in the mid 1990s, the rate of predation on lion tamarins in the reserve increased dramatically (Franklin et al. 2007a; Franklin et al. 2007b). The predation rate prior to 1996 was 0.18 golden lion tamarins per group per year. This rate increased to 0.55 lion tamarins per group per year from 1996-2004 (Franklin et al. 2007a; Franklin et al. 2007b). In conjunction with these changes in predation rates, population size decreased from 350 to approximately 220 individuals from 1995 to 2000 (Franklin and Dietz 2001). After testing the three hypotheses stated above, we examined how variation in predation affected population density and demography and, thus, mediated the observed changes in home range size.

The results of these three chapters make significant contributions to the understanding of resource and space use in social animals and to the conservation efforts in this endangered species. The results of my study on sleeping site use by golden lion tamarins can aid in a better understanding of their site requirements and the distribution of sleeping sites through the Reserve. It has long been thought that lion tamarins required tree holes for sleeping (Coimbra-Filho 1978; Valladares-Padua and Prado 1996). This is of particular concern given that only 7.5% of the original extent of the Atlantic Coastal Rainforest remains (Myers et al. 2000), with 90% of Poço das Antas Reserve being in various stages of secondary succession (Dietz and Baker 1993; Pessamilio 1994). My study shows that there are a large number of tree holes used as sleeping sites by golden lion tamarins, with the majority of groups choosing a small number of tree holes to which they return repeatedly. Tree holes

used frequently are found in larger trees, on hillsides, surrounded by other large trees. Lion tamarins also use bamboo, vine tangles, and palm trees frequently, with a few groups preferentially choosing bamboo over tree holes. The results of this study show that lion tamarins are adaptable to various habitat types and have found ample sleeping sites within regenerating forests.

My second study provides a comprehensive look at the three most frequently used home range calculation methods: Minimum convex polygon, grid cell, and kernel density estimators. Minimum convex polygon is still used in the vast majority of studies (Laver and Kelly 2008), despite its long-reported failings (van Winkle 1975; Swihart and Slade 1997; Seaman et al. 1999). My research shows systematic overestimation of home range size when calculated with minimum convex polygons, with many large sections of the home range containing no observations. Kernel density estimates provided a better representation of home range, and should be used in most studies. My research is the first examination of home range methods comparing calculations across years of data with multiple methods and data sampling techniques. I also provide a basis by which to calculate the number of years and study groups required for a good estimate of average home range size for a population.

My final chapter broadens the examination of home range size variation to include factors not commonly considered. It is the first simultaneous test of the effects of ecological constraints, demography, predation, and population density on variance in home range size. For the past 20 years, group size and energetic demands have dominated explanations of home range size (Clutton-Brock and Harvey 1977; Terborgh 1983; Chapman 1990; Wrangham et al. 1993). My results show that

individuals are capable of planning for the future: groups occupy larger home ranges when the potential for reproductive output is the greatest. This chapter also shows the dramatic effect predation can have on group demography and the resulting effect on ranging. Increased predation results in smaller lion tamarin home ranges because of the combined effects of decreased group size (i.e. decreased energetic constraints), fewer adult natal males in the group (i.e. diminished group defense and/or reduced need for “prospecting”), and fewer reproductive females in the group (i.e. less future reproductive potential), which is offset by lower population density (i.e. range expansion due to reduced pressure from neighboring groups). Groups in large ranges had greater reproductive success, producing more litters and infants than smaller ranges.

In addition to these contributions, my findings will aid in conservation planning for the golden lion tamarin. The first chapter allows a better understanding of the sleeping site requirements of golden lion tamarins. I provide a list of species commonly used by the lion tamarins for sleeping and a breakdown of the frequency with which each site type is used. This information will improve the planning of corridors between forest fragments containing golden lion tamarins. The viability of many endangered populations relies on the ability of individuals to successfully use the matrix that surrounds habitat fragments (Laurance 1994; Pires et al. 2002), either for resources or as a corridor to other habitat fragments. In cases where the distance between habitat fragments is greater than a day of travel, food and sleeping sites may be necessary in the intervening space. The first chapter provides corridor planners an idea of the types of species that golden lion tamarins can use for sleeping. The second

and third chapters provide information on the extent of golden lion tamarin ranging and provide conservation managers with a better understanding of the extent of forest that is required to successfully support a golden lion tamarin group, the variation in those requirements, as well as what factors alter the use of space by golden lion tamarins.

Chapter 1: Tree and Forest Characteristics Influence Sleeping Site Choice by Golden Lion Tamarins

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Abstract

Lion tamarin monkeys are among a small number of primates that repeatedly use a few tree holes for the majority of their sleeping sites. In order to better understand why lion tamarins rely on tree holes as sleeping sites we compared the physical characteristics of frequently used sleeping sites, infrequently used sleeping sites and randomly selected forest locations at multiple spatial scales. From 1990 to 2004 we recorded 5235 occurrences of sleeping site use by 10 groups of golden lion tamarins (*Leontopithecus rosalia*) in Poço das Antas Reserve, Rio de Janeiro State, Brazil. Of those, 63.6% were tree holes. Bamboo accounted for an additional 17.5% of observations. Frequently used tree holes were more likely to be found in living trees and their entrances were at lower canopy heights than infrequently used tree holes. We also found that frequently used sleeping sites, in comparison to random sites, were more likely to be found on hillsides, be close to other large trees, have a lower percent of canopy cover, and have larger DBH. Topography and small-scale variables were more accurate than were habitat-level classifications in predicting frequently used sleeping sites. There are ample tree holes available to these lion tamarins but few preferred sites to which they return repeatedly. The lion tamarins find these preferred sites wherever they occur including in mature forest and in relics of older forest embedded in a matrix of secondary forest.

Introduction

Sleeping sites are thought to serve several functions: protect occupants from inclement weather (Anderson 1998; Anderson 2000; Aquino and Encarnación 1986), provide proximate early morning and late afternoon access to foraging sites (Chapman 1989; Chapman et al. 1989; Heymann 1995; von Hippel 1998), and protect occupants from predators, parasites, and disease (Anderson 1998; Anderson 2000; Caine et al. 1992). Sleeping trees may be chosen based on physical characteristics of the forest surrounding the tree (Dawson 1979; Garcia and Braza 1993) and/or physical characteristics of the individual tree (Anderson 2000; Day and Elwood 1999).

Factors that have been associated with sleeping site choice include the diameter at breast height (DBH) of the tree (Aguirre et al. 2003; Chapman 1989; Day and Elwood 1999), location in relation to foraging resources (Day and Elwood 1999; Hamilton 1982; Heymann 1995; Mendes Pontes and Soares 2005), percent canopy cover (Garcia and Braza 1993), height of first branch (Day and Elwood 1999), crown height (Day and Elwood 1999), height of tree (Day and Elwood 1999; Peh and Sodhi 2002; Tenaza and Tilson 1986; Wahungu 2001; Zhang 1995), presence of lianas or other vines (Caine et al. 1992; Day and Elwood 1999; Garcia and Braza 1993; Tenaza and Tilson 1986), degree of concealment (Caine et al. 1992), whether the tree is living or dead (Carey et al. 1997; Schmid 1998), and the location in relation to groups of congeners (Heymann 1995). In addition, some species choose to sleep in tree species that are included in their diet (Brooke et al. 2000).

Each sleeping site function may predict a different suite of site characteristics. For example, protection from weather and predators would both emphasize the physical characteristics of the tree and the degree of cover provided by the surrounding vegetation. Both height and degree of cover are believed to aid in protection from predators (Anderson 2000; Caine et al. 1992). Live trees with greater DBH better insulate occupants from weather conditions (Schmid 1998; Wiebe 2001). Occupants should choose a sleeping site that balances the priorities of the site functions or addresses the function most crucial to survival and reproduction for that individual.

Lion tamarins, members of the family Callitrichidae, are small-bodied primates which feed primarily on insects and fruit. Wild lion tamarins sleep mainly in naturally occurring tree cavities (Coimbra-Filho 1978; Kierulff et al. 2002; Raboy et al. 2004; Valladares-Padua and Prado 1996). Coimbra-Filho (1978) suggested that a scarcity of sleeping sites may limit golden lion tamarin distribution. While golden lion tamarins have been observed sleeping in sites other than tree holes, this may be the result of insufficient mature forest and a paucity of adequate tree holes (Dietz et al. 1997). This hypothesis is supported by the observation that golden-headed lion tamarins (*Leontopithecus chrysomelas*) in Una Biological Reserve, which has more mature forest than the areas currently inhabited by golden lion tamarins, sleep predominantly in tree holes in mature or shade-crop forest (Raboy et al. 2004).

Over the course of the last 10 years, the monitored population of golden lion tamarins at Poço das Antas Reserve has been greatly reduced, primarily due to predation. On at least 16 occasions, multiple individuals and, occasionally, entire

social groups, disappeared from their home ranges. In several instances, tamarin remains were found in the vicinity of the sleeping site and excavated tree cavities indicated that nocturnal or crepuscular predators had enlarged the cavity opening in order to extract the tamarins (see Franklin *et al.*, in press, for a more complete description). The increase in predation at sleeping sites coupled with evidence that predators were able to breach some frequently used tree cavities prompted us to examine the physical characteristics of tamarin sleeping sites in a conservation unit covered mainly by secondary forest.

The objective of this research was to 1) describe the physical and spatial characteristics of golden lion tamarin sleeping sites, 2) determine which factors distinguish frequently used sleeping sites from infrequently used sleeping sites and sleeping sites from random sites, 3) determine if the availability of mature forest limits tree hole use by lion tamarins, and 4) examine the functions of sleeping sites in light of their physical characteristics and locations.

Methods

Study Site and Population

This study was conducted at Poço das Antas Reserve (22°30-33'S, 42°15-19'W), Rio de Janeiro State, Brazil. The reserve is a 6300-ha Atlantic Coastal rainforest remnant that is a mosaic of mature, secondary and swamp forests and grasslands (Dietz and Baker 1993; Dietz et al. 1997). The topography of the reserve ranges from 20 to 200 meters above sea level with seasonal precipitation (Dietz et al. 1997). The population of golden lion tamarins in the reserve comprises approximately 230 individuals (Rylands et al. 2002). Golden lion tamarins in this population are

trapped and marked semiannually. All groups are habituated to the presence of human observers and contain at least one radio-collared individual. While the number of study groups monitored changes over time, at any one time we actively follow at least eight groups of lion tamarins.

Data Collection

Study groups are followed once or twice a week from when they exit a sleeping site in the morning until they enter a sleeping site in the evening. Locations are recorded at 20 minute intervals throughout the day. We record the time of exit from and entrance into the sleeping site. Sunrise and sunset times were obtained from the U.S. Naval Observatory (<http://aa.usno.navy.mil/data/>).

Infrequently vs. Frequently Used Sleeping Sites

Data on tamarin movements and sleeping sites were collected between 1990 and 2004 by the researchers and trained field assistants. During this time we recorded data on 10 group home ranges. A “group home range” is defined as a geographic area used by a group of golden lion tamarins. While membership of the group may change over time, the geographic area occupied remains relatively constant.

Sleeping sites were categorized as frequently used if they accounted for at least 10% of observations for a group range. All groups were observed at least 300 times with the exception of one group. For this group, for which we had only 117 records, we used a minimum of 8 observations as a cutoff for classification as frequently used. We employed this standard because the group used only four sites more than twice, with the least frequently observed of these recorded on 8 occasions. Infrequently and frequently used sleeping sites were compared on two levels: macro-

site (habitat) and characteristics of individual trees used as sleeping sites. The macro-site variables included habitat type (mature or secondary) and aspect (lowland or hillside) and were determined using an IKONOS satellite image (approx. 20 m resolution). For each sleeping site we recorded the following tree characteristics: sleeping site type, height of tree, height of sleeping site or entrance to site (in the case of tree holes), DBH, and whether the tree was living or dead. Whenever possible, trees were identified to the level of family. The seven sleeping site types are defined as follows:

Tree Hole – Cavity formed in the trunk of a dead or living tree

Bamboo – Shelter at ground level inside a dense stand of bamboo

Vine Tangle – Dense tangle composed of vines supported by tree branches

Bromeliad – Shelter formed by an epiphytic bromeliad supported by tree branches

Palm – Site in the bole of a palm tree under living or dead palm leaves

Leaf or Bird Nest – Nest in a tree built by another animal

Tree Branch or Fork – Site on a tree branch or in the fork of two branches

Random vs. Frequently Used Sleeping Sites

In order to determine if sleeping sites are selected randomly relative to characteristics of existing forest, we documented the frequency of use of sleeping sites for 6 groups of lion tamarins from January-December, 2003. Frequently used sites were defined as those that accounted for at least 10% of observations. Forest and tree characteristics of frequently used sleeping sites were compared to randomly selected points in each home range. Group home ranges were determined using the fixed kernel density estimator in the Animal Movement Analysis Extension for

ArcView, version 3.2 (Environmental Systems Research Institute, Inc., Redlands, USA). GPS coordinates for random sites within each group home range were created using a random number generator. The sleeping and random sites were compared at three levels: macro-site (habitat), micro-site (0.01 ha = 100 m²), and tree characteristics. The macro-site characteristics were determined as described for infrequently and frequently used sites. We recorded the micro-site characteristics using a modified point-quarter method (Krebs 1999). At each random site we selected the closest tree of sufficient size to be a sleeping tree (i.e. with a DBH of at least 21 cm, the smallest known DBH for a sleeping tree during 2003). This selected tree became the point of reference for the point-quarter method, also called the “central tree.” Each quadrant was 25 m², with a total area around each tree measuring 100 m². For each site (random and sleeping), in each quadrant, we recorded the height of the tallest tree, number of lianas, number of trees, percent canopy cover, and the distance to the nearest tree of sufficient size to be a sleeping tree (same criterion as the selection of the central tree). Tree characteristics were also recorded for all sites including tree height, bole height, the number of vines attached to the tree, and DBH. For random sites we measured the characteristics of the central tree.

Statistical Analyses

Comparison of tree-supported sleeping sites

We tested differences among tree-supported sleeping sites (tree holes, bromeliads, vine tangles, nests, and tree branches and forks) in DBH, tree height, and height of sleeping site entrance using one-way ANOVAs with group home range identity included as a covariate. Since three separate comparisons were done, the

alpha level for each test was adjusted using a Bonferroni-type correction to 0.01667 (total experiment-wise alpha of 0.05). Pairwise comparisons followed each ANOVA. Again, given multiple comparisons, the alpha level was adjusted to 0.005 (10 comparisons for a total alpha of 0.05 for each dependent variable) to control experiment-wise error. Statistical assumptions of normality and homogeneity of variance were met for each test.

Infrequently vs. Frequently Used Sleeping Sites

The analysis of infrequently vs. frequently used sleeping sites included only tree holes. For the macro-level characteristics, we used chi-square analyses to test the relationship between infrequently vs. frequently used sleeping sites for both mature vs. secondary forest and hillside vs. lowland forest. A separate analysis was done for each group home range with effects across group home ranges evaluated using Cochran-Mantel-Haenszel statistics (Hollander and Wolfe 1999). An alpha level of 0.05 was used to determine significance.

At the tree level, we tested the probability of distinguishing a frequently used sleeping site from an infrequently used sleeping site using a logistic regression. Selection of variables was determined using backward elimination with a 0.05 alpha cutoff for inclusion in the model. The fit of the logistic model was determined to be appropriate by a Hosmer and Lemeshow test for goodness of fit ($\chi^2 = 8.95$, $P = 0.347$; Hosmer & Lemeshow, 1989). In order to control for effects of lion tamarin group identity on sleeping site selection, group identity was included as a covariate in the model.

Random vs. Frequently Used Sleeping Sites

For the macro-level characteristics, exact tests were used to test the relationship between sleeping vs. random sites for both mature vs. secondary forest and hillside vs. lowland forest. A separate analysis was done for each group with effects across groups evaluated using Cochran-Mantel-Haenszel (Q_{CMH}) statistics (Hollander and Wolfe 1999). An alpha level of 0.05 was used to determine significance.

For the comparison of sleeping to random sites on both the micro and tree level, we tested the probability of distinguishing a frequently used sleeping site from a random site using a logistic regression. Selection of variables was determined using backward elimination with a 0.05 alpha cutoff for inclusion in the model. For each analysis the fit of the logistic model was determined to be appropriate by a Hosmer and Lemeshow test for goodness of fit (micro-level: $\chi_8^2 = 13.42$, $P = 0.098$; tree level: $\chi_7^2 = 9.86$, $P = 0.1968$; (Hosmer and Lemeshow 1989). As for the other analyses, group identity was included in the model as a covariate.

Results

From 1990 to 2004 we collected 5235 records of sleeping site use. The four most frequently selected sleeping site types were tree holes (63.6%), bamboo (17.5%), vine tangles (9.6%), and bromeliads (4.7%, Table 1). Tree hole use among the ten groups ranged from 26.2%, for a group that primarily used two bamboo sites, to 91%. All groups, except the one that used primarily bamboo, used tree holes on a majority of the observed days. Bamboo accounted for more than 20% of observations

for four groups. Of the 3330 tree hole records, we identified the taxonomic family for 1913 tree records (Table 2).

All groups used a small number of sleeping sites frequently. A total of 1530 unique sleeping sites were used, with 1128 of those used only once (Figure 1). The remaining 402 sites were used more than once (a total of 4107 observations), 266 of these sites were tree holes (66.2%). Tree holes represented 85.3% of the sites used 8 or more times (Table 1) and bamboo another 11.6%.

On 1170 days we recorded both the morning sleeping site and the evening sleeping site used by a focal group. The lion tamarins returned to the site that they had used in the morning on 591 days (50.5%). Of those sites, 441 (74.6%) were tree holes and another 130 (22.0%) were bamboo.

In the morning, the monkeys left the sleeping site an average of 9.7 ± 0.4 minutes after sunrise (range of group averages: 6.8 to 14.4 min) and entered their sites in the evening an average of 81.6 ± 0.7 minutes before sunset (range of group averages: 91.1 to 73.4 min).

Comparison of tree-supported sleeping sites

Of the 1530 unique sleeping sites, 1349 were tree-supported sites including tree holes, bromeliads, vine tangles, nests constructed by other animals (i.e., bird nests and leaf nests), and tree branches and forks. Several observations were excluded from the analyses because of missing measurements of tree height (9), DBH (130) and height of sleeping site entrance (23). There were no differences among types of tree-supported sleeping sites in the height of the trees that supported them [$F(4, 1326) = 2.46, P = 0.0438$]. We found a significant difference between sleeping site

types in tree DBH [$F(4, 1205) = 32.31, P < 0.0001$, Figure 2]. Both tree hole (46.2 ± 0.9 cm) and bromeliad sites (47.1 ± 1.8 cm) had significantly larger DBH than did either vine tangle (32.1 ± 1.1 cm) or leaf or bird nest sites (27.6 ± 3.3 cm). Tree branch or fork sites (40.9 ± 5.1 cm) had an intermediate DBH and did not differ significantly from any of the other types. We found a significant difference among site types for height of entrance [$F(4, 1312) = 71.94, P < 0.0001$, Figure 3]. The height of tree hole entrances (6.5 ± 0.1 m) was significantly lower than that for bromeliads (8.9 ± 0.3 m), vine tangles (9.9 ± 0.2 m), tree branches or forks (9.4 ± 0.7 m), and leaf or bird nests (9.5 ± 0.5 m). No other types were significantly different from one another.

Infrequently vs. Frequently Used Sleeping Sites

On a macro-level there was no association between frequency of use of tree holes (frequently used vs. infrequently used) and either topography (hillside vs. lowland, not significant for any group, ($Q_{CMH} = 0.44, P = 0.51$) or habitat (mature vs. secondary forest, not significant for any group, ($Q_{CMH} = 0.03, P = 0.87$)). However, frequently used tree holes differed from infrequently used tree holes in the measured tree characteristics ($\chi^2_{11} = 35.73, P < 0.002$). Frequently used tree holes were more likely to be found in living trees ($\chi^2 = 11.50, P = 0.0007$). Of the 81 frequently used tree holes, 5 were located in dead trees, whereas 133 of the 555 infrequently used tree holes were in dead trees. Live trees were 6.8 times more likely to be used frequently than were dead trees. The height of entrance to tree holes was lower for frequently used sites (5.7 ± 0.2 m) than infrequently used sites (6.7 ± 0.3 ; $\chi^2 = 5.81, P = 0.02$). A

model including both living status and height of tree hole entrance correctly classified 68.2% of golden lion tamarin tree holes.

Random vs. Frequently Used Sleeping Sites

For the year 2003 we identified 22 frequently used sleeping sites: 19 tree holes and 3 bamboo stands. Trees and bamboo stands are incomparable on the measured characteristics; therefore the bamboo sites were excluded from the analyses. This also eliminated one tamarin group because its frequently used sites consisted solely of two bamboo sites, leaving six groups in the analyses.

On the macro-level we found no relationship between random vs. sleeping sites for mature vs. secondary forest (not significant for any group, overall trend $Q_{CMH} = 0.218, P = 0.64$). We found a significant relationship between the topography of the site (lowland vs. hillside) and whether the site was random or used for sleeping ($Q_{CMH} = 25.29, P < 0.0001$). For five of the six groups, sleeping sites were found more often in hillside forest than were random sites. Seventeen of the 19 sleeping sites were on hillside, whereas 6 of the 30 random sites were located on hillside.

The overall model for micro-level characteristics was significant ($\chi^2 = 42.02, P < 0.001$) with both distance to the nearest tree of at least 21 cm DBH and percent canopy cover included in the model. Sleeping sites were significantly closer to trees of at least 21 cm DBH (5.6 ± 0.5 m) than were random sites (8.9 ± 0.3 m; $\chi^2 = 6.30, P = 0.01$). Sleeping sites were also found in areas with a lower percent canopy cover (74.9 ± 1.0 %) than were random sites (81.3 ± 0.5 %; $\chi^2 = 6.71, P = 0.01$). The model correctly classified 94.7 % of observations.

For tree characteristics, the overall model was significant ($\chi^2_6 = 37.42$, $P < 0.001$) with only DBH included. Sleeping trees (47.3 ± 5.3 m) have a larger DBH than randomly selected trees (24.9 ± 0.5 m; $\chi^2 = 7.16$, $P = 0.007$). The model correctly classified 91.9% of all observations.

Discussion

Golden lion tamarins used a variety of sleeping sites, including tree holes, bamboo, vine tangles, and bromeliads. Groups varied in the frequency with which they used tree holes, with all but one group using tree holes on a majority of the nights observed. Tree holes are clearly an important resource for this population of golden lion tamarins. Approximately 64% of all sleeping site records were for tree holes, accounting for roughly 85% of sleeping sites that were used more than 8 times by any group. There are several possible explanations for frequent re-use of a particular type of sleeping site. One of the most prominent reasons is protection from predators. Hamilton (1982) noted that baboons living in the vicinity of a high density of predators opted to return to cliffs to sleep while those in areas of lower predator risk slept in trees. Although speculative, golden lion tamarin repeated use of tree holes is consistent with this function. Franklin *et al.* (2007a) hypothesized that golden lion tamarin use of a few sleeping sites coupled with an increased rate of scent marking prior to retirement and an increased speed of travel during this period may be the best strategy for minimizing predation risk. This behavior facilitates a rapid return to the sleeping site when crepuscular predators are active while ensuring that golden lion tamarins are safe within a sleeping site before nocturnal predators are present. The trade off between the re-use of “safe” sites and switching between sleeping sites

to deter predator knowledge of re-use has been noted in many studies (Boinski et al. 2000; Day and Elwood 1999).

While golden lion tamarins at Poço das Antas spend the majority of their nights in tree holes, these do not represent as large a portion of the sleeping sites as predicted based on previous research on this genus (Coimbra-Filho 1978; Kierulff et al. 2002; Raboy et al. 2004; Valladares-Padua and Prado 1996). In Poço das Antas, bamboo, vine tangles, and bromeliads accounted for an additional 32% of all sleeping site records with bamboo comprising almost 12% of frequently used sites. Given the degraded nature of the forest at Poço das Antas and the prevalence of bamboo planted as cattle fence in the previous century, bamboo may serve as an adaptive alternative sleeping site choice for golden lion tamarins. Mamede-Costa and Gobbi (1998) found that black lion tamarins in Morro do Diabolo State Park in southern Brazil use vine tangles almost exclusively, probably because tree holes were unavailable.

Alternatively, it could be that golden lion tamarins are opting to use this introduced species (bamboo) for sleeping sites because it is superior to tree holes in several of the important categories discussed in the introduction, most notably protection from predators. However, our anecdotal observations of two golden lion tamarin groups falling prey at bamboo sleeping sites decreases our belief that bamboo provides better protection from predators than a tree cavity in a large/healthy tree with a small entrance.

Tree-supported sleeping sites differed in expected ways. Those that had tree cavities or supported bromeliads large enough for the tamarins to sleep in had greater DBH than did the other tree-supported sites. The entrances to tree holes were

significantly lower than the entrances to other site types. These findings are not surprising given that most sites other than tree holes and bromeliads were located in the branches while most tree holes were in the tree trunk. Similarly, frequently used tree holes were more likely to have lower entrances than infrequently used holes. We speculate that the roughly 1 meter difference between the entrance heights of frequently used and infrequently used tree holes relates to depth of the tree cavity usable by tamarins. Lower tree holes probably have deeper usable cavities while higher tree holes have smaller mid-trunk holes. Our anecdotal observations support the idea that frequently used tree cavities are formed through ground-up decay to the central pith of pioneering, fast-growing tree species, but we have no systematic data to confirm this.

Frequently used tree holes were more likely to be found in living trees than infrequently used holes. Further, the DBH of sleeping sites was greater than the DBH of random sites. Both of these factors are consistent with preferences for sites that provide improved protection from the elements. Schmid (1998) found that insulation was best in living trees and gray mouse lemurs used these sites more often than dead trees. Live trees may also aid in protection from terrestrial predators by providing structural integrity that increases the difficulty of excavation. On several occasions during the last decade, predators in Poço das Antas extracted lion tamarins from their sleeping site at night by digging away rotted wood (see Franklin *et al.*, 2007a, 2007b, for a more complete description). The living tissue of the tree may prevent or deter this type of attack, as may the larger DBH of the tree. In addition, live trees may

remain warmer and drier or have fewer insects within them, and may decrease contact with insects carrying diseases, such as malaria (see Anderson 2000).

One might also speculate that sleeping in live trees is preferable to dead trees because live trees would provide more coverage and concealment from predators. Peetz *et al.* (1992) found that howler monkeys sleeping in defoliated trees were more prone to jaguar predation. Likewise, the height of the tree and the degree of concealment of the location are two main factors predicted to protect occupants of a sleeping site from predators (Anderson 2000; Caine *et al.* 1992). However, our data showed that sleeping sites, in comparison to random sites, were more likely to have a lower percent of canopy cover. It's possible that less cover is preferable in some situations in that it allows early detection of predators (Treves 2002). Despite having lower canopy cover, golden lion tamarin sleeping sites were closer to other large trees than random sites. The close proximity of other large trees may provide useable escape routes via connectivity between trees and is also consistent with golden lion tamarin frequent re-use of sites in that re-use may facilitate an intimate knowledge of escape routes (Strushaker 1967). This is in keeping with other findings of callitrichid sleeping site choice (Caine *et al.* 1992; Day and Elwood 1999). See Lima *et al.* (2005) for discussion of the trade off between sleeping site location and sleep quality.

A large number of tree holes were used only once or, at most, a few times. This information combined with the fact that tamarins did not choose to sleep only in mature forest indicates that sleeping site choice is not driven by a lack of tree holes as was suggested by Coimbra-Filho (1978) and Dietz *et al.* (1997). However, it is possible that aspects of the tree holes the tamarins used only once or a few times were

inferior to the ones used many times, most notably that tree holes in dead trees were less favorable. The use of tree holes found in small clusters of large trees on hillsides suggests that these patches are relics of older forest embedded in a matrix of younger secondary forest in early and mid stages of re-growth. Thus lion tamarins may be choosing larger and older trees, but these patches of mature forest are not identified as such with the use of satellite imagery because they occur at a finer scale, only a handful of large trees surrounded by secondary forest.

In summary, macro-level habitat characteristics (mature vs. secondary forest), are not as useful in predicting lion tamarin sleeping site locations as are the topography of the area and micro-level and tree characteristics. There are ample tree holes available to the tamarins but few sites to which the tamarins return repeatedly. The lion tamarins find these preferred sites wherever they occur including in mature forest and in relics of older forest embedded in a matrix of secondary forest.

Acknowledgements

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Tables

Table 1. The frequency of use of each sleeping site type and the number of sleeping sites used more than 8 times by type.

Sleeping Site Type	Number of Sites	Number of Times Used	Percentage of Time Used (range of group percent use)	Number of sites of each type used more than 8 times	Percentage of more than 8 uses
Tree Hole	645	3330	63.6 (26.2 – 91.0)	81	85.3
Bamboo	78	916	17.5 (0 – 53.7)	11	11.6
Vine Tangle	443	503	9.6 (6.0 – 18.2)	0	0
Bromeliad	194	247	4.7 (0 – 26.2)	0	0
Palm	36	96	1.8 (0 – 4.2)	3	3.1
Leaf or Bird Nest	46	53	1.0 (0 – 4.3)	0	0
Tree Branch or Fork	21	21	0.4 (0 – 1.0)	0	0
Other and Unknown	67	69	1.3 (0 – 2.6)	0	0

Table 2. The frequency of use of each tree family for tree holes.

Tree Family	Number of Times Used	Percent of Use
Bignoniaceae	779	23.4
Moraceae	313	9.4
Anacardiaceae	196	5.9
Lauraceae	189	5.7
Leguminosae	155	4.7
Guttiferae	110	3.3
Palmae	42	1.3
Melastomataceae	39	1.2
Apocynaceae	31	0.9
Meliaceae	31	0.9
Annonaceae	7	0.2
Sapotaceae	7	0.2
Bombacaceae	5	0.2
Lecythidaceae	5	0.2
Urticaceae	4	0.1
Unidentified	1417	42.6

Figure Legends

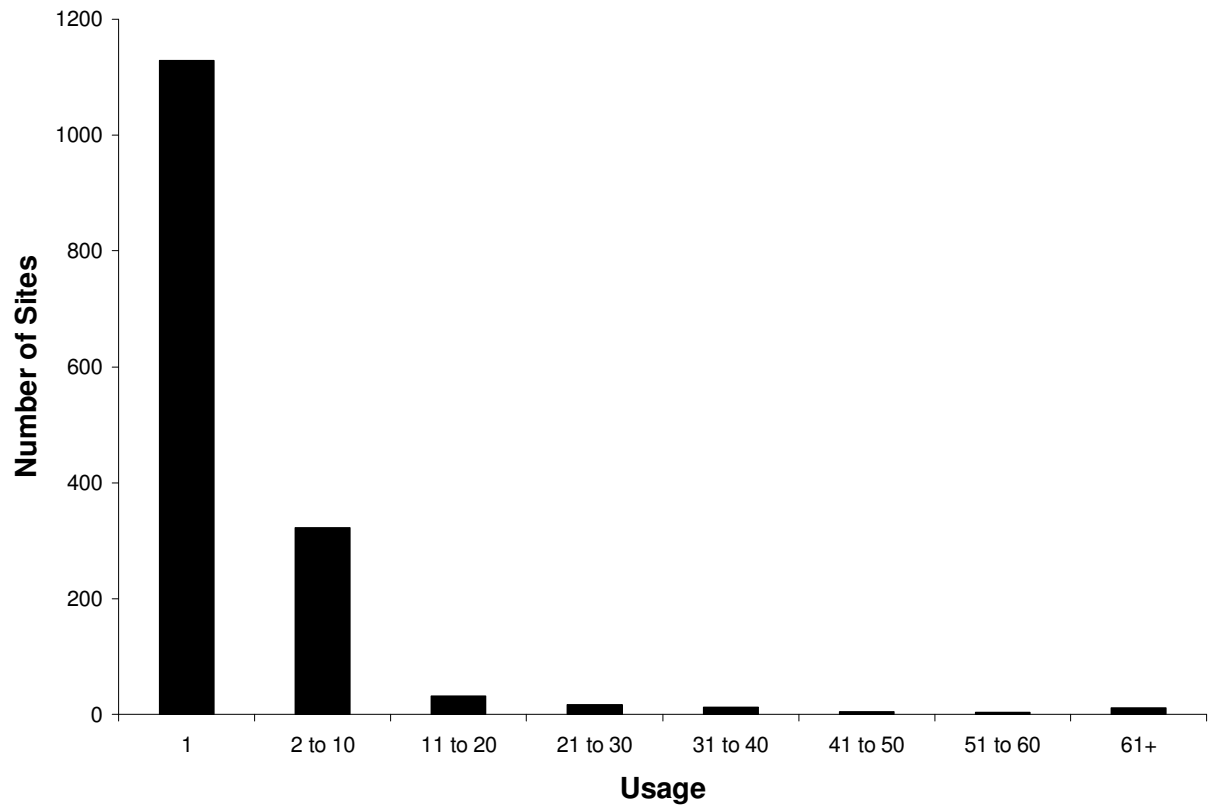
Figure 1. The frequency of use of unique sleeping sites.

Figure 2. DBH (in cm) \pm SE for all tree-supported sleeping sites.

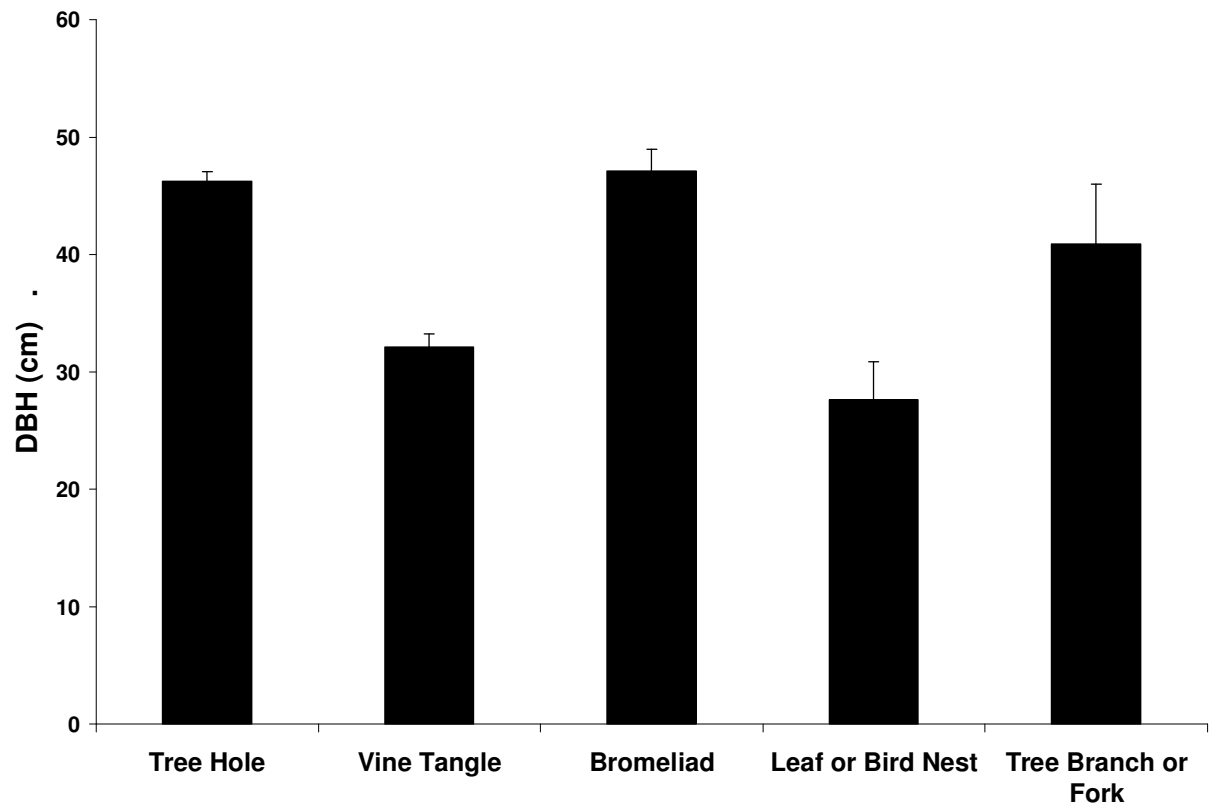
Figure 3. Sleeping site entrance height (m) \pm SE for all tree-supported sleeping sites.

Figures

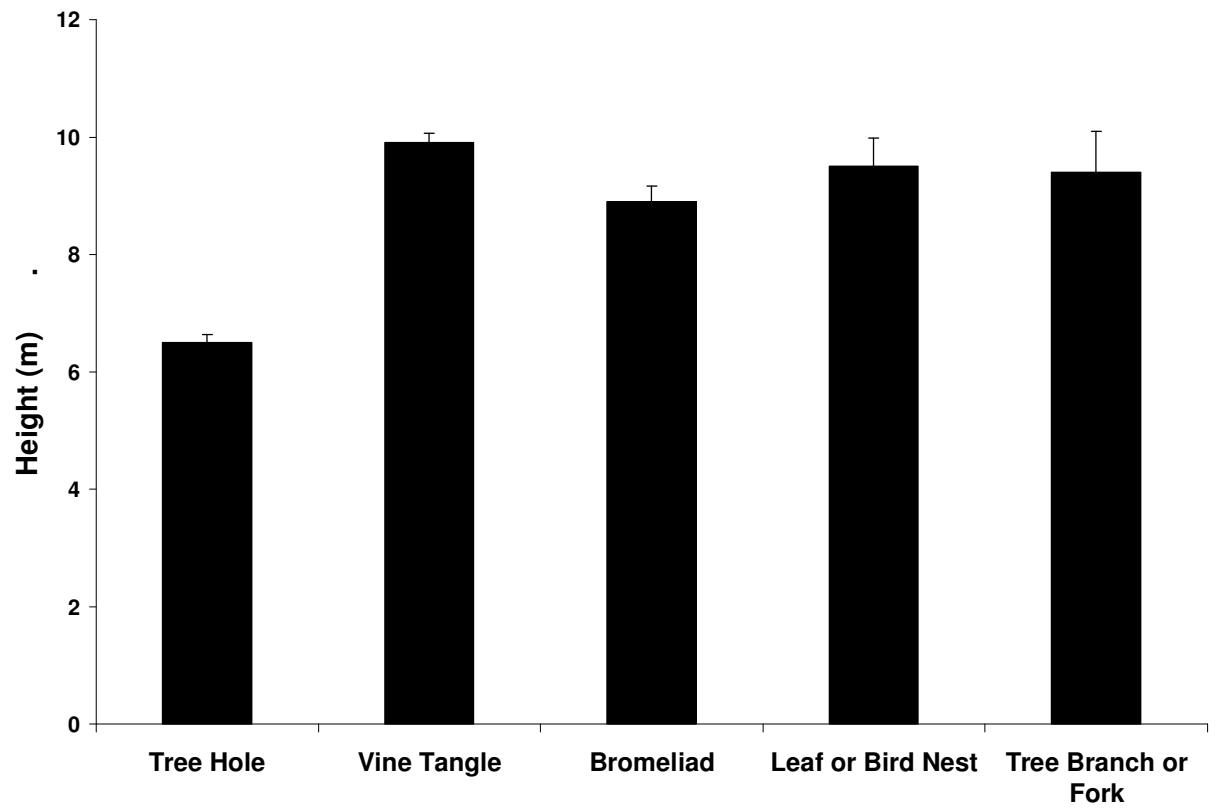
(Figure 1)



(Figure 2)



(Figure 3)



Chapter 2: Comparison of Home Range Calculation Methods: Golden Lion Tamarins as a Case Study

Abstract

Home range size can be affected by many abiotic, habitat, and social factors, but estimates can also be influenced by sample size and choice of analytical methods. To illustrate the effects of these factors on home range size, we analyze data collected on 15 groups of golden lion tamarins, *Leontopithecus rosalia*, over a 19-year study period using three common home range calculation techniques: minimum convex polygon (MCP), grid cell methods, and kernel density estimators. MCP produced significantly larger, and the grid-cell method produced significantly smaller home ranges than kernel methods when all data were used. There was no difference between h_{LSCV} and h_{REF} bandwidth selection methods. Home range estimates using statistically independent observations were larger than those produced using all available data. When using statistically independent data, grid cell methods produced a significantly smaller home range size than either kernel or MCP, which were not significantly different. We preferred the fixed kernel method for golden lion tamarin home ranges due to its ability to generate probability of use and produce graphic shapes reflecting the spatial distribution of the observations. For the majority of study groups, observations were statistically independent when separated by approximately 3 hours. However, there is a trade-off between statistical independence and sample size, which may prohibit home range estimation using independent points in many studies. Home ranges for golden lion tamarin groups fell between 17.4 and 118.2 ha, with an average home range size of 49.2 ha. Despite significant within-group variation, we found no overall seasonal or temporal trends within yearly group home range sizes. Home range sizes did fluctuate across years for groups, and the

population as a whole. Using a dataset sampled over a very long time frame may mask ranging responses to fluctuating factors like population density, predation pressure, and rainfall and overestimate range size due to shift in geographic location over time. Based on our calculations of variation within the population, 8 groups are required for an adequate measure of population average home range size for a given year.

Introduction

A home range is defined as the area occupied by an animal or animal group during a given time period (Burt 1943; Kernohan et al. 2001) and differs from a territory, which is actively defended against conspecifics (Burt 1943). The shape and size of an animal's home range may reflect selection pressures (Schoener 1981) and are influenced by abiotic, habitat, and social factors including season (Burt 1943), group biomass (Milton and May 1976; Dietz et al. 1997; Kelt and Van Vuren 2001), resource distribution (Law and Dickman 1998; Kelt and Van Vuren 2001; Raboy and Dietz 2004; Mitchell and Powell 2007), habitat composition (Kierulff et al. 2002), and energetic requirements (McNab 1963; Mace et al. 1983). Comparison of home ranges between and within species may help clarify the basis of observed population and community-level differences (Schoener 1981). In addition to the adaptive significance of home range differences, home range calculations provide an estimate of spatial requirements for a population or species, which is important for planning conservation management activities (Singleton and van Schaik 2001).

In this paper, we provide guidance to field biologists in selecting the home range method appropriate to their objectives and in designing a data collection scheme that meets the needs of those goals. While many methods have been used to calculate home range, the three most common are minimum convex polygon, quadrat or grid cells, and kernel density estimators (Kernohan et al. 2001). Minimum convex polygons (MCPs) connect the outermost points of a set of observations (Mohr 1947). The three main drawbacks of using MCPs are that they tend to include area not traversed by the study organism, the final home range size and shape is strongly

dependent on outlying points, and this method provides little information on the internal configuration of the home range (Harris et al. 1990). Grid cell methods involve overlaying a grid on a plot of the observational data set (Siniff and Tester 1965; White and Garrott 1990). Typically, only grid cells that contain observation locations are included in the home range estimate, though some adaptations are possible (see White and Garrott 1990). While grid cell methods are not as accurate as contour methods (Kernohan et al. 2001), they do provide a description of the extent of ranging and a simple measure of intensity of use by counting the number of observation points in each cell (White and Garrott 1990). However, the size of the grid cell can have a large impact on home range estimates (White and Garrott 1990). Kernel methods, or utilization distributions, estimate the probability of use across the ranging area (van Winkle 1975). Through an examination of the distribution of data points, kernel methods create a home range plot corresponding to a specific probability of use. For example, a 95% kernel home range represents the area in which the study organism's probability of occurrence at any point in time is 95%. One benefit of the kernel method is the ability to estimate the probability of use at any point in the home range of the organism (Marzluff et al. 2001; Marzluff et al. 2004), a technique that facilitates examination of habitat selection (see volume 70 of the *Journal of Wildlife Management* for a review and future research directions, 2006).

There are two main methods of calculating home range areas using kernel distributions: fixed and adaptive distributions. The distinction between these two is related to how they deal with bandwidth, h . Bandwidth determines the influence of neighboring points on the calculated probability of use at a focal point (Silverman

1986). As bandwidth increases, so does the neighborhood (distance from the focal point) used to calculate probability (Seaman and Powell 1996). Bandwidth choice strongly affects kernel performance (Silverman 1986; Seaman et al. 1999; Kernohan et al. 2001). Very large values of h produce large home ranges with little internal detail (Silverman 1986; Worton 1989), while small h values provide more internal structure but can result in a home range comprising many disconnected polygons (Hemson et al. 2005; Gitzen et al. 2006). The three main options for bandwidth selection are reference (h_{REF}), least squares cross-validation (h_{LSCV}), and plug-in or solve-the-equation methods. H_{REF} assumes the data follow a bivariate normal distribution. When the true distribution of points is multimodal, h_{REF} tends to overestimate home range size (Seaman et al. 1999) by oversmoothing across multiple peaks (Silverman 1986). H_{LSCV} creates a distribution that attempts to mimic the true, but unknown, probability function by minimizing the estimated error between the calculated and true surfaces (Silverman 1986; Hemson et al. 2005; Buskirk and Millspaugh 2006). H_{LSCV} can occasionally produce inconsistent results or a set of disconnected polygons (Sain et al. 1994; Blundell et al. 2001; Kernohan et al. 2001), but outperforms h_{REF} for more complex density distributions (Kernohan et al. 2001; Gitzen and Millspaugh 2003). Recent plug-in and solve-the equation methods for determining h have shown decreased sampling variability (Gitzen et al. 2006; Jones et al. 1996; Wand and Jones 1995; see Loader 1999 for contrasting results). Unfortunately, these methods currently are not available in the most popular home range calculation software packages. While there is no consensus on the best bandwidth selection method, h_{LSCV} is a common choice for home range studies

(Millsbaugh et al. 2006). When comparing kernel methods, Seaman et al. (1999) found that fixed kernel estimates employing h_{LSCV} produced the smallest number of weak matches to the original distribution.

A fixed kernel uses a single bandwidth calculation across the entire observation area to determine the neighborhood of influential observations. An adaptive kernel allows selection of different bandwidths at each observation point (Kernohan et al. 2001). The fixed kernel method is commonly preferred to the adaptive kernel method (Millsbaugh et al. 2006) due to its lower level of bias (Kernohan et al. 2001) and its increased accuracy and precision (Worton 1995; Seaman and Powell 1996; Seaman et al. 1999).

Apart from bandwidth, two additional factors need to be considered when using a kernel calculation method: sample size and independence of data points. While both bandwidth selection method and sample size contribute to kernel performance, sample size may play a larger role (Gitzen and Millsbaugh 2003). An increase in sample size results in a decrease in variability of calculated home range size when examined over randomized subsets of data (Arthur and Schwartz 1999). Several studies have looked at the minimum sample size necessary to calculate a kernel density estimate. Arthur and Schwartz (1999) found that kernel estimates require a minimum sample size of 80 observation points for high accuracy and precision. Seaman et al. (1999) found that a minimum of 30-50 independent observations are necessary when using h_{LSCV} . Girard et al. (2002) reported a minimum of 100-300 observations to estimate ranging for a year, and 30-100 for a season. However, performance of kernel estimations using h_{LSCV} increases with

sample size, up to a threshold which typically peaks around 90-100 independent observations (Seaman et al. 1999). Because of the strong effect sample size can have on home range estimates, it is important for authors to report sample size in order to facilitate comparison across studies (Seaman et al. 1999).

Recommended sample size estimates assume the use of independent observations (Millspaugh et al. 2006). Kernel methods have been shown to produce more accurate results when using independent observations (Harris et al. 1990), with both study duration and sampling intensity impacting the degree of autocorrelation in a given observational dataset (Fieberg 2007a). However, there is ongoing debate in the literature as to whether observation points should be statistically or biologically independent (see Barg et al. 2005; Kernohan et al. 2001; McNay et al. 1994; Swihart and Slade 1997). Data points are considered independent when the location at one time is not a function of the location at the next sample time (Schoener 1981; Swihart and Slade 1985). The main difference between biological and statistical independence is the method of choosing the distance and, therefore, time period required before consecutive points are considered independent. Schoener's ratio is the most frequently used method to calculate statistical independence (Kernohan et al. 2001). This method uses travel speed and distance from the geometric center of observations to estimate the time interval between independent observations (Swihart and Slade 1985, 1986, 1997). In practice, several studies have reported difficulty in reaching statistical independence in their samples using this method (McNay et al. 1994; Hansteen et al. 1997), with the behavior of the study animal possibly interfering with the ability to achieve independence (McNay et al. 1994). For example, researchers

studying migrating animals often have difficulty achieving a statistically independent dataset (see review in Kernohan et al. 2001). Another difficulty is that the act of paring down a dataset to only independent observations reduces sample size and, if this reduction is severe, can cause an underestimation of home range (Rooney et al. 1998; Kernohan et al. 2001). This reduction may also change the shape of the home range into something not accurately reflecting the biology of the organism (Barg et al. 2005). As a result, some authors suggest that it may be more important to focus on systematic or random sampling rather than on trying to collect sufficient independent points (McNay et al. 1994; Fieberg 2007a). Both systematic and random samples are considered representative of an animal's space use (Fieberg 2007b). Methods for identifying biologically independent data include sampling at intervals long enough to allow an animal to have moved to any point in its home range (Lair 1987). A similar interpretation of biological independence is that the study organism has had sufficient time to cross its entire home range between consecutive observations (Barg et al. 2005).

As a case study of the impact of home range analytical methods on home range estimates, we examine 19 years of spatial movement data collected on 15 groups of wild golden lion tamarins in Poço das Antas Reserve, Brazil. Previous estimates of home range size for golden lion tamarin groups in this reserve range between 21.3 and 73 ha, with an average of 45.2 ha, calculated using a modified grid cell approach (Dietz et al. 1997). Two groups of golden lion tamarins in the nearby União Reserve have home ranges of 73 and 96 ha, estimated using MCP (Lapenta et al. 2007). Congeners have been reported to occupy larger home ranges: golden-

headed lion tamarins (*L. chrysomelas*) average 123 ha, using a fixed kernel with h_{LSCV} (Raboy and Dietz 2004); black lion tamarin (*L. chrysopygus*) home ranges are estimated at between 64 and 276 ha, using the grid cell method and MCP (Valladares-Padua and Cullen 1994; Albernaz 1997; Passos 1998); and black-faced lion tamarins (*L. caissara*) have home ranges estimated at 250 ha, using an unreported calculation method (IPE 2007). The wide range of home range estimates documented across the genus may represent biological differences at the species or population level; however, it is difficult or impossible to compare these results as they used different calculation methods, sampling intervals, and sample sizes.

We use long-term data from our study population to: 1) compare home range sizes calculated using MCP, grid cell, and kernel estimates, 2) examine the impact of statistically independent and biologically independent data points on final home range size, 3) determine the effect of using h_{LSCV} versus h_{REF} on home range size and numbers of disconnected polygons, 4) explore the impact of time of day and seasonality on home range estimates, and 5) give recommendations for study duration and the number of groups or individuals required to give an adequate picture of ranging for a population.

Methods

Study Site and Data Collection

We collected data on movements of golden lion tamarins in Poço das Antas Biological Reserve (22°30-33'S, 42°15-19'W), Rio de Janeiro State, Brazil from January 1987 through January 2006. The reserve is a 6300 ha Atlantic Coastal rainforest remnant, containing a mosaic of mature, secondary and swamp forests and

grasslands (Dietz and Baker 1993; Dietz et al. 1997). The topography of the reserve ranges from 20 to 200 meters above sea level with seasonal precipitation (Dietz et al. 1997). The population of golden lion tamarins in the reserve comprises approximately 230 individuals (Rylands et al. 2002). Golden lion tamarins in this population are trapped and marked semiannually. All groups are habituated to the presence of human observers and contain at least one radio-collared individual. While the number of study groups monitored changed over time, within any one year we followed at least eight focal groups of lion tamarins, recording demographic and spatial information for an additional 5-7 groups. Once or twice a week, focal groups were followed from when they exited a sleeping site in the morning until they entered a sleeping site in the evening. Group locations were recorded at 20 min intervals throughout the day, using maps and GPS. Additional spatial data came from weekly surveys of demography and locations of all known groups in the study area, including the ~8 focal groups.

Home Range Calculation Methods

In this study, home range sizes were calculated using minimum convex polygons, grid cell counts, and fixed kernel density estimates for each group for each year (June-May). Years were classified as June-May to correspond with the mating seasons documented for this species (Dietz et al. 1994). A total of 144 home ranges (# groups x years studied/group) were calculated with each of the three methods. The shortest number of years of study for a group was 4, with the longest studied for 19 years. All home ranges were generated using the Animal Movement Analysis Extension (Hooge and Eichenlaub 1997) in ArcView 3.2 (Environmental Systems

Research Institute, Inc., Redlands, USA). We chose this software as it is frequently used by field researchers and the home range calculation extension has been well documented (see Hooge and Eichenlaub 1997). For the grid cell approach, we calculated 50 m² cells and included only grid cells which contained observations, instead of the “straight line method”, which also includes unoccupied cells located between consecutive observations (White and Garrott 1990). We used the 100% MCP option, which is the default in the Animal Movement Analysis Extension. In the kernel analysis, we calculated a 95% fixed-kernel estimate for total home range and 50% for estimating core areas. The Animal Movement Analysis Extension allows for choice of % probability of use at 5% intervals between 5-95%. We compared the three methods of home range calculation twice, once using all data and again using only statistically independent data.

Bandwidth Selection

We calculated both 95% and 50% fixed kernels using both h_{LSCV} and h_{REF} bandwidth selection options. H_{LSCV} may fail due to closely clustered points (Hemson et al. 2005) or repeated use of the same location (Silverman 1986). In ArcView, a failure of h_{LSCV} causes the program to revert to h_{REF} . Hemson et al. (2005) reported a high failure rate for h_{LSCV} , especially with larger sample sizes. There were no instances of h_{LSCV} failure in any of our datasets, though some calculated home ranges contained many disconnected polygons.

Data Independence

To estimate the interval between statistically independent points, we calculated Schoener’s ratio for all groups for each year of observation (group/year).

Schoener's ratio is t^2/r^2 , where t is the average distance between successive observations and r is the average distance between observations and the geometric center of the range (Schoener 1981; Swihart and Slade 1985). Swihart and Slade (1985) determined that data points were independent when $t^2/r^2 = 2$. We calculated t^2/r^2 at increasing intervals between points until independence was reached, i.e. Schoener's ratio = 2. As consecutive days of observation were not available for all groups, we calculated Schoener's ratio looking within full days of observation. Thus a failure to find statistical independence across the whole group/year dataset indicates only that observations need to be separated by more than a day in order to be statistically independent, rather than a lack of independence across the entire sample.

We compared the time required to reach statistical independence (using Schoener's ratio) with time to our measure of biological independence. In order to be biologically independent, time between observations must be sufficient to allow study animals to travel from one point in their home range to any other point (Lair 1987). For this measure, we replaced the distance method in Schoener's ratio with the average distance between all points in the sample. We randomly shuffled the points in each group/year dataset 1000 times and calculated the average distance between pairs of points. We substituted the resulting number for the variable r in Schoener's formula. The remainder of the measure was calculated following the procedure stated for Schoener's ratio. To the best of our knowledge, the method we used for calculating biological independence is novel; though other options are also available (see Lair 1987; Barg et al. 2005).

Disconnected Polygons

To test whether h_{LSCV} produced a greater number of disconnected polygons than h_{REF} , we counted the number of polygons produced by each method in both 95% and 50% probability areas. We also counted disconnected polygons in home ranges using all, biologically independent, and statistically independent data.

Seasonal and Time of Day Comparisons

To compare the effect of seasonality on home range size, we divided each group/year into wet and dry seasons. Statistically independent points were used for this analysis. We classified each month in a dataset as occurring during the wet or dry season by comparing the total rainfall during that month with the average monthly rainfall for that dataset. If the difference between these two figures fell outside a two-standard-error confidence interval, the month was classified as being dry (negative) or wet (positive). Months that did not exceed the two standard error threshold in either direction were classified according to the months surrounding them. For example, if October did not fall outside the confidence interval but both September and November were classified as wet, October was also classified as wet. Study year 2005-2006 was excluded from seasonal analyses as observations did not span the entire year.

We used four sources of rainfall data for our analyses. Daily precipitation totals were collected at our field station from June 1987 to May 1991 and June 1993 through May 2001 by L. Olivera (unpublished data), from January 1998 through May 1999 (Miller and Dietz 2005), and from 2005 to 2008 (J. M. Dietz unpublished data). To verify the information collected and to fill in any gaps that exist in our climate

data, we also used a gridded precipitation dataset created by Silva et al. (2007). V.B.S. Silva provided estimated rainfall data for the grid cell closest to our field site, using 22.5S, 42.3W as the target location. We compared these data to the data collected at our field site and found approximately 90% agreement on month classifications. Since the gridded data tend to underestimate the number of dry days (Silva et al. 2007), we used the information collected at our field site in instances where the datasets produced conflicting results.

In order to examine the impact of time of day on home range estimates, we categorized each day into 4 time periods: onset of activity-8AM, 8AM-11AM, 11AM-2PM, and 2PM-cessation of activity. We used all observations for each group/year to maximize the number of datasets available for this analysis. All calculations were done using fixed kernel with the h_{LSCV} bandwidth option. To determine whether it is necessary to include an equal number of observations for each time period, we also compared home range calculations using time-balanced and unbalanced data for each group/year. Time-balanced datasets consisted of an equal number of randomly-selected points for each time period. We calculated home ranges using fixed kernel with h_{LSCV} for both time analyses and for the seasonal comparison. Following the recommendations of Girard et al. (2002) and Seaman et al. (1999), home ranges were calculated only for group/year datasets containing at least 100 observations.

Population and Group Estimation

We used the variance in home range size in this study to determine the minimum number of years of observation necessary to estimate a group's home range

size, and the number of groups necessary to estimate the average home range size for a population. We used the following derivation of a confidence interval calculation (Sokal and Rohlf 1995) in order to calculate sample size necessary to detect significant differences:

$$n \geq \frac{t_{\alpha,(df)}^2 * \sigma^2}{L^2}$$

where $t_{\alpha,(df)}$ is the two-tailed t value for a given α and degrees of freedom (df), σ is the standard deviation, and L is one half the length of the desired confidence interval. The method is iterative until the df for the t value matches the resulting n value. We calculated n for $\alpha=0.05$ and $\alpha=0.1$ using two estimates of σ : standard deviation for all home range calculations and the average standard deviation for groups across study years. We used confidence interval lengths of 10 ha (L=5) and 5 ha (L=2.5), representing 10 and 20% of the average home range size, respectively. Variance estimates were taken from kernel home ranges calculated using the h_{LSCV} bandwidth option.

Given the likely variability of home range estimates and the narrow confidence intervals desired, some field studies may not produce a sample size adequate to reach the calculated n value. Therefore, we also used an alternative, and novel, approach to determine the number of groups required to obtain an estimate of average home range size at the population level. We randomly resampled (with replacement) 1 home range value from each group. For each sample drawn we calculated the mean for a random selection of 2, 3, 4, ..., 14 groups. This process was

repeated 1000 times. We then calculated the standard deviation of home range averages for each of these numbers of included groups. Using the formula given above, we calculated the n for each group, repeating the analysis until the resulting n matched the number of groups used to calculate the mean. We used a similar method to calculate the number of years of data required to estimate a group's home range size. For each group we randomly selected 2-19 years and calculated an average group home range size, repeating this process 1000 times. We then took the standard deviation of these averages and used the formula given above to calculate n. We repeated the analysis until the number of years used in the estimate of standard deviation matched the resulting n value.

In addition to understanding the amount of data required to adequately estimate mean ranging, both at the population and group level, it is also important to understand the impact of changes in home range position over time. Using the final kernel home range measurements, we calculated the percent overlap between one group/year and the subsequent year using the following formula:

$$\% \text{ Inter-Year Overlap} = \frac{\text{Area of Overlap between Years 1 and 2}}{\text{Total Area of Year 1}}$$

From these overlap percentages, we calculated an average inter-year overlap for each group and an average inter-year overlap across groups.

Statistical Analyses

We compared methods of home range calculation, impact of time of day, and seasonality using one-way analyses of variance (ANOVA). Bandwidth selection and

independence of data were analyzed using a 2x3 analysis of variance. For all analyses, group was included as a subject variable and, where appropriate, year and the number of data points were incorporated as random covariates. For all analyses we used an alpha level of 0.05. We used Tukey's tests for multiple comparisons to control for experiment-wise error.

The statistical assumption of normality was met for the tests of home range calculation method; however, variance differences exceeded acceptable limits. In order to control for heterogeneity of variance, we included the home range calculation method as a variance group in the final model, allowing a separate measure of variance for each method. The assumptions of homogeneity of variance and normality were met for the test of time-balanced versus unbalanced data and for all two-way ANOVAs comparing independence and bandwidth selection methods: 95% kernel home range size, 50% kernel core area size, number of disconnected polygons in the 95% kernel, and number of disconnected polygons in the 50% kernel. The statistical assumption of homogeneity of variance was met for the seasonality and time of day analyses, but data were log transformed to meet the assumption of normality for both the 95% and 50% kernel methods.

Results

Independence of Observations

For most groups, statistical independence between successive data points was achieved when points were separated by ten 20-minute steps, or 200 min. However, for a few groups, the intervals between data points never achieved statistical or biological independence. Since groups were not always observed on consecutive

days, independence had to be reached during one day of data collection, typically 10-14 hours.

The time interval between observations required for independence using Schoener's ratio was significantly correlated with the time required to reach biological independence ($R= 0.82$, $P<0.0001$). With the exception of a few groups, the biologically independent time interval was smaller than that of its corresponding statistically independent interval. Average times to independence based on categorical group travel speeds and estimated home range sizes are given in Table 1. Travel speeds and home range sizes were categorized according to the mean \pm 1 SD. For example, small home ranges were those that fell below 1 SD of the home range size mean.

Home Range Methods

When using all data, there was a significant difference in home range size among the three calculation methods [Fig. 1a; $F(2, 21.9)=24.3$, $P<0.0001$]. MCP (71.1 ± 2.38 ha) produced larger home ranges than either kernel (49.1 ± 1.37 ha; $t=4.48$, $P=0.005$) or the grid cell method (41.1 ± 1.1 ha; $t=7.02$, $P<0.0001$). Home range size using kernel methods was significantly larger than grid cell methods ($t=2.23$, $P=0.037$).

Using only statistically independent data, there was a significant difference in home range size for the three methods [e.g. Fig. 1a; $F(2, 17.2)=177.46$, $P<0.0001$]. The grid cell method (18.5 ± 0.52 ha) produced significantly smaller home ranges than either kernel (54.4 ± 1.61 ha; $t=11.84$, $P<0.0001$) or MCP methods (56.8 ± 2.12 ha; $t=15.6$, $P<0.0001$). There was no significant difference between MCP and kernel

methods ($t=0.75$, $P=0.95$). Despite this lack of difference, the degree of overlap between MCP and kernel home ranges was often less than 75%. MCP ranges often included areas in which no observations occurred (e.g., Fig. 1b). For statistically independent data, grid cell home range sizes were significantly correlated with the number of points included in the analysis ($R = 0.90$, $P<0.0001$). MCP range size was also correlated with number of points, but to a lesser degree ($R = 0.26$, $P=0.0025$). The relationship between kernel range size and the number of points included in the calculation was not significant ($R = -0.16$, $P=0.07$).

Bandwidth Selection Method and Independence of Data

The interaction between bandwidth selection option and data independence was not significant for 95% kernel home range [$F(2,781)=0.14$, $P=0.87$]. We found no significant main effect of bandwidth selection method between h_{LSCV} (49.6 ± 1.4 ha) and h_{REF} [51.2 ± 1.4 ha; $F(1, 518)=2.77$, $P=0.10$] but there was a significant main effect of data independence [$F(2, 580)= 19.97$, $P<0.0001$]. Home ranges including all data (41.2 ± 3.7 ha) were significantly smaller than home ranges including only statistically (55.2 ± 3.0 ha; $t=6.15$, $P<0.0001$) or biologically independent data (54.9 ± 2.9 ha; $t=6.07$, $p<0.0001$). However, range sizes calculated using biologically vs. statistically independent datasets were not significantly different ($t=0.26$, $P=0.80$).

There was no significant interaction between bandwidth selection option and data independence for core area [$F(2,781) = 0.01$, $P=0.99$]. Core area size (50% probability) was not significantly different between h_{LSCV} (6.00 ± 0.25 ha) and h_{REF} [6.41 ± 0.26 ha; $F(1, 518)=1.93$, $P=0.17$]. However, there was a significant main effect of data independence [$F(2, 260)= 16.89$, $P<0.0001$]. Core areas in home ranges

calculated using all data (5.24 ± 0.18 ha) were significantly smaller than either those in home ranges including only statistically independent data (7.46 ± 0.53 ha; $t=5.77$, $P<0.0001$) or those using biologically independent data (7.24 ± 0.53 ha; $t=5.45$, $P<0.001$). There was no significant difference between ranges calculated using biologically and statistically independent data ($t=0.76$, $P=0.45$).

Disconnected Polygons

The interaction between the bandwidth selection option and the data independence method was not significant for the number of disconnected polygons included in the 95% kernel home range [$F(2,783)=0.11$, $P=0.89$]. The number of disconnected polygons included in the 95% kernel home range was not significantly different between h_{LSCV} (1.77 ± 0.07) and h_{REF} bandwidth options [1.69 ± 0.08 ha; $F(1, 783)=1.60$, $P=0.21$]. No significant differences were found in the number of disconnected polygons in home ranges calculated using all data (1.82 ± 0.07 ha), biologically independent data (1.66 ± 0.11 ha), or statistically independent data [1.71 ± 0.13 ha; $F(1, 518)=1.88$, $P=0.17$].

The interaction between bandwidth selection and data independence was not significant for the number of disconnected polygons included in the 50% core area [$F(2,783)=0.19$, $P=0.83$]. We found no significant difference in number of disconnected polygons comprising the 50% core area for h_{LSCV} (2.18 ± 0.13) versus h_{REF} methods [2.09 ± 0.12 ha; $F(1, 783)=1.65$, $P=0.20$]. There was no significant difference in number of disconnected polygons in the core area calculated from all data ($2.28, \pm 0.21$ ha), biologically independent data (2.12 ± 0.11 ha), or statistically independent data [2.00 ± 0.12 ha; $F(2, 144)= 1.93$, $P=0.15$].

Seasonal and Time of Day Comparisons

We found no significant difference in home range size between wet (53.5 ± 4.17 ha) and dry seasons [49.8 ± 4.19 ha; $F(1, 164) = 2.82$, $P = 0.10$]. There was no significant difference between wet (10.5 ± 1.6 ha) and dry seasons (9.7 ± 1.5 ha) for core area size [$F(1, 165) = 1.38$, $P = 0.24$].

Data collected at different times of day showed significant differences in home range size [$F(3, 206) = 26.65$, $P < 0.0001$] and core area size [$F(3, 515) = 31.33$, $P < 0.0001$]. Each time category was significantly different ($P < 0.01$) from every other category except for core area size for the two mid-day categories, 8AM-11AM and 11AM-2PM ($t = 0.38$, $P = 0.98$; Table 2). For 125 of 144 group/years there was less than 70% overlap between home ranges calculated from data collected at the beginning or end of the day versus during the middle of the day. Home range size for data sets balanced for time interval (53.1 ± 5.1 ha) was not significantly different from unbalanced data sets [49.5 ± 5.3 ha; $F(1, 70) = 1.68$, $P = 0.20$], nor was there a significant difference between balanced (6.32 ± 0.78) and unbalanced data sets (5.44 ± 0.92) for core area size [$F(1, 64) = 2.81$, $P = 0.10$].

Golden Lion Tamarin Home Range Analyses

Since we found no difference in home range and core area size between biologically and statistically independent data, we chose to use statistically independent data for final golden lion tamarin home range calculations. All final home ranges and core areas were generated using fixed-kernel density estimates with h_{LSCV} . Following the recommendation in Girard et al. (2002) and Seaman et al. (1999), home ranges were calculated for each group/year that contained at least 100

observations. Given the roughly 3% difference between home range sizes using statistically independent data and all data, we opted to use all data for all home ranges, thus maximizing the number of ranges we could include in the summary. The minimum sample size included was 109 observations. The average sample size was 786 points. Over 96% of group/year datasets included observations for 9 or more months of the year.

Home range and core area sizes are given for each group/year in Appendix 1, along with bandwidth value, sample sizes, and the number of disconnected polygons in the home range and core areas. There was a high degree of variability in home range and core area size across groups. Home ranges for golden lion tamarin groups at Poço das Antas fell between 16.9 and 104.8 ha. The average home range size was 49.2 ha, ranging yearly from 40.0 to 60.4 ha (Figure 2). Core areas averaged 5.1 ha, with groups having a 50% probability of being found in an area as small as 10% of their home range. Yearly core areas averaged 2.2 to 8.4 ha (Figure 2). Both average home range size and average core area size decreased over the course of the study, with the change in core area being more consistent. Home range size within groups also changed across years. For example, while the average home range size for group BO was 55.3 ha, yearly home range sizes for the group varied from 22.6 to 80.3 ha. The same was true for core area use. Average core area size for BO was 5.1 ha, but it ranged from 0.9 to 13.4 ha.

As a means of comparing our findings to other studies we also report the range and average home ranges calculated using the grid cell method and MCP, for all data and independent data (Table 3). On average, MCP produced results 1.5 times

larger than kernel while grid cell produced results 0.88 times the size of kernel home range estimates.

Population and Group Estimation

As predicted, determining minimum sample sizes using the overall home range standard deviation, 17.5 ha, required data inputs that would not be available in most field studies (Table 4). For example, in order to produce an estimate of population home range size in which we are 95% confident the true mean falls within a 5 ha range we would require 190 samples. Because of the high level of variation between years for the same group, a minimum of 11 years is required to be 95% confident that the group's home range falls within a 5 ha range. The use of the resampled standard deviations required fewer data. Estimating a population home range value with 95% confidence and a 5 ha confidence interval required a minimum of 8 groups. Results for all tested confidence levels and interval lengths are given in Table 4 along with the standard deviations used in the test.

The average overlap in home range between one year and the next was 77% (range= 67-84%). The area of overlap among consecutive years was often consistent, with small changes occurring on the outer portion of the home range. For example, home ranges for group SA between June 1987 and May 1991 share an overlap region that represents 72-85% of the home range size for the years included (Figure 3). A home range calculated using combined data from June 1987 to May 1991 was 70.5 ha, while the area of common overlap for years 1987-1988 through 1990-1991 was 56.2 ha (Figure 4). Other consecutive years show a much lower area of overlap, such as group PP between 1992-1993 and 1993-1994 (Figure 5).

Discussion

Data collected from wild populations are subject to several sources of variation typically not included in statistical models used to calculate home ranges. In the following sections we identify these sources of variation and, generalizing from the results above, provide recommendations for home range studies using imperfect or incomplete data.

1) Home Range Definition

The operational definition of a home range can have a significant impact on methodological choices and interpretation of results and should reflect the goals of the study. For example, Singleton and van Schaik (2001) suggest that short studies may reflect only core areas of use and not full home ranges. Their definition of home range is based on the lifespan of an adult animal (Jolly 1972). As shown in the present study, a home range can fluctuate across years. Simply looking at one home range for the entire adult lifespan would limit the ability to evaluate the factors which affect home range change, and may not represent the correct experimental (observational) unit when studying group-dwelling animals, particularly those in relatively stable, rather than fission-fusion, groups. Based on our results, we recommend the use of the Kernohan et al. (2001) modification of Burt's (1943) definition, the range occupied during "normal" activities for a specific time period.

2) Home Range Calculation Method

While MCP methods produced the largest home range estimates when using all successive points, they were not different from estimates using kernel methods when only statistically independent data were included. However, as expected based

on reports by Harris et al. (1990), MCP produced home ranges that frequently included large areas with no observations (Fig. 1b). All areas within the MCP perimeter are equally valued, making an area containing no observations as important as an area containing many observations. Also, the shape of the MCP is dependent on the outermost points (Harris et al. 1990), not the distribution of all observations across space. Because of this lack of fit between distribution of data points and home range shape, we did not find MCP adequate for the estimation of home range size or for the examination of the relationship between neighboring group ranges.

The grid cell method produced a very conservative estimate of home range use. These home ranges only include cells that contain observations. Since the grid cell method is unable to extrapolate to the surrounding area, it may create an incomplete picture of the extent of the home range, resulting in a less accurate representation than that provided by kernel methods (Kernohan et al. 2001). The grid cell method also provides only a rudimentary method of determining intensity of use (count of observations in each grid cell). However, because it can be generated by hand and does identify heavily used areas, it has some benefits over kernel methods (ease of use) and MCP (measure of intensity of use), as long as researchers fully understand its properties: potential underestimation of ranging, grid cell size is critically important to the results (White and Garrott 1990), and performance is best with an independent sample (White and Garrott 1990). Researchers should take care to choose grid cell sizes that, at a minimum, cover group spread and measurement error.

Kernel methods are generally preferred for home range calculation (Worton 1989; Kernohan et al. 2001; Barg et al. 2005). The 95% kernel density estimate was the most accurate descriptor of range size and use for golden lion tamarins in our study. We found that home range estimates using kernel methods were not significantly correlated with sample size, while estimates from both MCP and grid cell methods were correlated with sample size. Unlike MCP, kernel home range estimates are influenced by the spatial distribution of all data points, not just the outermost points. Unlike grid cell methods, kernel estimates include areas near observation points but not containing them. Kernel estimates also provide a measure of probability of use at any point within the home range, making them ideal for use in habitat selection and behavior distribution models (Kernohan et al. 2001; Marzluff et al. 2001).

3) Bandwidth Selection Method

We found no difference in home range or core area size between h_{REF} and h_{LSCV} . This is not the result of data simply following a bivariate normal distribution as 78% of home ranges contained multiple centers of activity (disconnected polygons in the core area). This finding differs from Seaman et al. (1999) who found an overestimation of home range size when using h_{REF} with multimodal data. Unlike Hemson (2005), we found no evidence of an increase in failure rate of h_{LSCV} for home ranges with large sample sizes.

The time required for ArcView 3.2 to calculate a kernel estimate with h_{LSCV} varied with computing power and sample size, with a 1000+ observation dataset often taking several hours to run. For field researchers with time constraints, sub-optimal

computing power, and/or a large number of analyses, it might be prudent to check for differences in methods between a few test cases or use another software package, such as R (<http://www.r-project.org>), which can take advantage of computers with multi-core processors.

4) Sample Size and Data Independence

A common dilemma when estimating home ranges is whether to include only independent data points and suffer the consequences of reduced sample size or use all data, with dependent points potentially producing an inaccurate picture of the concentration of space use. We found that the use of non-independent sample points reduced the final size of the home range estimate, both for 95% kernel and 50% core areas. However, the difference in estimates was not large (~3%) at the 95% kernel level. If the use of independent sample points reduces sample size such that fixed kernel methods become inappropriate, it may be preferable to use a non-independent sample rather than switch to MCP or grid cell analyses. In our study the use of these methods produced estimates an average of 50% larger (MCP) or 12% smaller (grid) than the size of kernel home range estimates.

Another common problem in estimating home ranges is the large time interval often required to achieve statistical independence between sample points (McNay et al. 1994; Hansteen et al. 1997). For most groups in our study, time to independence was about 3 hours, which reduced the number of points included in the analysis to an average of 15% of the total points collected. An ideal home range method would include all observations but would weight points based on the amount of time separating them, valuing observations taken far apart in time more heavily. Such a

method would take advantage of a large sample size while accounting for autocorrelation between points (Katajisto and Moilanen 2006). While some modeling of this method has been attempted (e.g. Katajisto and Moilanen 2006), the option is not yet available in ‘off the shelf’ home range programs.

An alternative to statistically independent points is systematic sampling over the duration of the study (McNay et al. 1994; Fieberg 2007a), an approach that is facilitated by use of GPS radio collars. By using GPS collars, researchers can increase sample size and improve home range accuracy and precision (Arthur and Schwartz 1999). However, the cost and relatively large size of GPS collars limit their use (Wauters et al. 2007).

5) Seasonal and Temporal Variation

When looking at all study groups, we found no differences between home ranges categorized by season. However, 7 study groups had larger average home range size during the dry season and 8 groups showed larger home range sizes during the wet season. For example, Group 2M3 had an average home range size of 42.9 ha in dry months and 32.6 ha in wet months, while Group BO showed the opposite pattern, with an average home range size of 46.5 ha in the dry season and 65.7 ha in the wet season.

Similar to the findings for seasonality, we found no difference in home range size between datasets balanced for time and those including all data. However, home ranges calculated using data from 8AM-11AM or 11AM-2PM were much larger than those from early in the morning or later in the evening. This pattern may be due to use of a relatively small number of sleeping sites, thus concentrating use of space during

these times, or to wide-spread resources that are used during the primary feeding hours of the day (8AM - 2PM). Likewise, Raboy and Dietz (2004) cited resource and sleeping site distribution as the main factors affecting home range size in golden-headed lion tamarins.

While we found no clear trends of seasonal and temporal variation in home range estimates of golden lion tamarins at the population level, these sources can vary significantly at the group level. It is useful to conduct preliminary analyses on temporal and seasonal variation before making decisions on how to analyze or divide the data, thereby creating a sample that truly represents the extent of ranging over the time period included. This may mean balancing the data for the season or spacing samples across the day. For example, inclusion of nighttime locations for diurnal animals may be important for some species (see Fieberg 2007b).

6) Estimating Home Range across Years

Maynard-Smith (1974) and Wilson (1975) reasoned that animals should occupy the smallest home range size that provides energy required for survival and reproduction. However, animals may not always occupy the minimum home range size needed for baseline energy intake (Benson et al. 2006). Terborgh (1983) and Rylands (1986) argue that animals do not occupy the minimum area required in the time of observation, but rather the minimum area required for an adequate food supply to ensure survival in times of food scarcity. Hence, there may be a variety of possible home range sizes, with the lower boundary marking the minimal energy

intake required and the upper boundary at the point where there is no longer a fitness benefit for increased home range size (Kelt and Van Vuren 2001).

Small contractions and expansions in home range size between years may represent yearly fluctuations in population density, predation pressure, reproductive success, group size, group composition or leadership, food availability, weather patterns, and/or pressure from neighboring groups. Large perturbations in ranging may reflect significant changes in any of these sources, or the gain or loss of previously occupied territory. An example of pressure from outside groups can be seen in Group PP2 from 2003 to the present. Their home range is bordered by 3 other groups, with open pasture on the 4th side. Their home range size has declined steadily since 2003, with the group occupying only 17.4 ha in 2005-2006. With open pasture on one side of their range, PP2 was unable to shift their home range away from advances by three strong neighboring groups.

Changes in a group's home range size across years increase the potential for overestimation of ranging patterns if sampled over time periods that include these changes. Based on our calculations, 11 years of data are required in order to be 95% confident that a group's average home range falls within 5 ha. The home range calculated from a long-term dataset will almost always be larger than ranges calculated from its subsampled parts. An example of this effect is seen in Figure 5, where a substantial shift in home range occurred between the study years. If ranges from both years were combined, the home range estimate would be larger than either year alone. Seen separately, the change between years may represent a range shift due to one of the factors mentioned previously. In contrast, we noted instances in which

groups varied little in the area they occupied across several years (e.g. Figures 3 and 4). Similar to our recommendations for possible temporal and seasonal variation, we suggest that a multi-year dataset be subsampled and the degree of overlap between years calculated, prior to producing a multi-year estimate of home range.

7) Sample Sizes Necessary to Estimate Mean Range Sizes for Populations

There are three clear sources of variation that affect population home range averages: variance in home range size among groups in the population, variance in home range across years for a given group, and variance in the population mean over time. Based on our calculations, we are 95% confident that we can estimate the population mean for a given year within 5 ha if we include data for 8 groups of golden lion tamarins. Based on the data we collected, we can produce an accurate picture of population ranging for 12 of the 19 years of observation. This, taken in conjunction with the number of years required to accurately estimate the average home range for a group, means that we would require 11 years of data for 8 groups to calculate a mean population range at the 95% confidence level. This statement may be misleading, however, because the true population average home range size may increase or decrease over all or part of the study years. This change from year to year is critically important for conservation planning, particularly if the population mean increases over time, as reserves may not be large enough to hold a sufficient number of breeding groups to maintain genetic diversity in the population.

8) Interpreting Comparisons of Home Ranges across Studies

With adequate information on methodology and sample size, comparisons of home ranges between studies are valid and informative. In the present study, our

estimate of 50.5 ha for average home range size was similar to previous estimates for golden lion tamarins in Poço das Antas Biological Reserve, which gave 45.2 ha as an average using grid cell methods and all available data (Dietz et al. 1997). In our findings, grid cell methods produced estimates 12% smaller than kernel methods. Thus the difference between our findings and those of Dietz et al. (1997) are most likely the result of differing methodology and do not reflect biological differences. Golden lion tamarins at União Reserve occupied home ranges of 73 and 96 ha (Lapenta et al. 2007), using MCP and all available data. The mean MCP value for home ranges at Poço das Antas Biological Reserve was 71.1 ha with a standard deviation of 28.0 ha. Both of the values from União Reserve fall within 1 standard deviation of the mean from Poço das Antas Biological Reserve. Given this similarity, we would predict that the kernel home range estimate for lion tamarins in União Reserve would approximate that for tamarins in Poço das Antas Reserve, about 50 ha. Unless the methods of calculating ranges and sample sizes are clearly stated, comparisons with results from other studies may be incorrect, misleading, or both.

Acknowledgements

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this manuscript. This research complies with the guidelines of the University of Maryland Animal Care and Use Committee and all applicable Brazilian laws.

Tables

Table 1. Time in minutes (\pm SE) to statistical and biological independence by travel speed and home range size categories. Statistical independence was calculated using Schoener's ratio while biological independence was calculated by randomization of data. Travel speed and home range size categories are based on the mean \pm 1 SD.

		Statistical Independence	Biological Independence
Travel Speed	Slow	236.2 \pm 22.2	213.5 \pm 10.0
	Average	199.9 \pm 10.4	167.9 \pm 4.7
	Fast	159.3 \pm 11.4	134.4 \pm 4.5
Home Range Size	Small	180.9 \pm 17.3	144.4 \pm 6.5
	Medium	205.5 \pm 17.0	167.3 \pm 8.5
	Large	202.3 \pm 17.4	183.5 \pm 10.4

Table 2. Home range and core area sizes for each time category (\pm SE). Each time category was significantly different ($P < 0.01$) from every other category except for core area size for 8AM-11AM and 11AM-2PM.

	Home Range Size (95% kernel)	Core Area Size (50% kernel)
Sleeping Site to 8 AM	42.9 \pm 1.4	5.0 \pm 0.27
8 AM to 11 AM	53.9 \pm 1.6	7.1 \pm 0.37
11 AM to 2 PM	48.5 \pm 1.6	7.0 \pm 0.33
2 PM to Sleeping Site	35.3 \pm 1.3	4.2 \pm 0.28

Table 3. Home range average and ranges (ha) calculated with all and independent data using the grid cell method and MCP.

	Grid Cell		MCP	
Data Used	All	Independent	All	Independent
Minimum	12.0	4.8	19.4	14.7
Maximum	79.0	32	245.9	224.2
Mean	41.1	18.5	71.1	56.8
SD	12.7	6.1	28.0	24.7

Table 4. The number of samples required to achieve specified confidence levels and interval lengths (2L) for estimating population home range size and group home range size using two approaches for calculating standard deviations, actual and resampled. Actual standard deviation values are 17.5 ha for population home range and 13.4 for group home range. Standard deviations used in the resampled analysis are in parentheses preceded by the number of samples.

Method	Actual Standard Deviation				Resampled Standard Deviation			
Parameter	Population Home Range		Group Home Range		Population Home Range		Group Home Range	
Confidence Level (%)	95	90	95	90	95	90	95	90
2L = 5	190	135	112	80	8 (3.7)	8 (4.2)	11 (3.6)	9 (4.1)
2L = 10	48	34	30	21	6 (5.5)	5 (6.4)	7 (5.1)	5 (5.9)

Figure Legends

Figure 1. Three methods of home range calculation for group BO in 1997-1998 using all data (a), and statistically independent data (b). Kernel home ranges are outlines in black, MCP is cross-hatched, and grid cells are colored in dark grey. Data points are included in 1b.

Figure 2. Average home range (ha) and core area (ha) across groups for 1987-1988 to 2005-2006.

Figure 3. Variation in home range location over time: SA home ranges for June 1987 – May 1991. The light grey area represents the 56.2 ha overlap region common to all 4 years for this group. The patterned areas represent overlap between consecutive years not included in the common overlap. The colored areas represent home range area exclusive to one year of study.

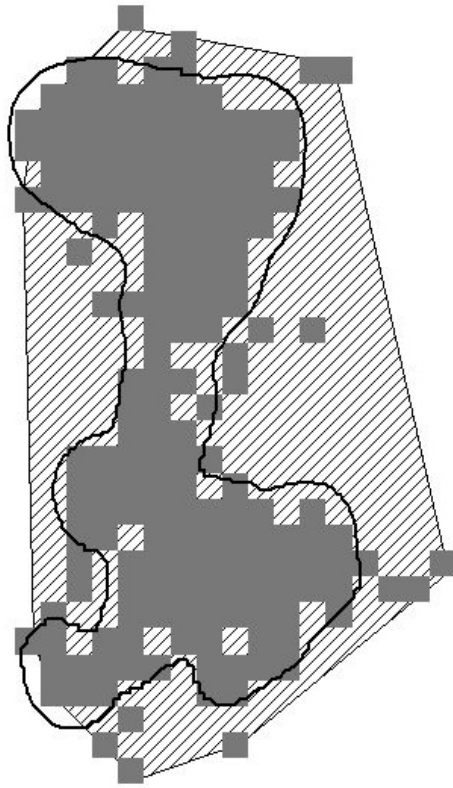
Figure 4. The home range for group SA calculated from June 1987 to May 1991 is 70.5 ha. The area of overlap among yearly home ranges calculated from year 1987-1988 to 1990-1991 is 56.2 ha and is outline with the dashed line (from Figure 3).

Figure 5. Home ranges for PP for 1992-1993 (black) and 1993-1994 (striped). The area of overlap of group ranges between years is represented in grey.

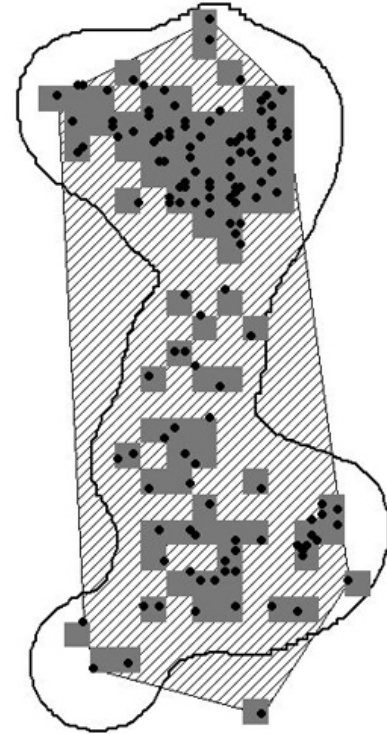
Figures

(Figure 1)

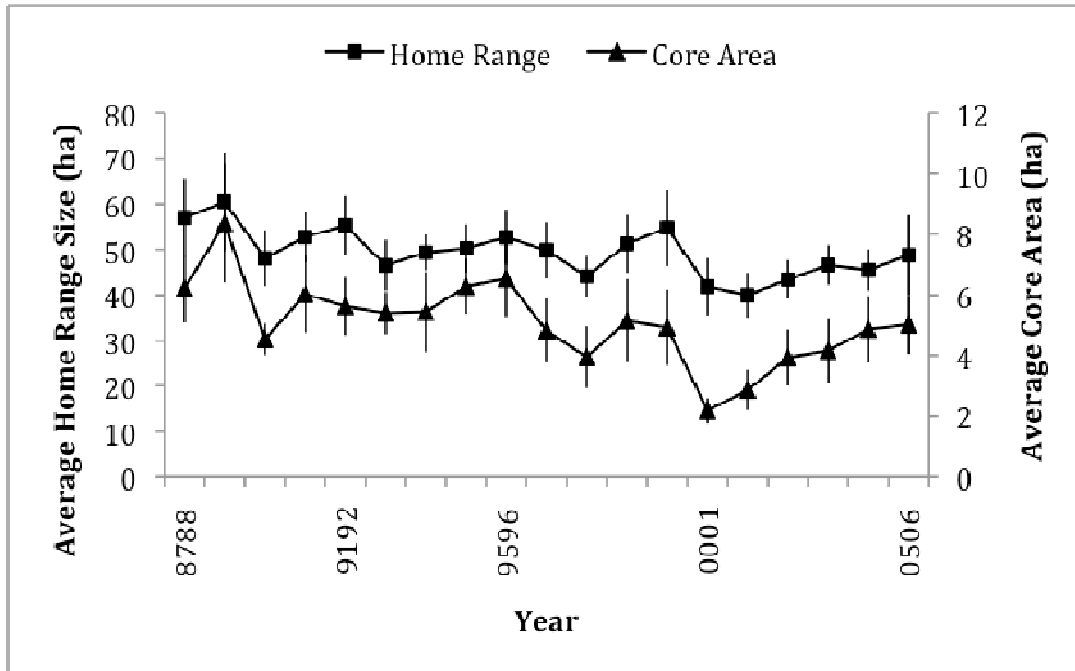
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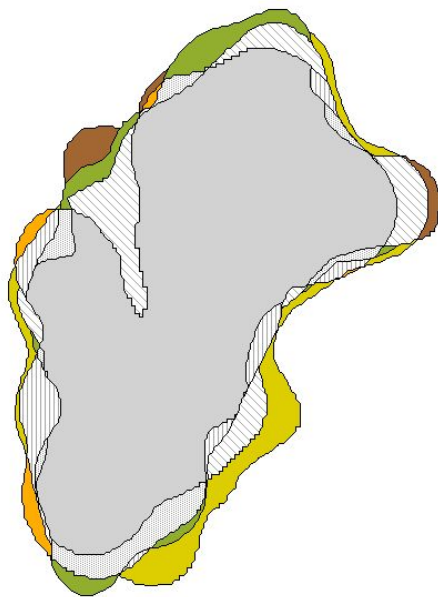
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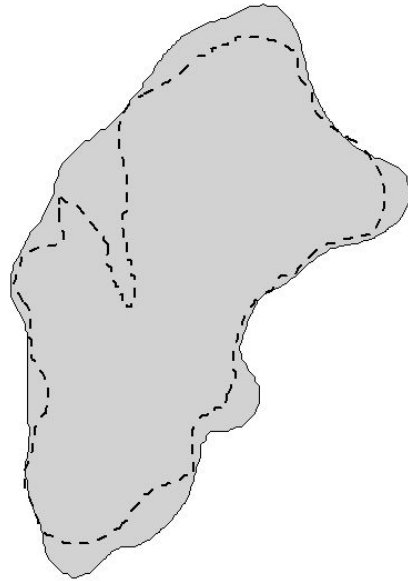
(Figure 2)



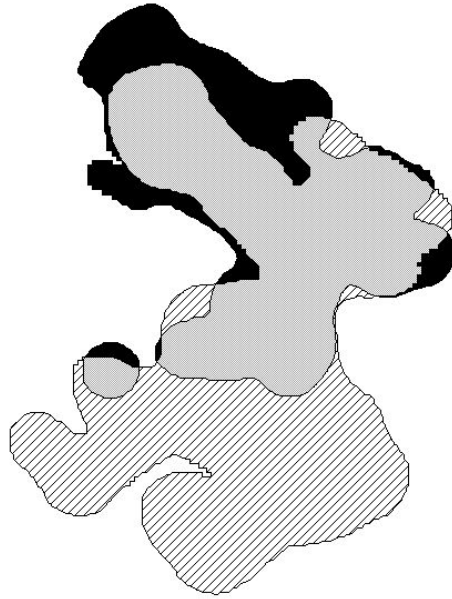
(Figure 3)



(Figure 4)



(Figure 5)



Chapter 3: What Influences Home Range Size? Re-examining the Ecological Constraints Hypothesis

Abstract

For the past 20 years, the ecological constraints hypothesis has been the dominant explanation of home range size variation. This hypothesis states that as group size increases, energetic demand also increases, causing groups to travel further and occupy larger home ranges in order to meet basic needs for survival and reproduction. In this paper we use 19 years of data on golden lion tamarins, *Leontopithecus rosalia*, to examine three hypotheses explaining variation in home range size: ecological constraints, male presence, and female presence. We also looked at how changes in predation level and population density affected home range size and group composition. As predicted by the ecological constraints hypothesis, big groups occupied large home ranges. However, group size alone was insufficient to explain home range size variation. Larger home ranges were also occupied by groups containing adult natal males, more than one potentially reproductive male, and/or more than one reproductive female. In contrast, the presence of adult natal females had no effect on home range size. Variation in predation and population density resulted in significant changes in group demography, which mediated changes in range use. In comparison with periods of low predation, periods of high predation were characterized by groups containing significantly fewer reproductive females and adult natal males. Group size was significantly reduced during periods of high predation, as were population density and home range size. Population density and predation rate were significant predictors of average annual home range size, with both factors having a negative impact on ranging. The results of this study indicate that while larger groups do use larger home ranges, predation-mediated changes in

group composition and population density cause significantly greater changes in ranging patterns. The number of reproductive females in the group and, therefore, the number of potential offspring, also has a large effect on range size. Large home ranges supported allowed for greater number of litters and infants. Taken together, our results show that home range size is affected by much more than absolute group size, with predation and reproductive potential playing key roles.

Introduction

Animals are thought to occupy the smallest home ranges adequate to provide energy sufficient for survival and reproduction (Maynard Smith 1974; Wilson 1975), a hypothesis supported by the relationship found between body size, energetic demands, and home range size (McNab 1963; Milton and May 1976; Mace et al. 1983). Extending this logic to use of space in social animals, as group size increases, travel should increase due to greater food requirements and heightened intra-group foraging competition (Clutton-Brock and Harvey 1977; Terborgh 1983; Chapman 1990; Wrangham et al. 1993). This ecological constraints model has been the dominant explanation of home range size for the last 20 years, with support for the hypothesis coming from many studies (Herrera and MacDonald 1989; Barton et al. 1992; Watts 1998; Gillespie and Chapman 2001; Dias and Strier 2003).

Recent reports suggest that food availability and group size may be insufficient to predict travel patterns (Adams 2001; Struhsaker 2006). Space use may reflect the combined effects of several factors acting at different levels (Chapman and Chapman 2000a), including breeding system (Clutton-Brock and Harvey 1977), social factors (Chapman and Pavelka 2005; Struhsaker 2006), and population density (Benson et al. 2006; Horiuchi 2006). Independent of the effect of group size, home range size may be related to the numbers of adult males and females in a group. An increase in the number of adult males may increase home range size because of heightened defense capabilities (Peres 1989; Lehmann and Boesch 2003), with adult females potentially contributing to group defense in some taxa (Lehmann and Boesch 2003). In addition to defense, the assessment of potential breeding vacancies in

neighboring groups, such as during intergroup encounters (Garber et al. 1993; Baker and Dietz 1996; Lazaro-Perea 2001), may also affect ranging patterns. Finally, for population density, Huxley (1934) postulated that when density increases, heightened pressure from neighboring groups on the outside of a home range results in a decrease in home range size. A negative relationship between population density and home range size has been found in several taxa: birds (Huxley 1934; Holmes 1970), social carnivores (Benson et al. 2006), ungulates (Kjellander et al. 2004), bears (Dahle and Swenson 2003), pigs (Saunders and McLeod 1999), and primates (Horiuchi 2006).

To our knowledge, no study has examined the effects of all these factors on home range size. We use 19 years of data collected on golden lion tamarins, *Leontopithecus rosalia*, at Poço das Antas Reserve, Brazil to test three non-mutually exclusive hypotheses explaining variation in home range size: ecological constraints, male presence, and female presence. Golden lion tamarins are cooperative breeding primates that feed on fruits and insects, live in groups ranging in size from 3 to 14 individuals, and defend partially overlapping territories (Peres 1989; Miller and Dietz 2005; Lapenta et al. 2007) that range in size from 17.4 to 87.7 ha (see Hankerson and Dietz, Chapter 2 of this dissertation). Golden lion tamarins are an appropriate model to examine these hypotheses of home range size variability because 1) they exhibit large variation in home range size (Hankerson and Dietz, Chapter 2 of this dissertation), 2) like many callitrichids, golden lion tamarins have a variable mating system, including monogamy, polygyny, polyandry, and polygynandry (Baker et al. 2002), and 3) as described below, golden lion tamarins at Poço das Antas Reserve have experienced large shifts in population density and predation risk.

We examine the ecological constraints hypothesis by testing two predictions. First, if space use is determined by energetic demands, there will be a positive relationship between group size, or biomass, and home range size. Second, groups in high quality habitat will have smaller home ranges than groups in poor quality habitat. Next, we examine the male presence hypothesis by looking at the impact of the number of males, both potentially breeding and natal, on home range size. The presence of multiple adult males in the group may increase home range size for various reasons, including increased defensive capabilities of the group or increased travel to find breeding positions in neighboring groups (“prospecting”). Finally, we test if the presence of more than one adult female in the group affects home range size due to one of three reasons: 1) additional reproductive females may result in increased reproductive output and, thus, the need for additional resources; 2) the presence of multiple reproductive females or adult natal females requires increased travel to “prospect” for breeding opportunities; or, 3) additional reproductive or adult natal females allows the group to defend a larger area and, therefore, more resources. If we see a difference in home range size between groups containing one vs. two reproductive females but no difference in home range size between groups with vs. without adult natal females, then there is support for the reproductive output explanation. Otherwise, the effect may be due to one or more alternative explanations. The male and female defense explanation for increased group size and the reproductive output explanation are both logical extensions of the ecological constraints hypothesis. Like ecological constraints, the female and male defense hypotheses predict larger numbers of individuals occupying larger home range.

Likewise, the reproductive potential explanation predicts larger space for a larger group size in the future.

In this and other studies on social mammals, predation has been identified as the cause of large changes in population and group demography and dynamics (Anderson 1986; Caine 1993; Stanford 1995; Stanford 1998). Starting in the mid 1990s, the rate of predation on lion tamarins in the reserve increased dramatically (Franklin et al. 2007a; Franklin et al. 2007b). Prior to this time, the majority of predation events involved the loss of single individuals, with an occasional event involving multiple lion tamarins. However, from May 1996 through March 2004 partial or whole groups commonly fell victim to predators in the reserve (Franklin et al. 2007a; Franklin et al. 2007b). The predation rate prior to 1996 was 0.18 golden lion tamarins per group per year, increasing to 0.55 lion tamarins per group per year from 1996-2004 (Franklin et al. 2007a; Franklin et al. 2007b). To better understand how variation in predation and resulting changes in population density mediate changes in range use we examined differences in group demography, group size, and population density during periods of high and low predation.

Methods

Study Site and Data Collection

We collected data on group composition and movement of golden lion tamarins in Poço das Antas Biological Reserve (22°30-33'S, 42°15-19'W), Rio de Janeiro State, Brazil from January 1987 through January 2006. The reserve is a 6300-ha Atlantic Coastal rainforest remnant, containing a mosaic of mature, secondary and swamp forests and grasslands (Dietz and Baker 1993; Dietz et al. 1997). Golden lion

tamarins in this population are trapped, marked, and weighed semiannually. All study groups are habituated to the presence of human observers and contain at least one radio-collared individual. While the number of study groups monitored changes over time, at any one time we actively follow at least eight focal groups of lion tamarins, while recording demographic and spatial information for an additional 5-7 groups. Once or twice a week, focal groups are followed from when they exit a sleeping site in the morning until they enter a sleeping site in the evening. Group spatial locations are recorded at 20 min intervals throughout the day. Additional spatial data come from a weekly census of individuals in all groups in the study area, including the ~8 focal groups.

Home Range Size

Home range sizes were calculated using fixed kernel density estimates for each group for each year (June-May) using the Animal Movement Analysis Extension (Hooge and Eichenlaub 1997) in ArcView 3.2 (Environmental Systems Research Institute, Inc., Redlands, USA). Years were classified as June-May to correspond with the mating seasons documented for this species (Dietz et al. 1994). We used a 95% fixed-kernel estimate for total home range (see Hankerson and Dietz, Chapter 2 of this dissertation for details of home range calculation).

Group Size, Age Structure, and Social Status

Group membership was noted on each day of observation. For each day, we recorded the number of adults (> 18 months of age), subadults (10-18 months), juveniles (4-9 months), and infants (0-12 weeks of age) in the group. Golden lion tamarins reach sexual maturity between 15 and 20 months of age (Dietz et al. 1994).

The age of unknown individuals entering a study group was estimated using protocol established by Dietz et al. (1994).

For a yearly measure of group size, we averaged daily estimates of group composition for the year, excluding infants. We also calculated averages for each age category and noted the social status of all adults. All females that had given birth in that group during the current or previous year were counted as reproductive females. Adult males not closely related to the breeding female(s) were considered potentially reproductive. For each year for each group, we classified the group as containing one or two reproductive females, one or more potentially reproductive males, and by the presence or absence of adult natal males and adult natal females.

Group Biomass

Group biomass has been considered a more appropriate measure of energetic needs than group size in golden lion tamarins (Dietz et al. 1997; Miller and Dietz 2005). As with group size, we calculated the biomass of each group for each day. Since each individual in the group presumably contributes to biomass in proportion to their energetic requirements, we included weights of infants in calculating group biomass. For a yearly measure of group biomass, we averaged the daily measurements of biomass. We used weights of 620 and 598 g for adult males and non-gravid adult females, respectively (Dietz et al. 1994). Weights for pregnant females, infants, juveniles, and subadults were calculated using weights recorded during semi-annual captures.

We estimated the weights of pregnant females using 223 measurements recorded for 106 pregnant females captured during semi-annual physical

examinations. Pregnant females were categorized as being in the early, mid, or late stage of pregnancy. To assess the change in female weight during pregnancy we used a one-way ANOVA of female pregnancy stages (non-gravid, early, mid, late). Female identity was included as a subject variable in the model to account for variation among individuals. If a female was weighed at a specific stage in more than one pregnancy, we used an average weight for that female in that stage. As expected, pregnancy stage had a significant effect on body mass [F(3, 107)= 117.3, P<0.0001]. We found that females in the early stage of pregnancy (599 ± 4.5 g) did not differ in body mass from non-gravid females (604 ± 2.4 g, P=0.78). All other stages were significantly different (P<0.0001). Females in the second and third trimesters averaged 633 ± 4.8 g and 698 ± 4.7 g, respectively.

Juvenile and subadult weights were generated from a regression plot of 968 weights taken during examinations. Age in months was a significant predictor of weight [$r^2=0.86$, F(2, 1346)= 4017.5, P<0.0001]. The data fit a quadratic curve with the following regression equation:

$$y = -0.7229x^2 + 33.998x + 148.04$$

where y is weight (g) and x is age in months. Since this equation consistently overestimated the weights of individuals < 3 months of age, we generated a separate regression equation for infants. We included weights from 87 infants with age in weeks as the predictor variable. Age in weeks was a significant predictor of weight [$r^2=0.54$, F(1, 84)= 98.7, P<0.0001]. The relationship was linear and is reflected by the following regression equation:

$$y = 16.177x + 55.504$$

where y is weight (g) and x is age in weeks. The age (weeks or months) of each infant, juvenile, and subadult in the group was calculated for each day and the corresponding weight was used in calculations of group biomass.

Habitat Quality

We used the amount of swamp forest and dense forest in a home range as an estimate of habitat quality and food availability. Swamp forest has a larger number of fruits available than other habitat types in the reserve (Dietz and Baker 1993; Miller and Dietz 2005) and also provides food during times of food scarcity (Dietz and Baker 1993; Dietz et al. 1997). In addition to fruit, swamp forest contains more vertebrate prey per hectare than other habitat types (Domingues et al. 1989; Dietz et al. 1997). Dense forest contains twice the number of insects per hectare than non-dense forest (Domingues et al. 1989). The number of hectares of swamp and dense forests in home ranges are highly correlated ($r=0.84$, $P<0.0001$).

We calculated an index of habitat quality for each home range by overlaying ranges on habitat maps and calculating the percentages of swamp and dense forest using ArcView 3.2 (Environmental Systems Research Institute, Inc., Redlands, USA). The percentages of swamp and dense forests were combined into one measure of habitat quality using a principal component analysis. The first principal component contained equal loadings of both swamp and dense forest and accounted for 82.3% of the variance.

Population Density

We calculated the total area used by the study population by overlaying yearly home ranges for all study groups. This approach ensured that areas of home range

overlap between groups were counted only once in the estimate of population range size. Average group sizes for each year, not including infants, were totaled to create an estimate of study population size. Population density was calculated for each year by dividing the population size by the population range size expressed as the number of golden lion tamarins per hectare.

Predation Rate

In order to test for the impact of predation rate on home range use we classified January 1987-May 1995 and June 2004-January 2006 as periods of low levels of predation in the reserve and June 1995-May 2004 as a period of high predation (Franklin et al. 2007a; Franklin et al. 2007b). We identified the beginning of the period of high predation as the first full year after the first large-scale predation event, in April 1995. We chose to end the high predation period in June 2004 as there were no instances of group-level predation in late 2003 and early 2004, and only a few single-individual events following this time period.

Statistical Analyses

To test the ecological constraints hypothesis, we measured the effect of habitat quality and group biomass on home range size in two ways. First, we used a multiple regression with one value of biomass and one value of habitat quality for each group averaged over the years of study. All statistical assumptions were met. We used a stepwise selection process for inclusion in the model, with $\alpha=0.15$ for entry into the model. This analysis examined whether groups that tend to be large have larger average home ranges. Our second test of this hypothesis allowed us to look at how groups changed home range size as group size changed. For this analysis, we

classified groups as small (< 4.5 individuals), medium (4.5-7.9 individuals), or large (> 8 individuals). This categorical variable was used in a one-way analysis of variance, which included group identity as a subject variable, year as a repeated measure, habitat quality as a random covariate, and home range size as the response variable. All statistical assumptions were met. To verify our assumption that group biomass was a strong predictor of group size, we calculated a correlation of average group size and average group biomass.

For hypotheses relating to the presence of adult males and adult females, we ran a repeated measures mixed-model ANOVA including the categorical number of potentially breeding males, the categorical number of breeding females, the presence/absence of adult natal males, and the presence/absence of adult natal females. Average group biomass was included as a covariate to control for the effect of changing group size on composition. Group identity was included as a subject variable, with year being the repeated measure. Assumptions of normality and homogeneity of variance were met. All interactions were non-significant and were removed prior to the final run of the model.

Repeated-measures ANOVAs were used to test the effect of predation on each of the variables: number of potentially reproductive males, number of reproductive females, number of natal adult males, number of natal adult females, group biomass, group size, population density, and home range size. We used yearly averages for each response variable. Two groups were left out of the analyses because they occurred in one but not both of the predation conditions. Each of these analyses included group as a subject variable and year as the repeated measure. Assumptions

of normality were met for group biomass, group size, and home range size. For the other analyses, in order to verify the outcome of the ANOVA, we randomized the response variable and ran 5000 iterations of each ANOVA. The p-value reported for each ANOVA is the percentage of trials, out of 5000, in which the trial F value was greater than the test (actual) F value.

In order to determine the effect of predation and population density on home range size, we ran a multiple regression including predation and population density as independent variables and average home range size for each year as the response variable. A stepwise selection process was used with an alpha of 0.15 as the cutoff for entering the model. All statistical assumptions of multiple regression were met.

Results

Ecological Constraints Hypothesis

Group size and group biomass were highly correlated ($r^2 = 0.98$, $P < 0.0001$). Average group biomass was a significant predictor of average home range size [$r^2 = 0.32$, $F(1, 12) = 5.7$, $P = 0.03$; Figure 1a]. However, habitat quality did not reach the 0.15 cutoff to enter the model (Figure 1b), thus indicating a lack of support for the second prediction of the ecological constraints hypothesis, that ranges should be smaller in high quality habitat.

For the analysis of the categorical group size variable, there was a significant difference among groups sizes for home range size [$F(2,132) = 11.53$, $P < 0.0001$]. Large groups (66.9 ± 3.71 ha) had larger home ranges than either small (46.7 ± 1.99 ha; $t = 4.76$, $P < 0.0001$) or medium groups (49.7 ± 1.96 ha; $t = 4.10$, $P < 0.0001$). Home

range sizes for small and medium-sized groups were not significantly different ($t=1.06$, $P=0.54$).

Male and Female Presence Hypotheses

As predicted by the male presence hypothesis, both categories of males had a significant effect on home range size. Groups with two or more potentially breeding males (53.0 ± 6.94 ha) had larger home ranges than groups with only one breeding male [40.2 ± 5.83 ha; $F(1,130)=20.29$, $P<0.0001$]. Groups with at least one adult natal male had larger home ranges (51.2 ± 7.66 ha) than groups with no adult natal males [42.0 ± 5.12 ha; $F(1,130)=6.26$, $P=0.014$].

For the female presence hypothesis, groups with only one reproductive female (41.8 ± 5.54 ha) had smaller home ranges than groups with two reproductive females [51.4 ± 7.27 ha; $F(1,30)=8.51$, $P=0.004$]. However, there was no significant difference in home range size between groups containing at least one adult natal female (47.7 ± 7.00 ha) and groups with no adult natal females [45.5 ± 5.76 ha; $F(1,130)=0.56$, $P=0.46$]. All interactions between the categorical variables were non-significant and were removed from the final model. The interaction of home range size and the number of reproductive males and females is shown in Figure 2. All analyses of male and female presence included group biomass as a covariate to control for the effect of group size.

Effects of Predation and Changes in Population Density

As expected, group biomass was significantly smaller during periods of high predation (2528 ± 134.5 g) than in periods of low predation [3311 ± 114.8 g; $F(1, 119)=19.6$, $P<0.0001$]. Likewise, average group size during the period of high

predation was 4.4 individuals, not including infants, while it was 6.0 individuals during low predation. Home range size was significantly reduced during high predation (52.6 ± 1.88 ha) compared to periods of low predation [45.3 ± 2.20 ha; $F(1,119)=6.36$, $P=0.013$).

Group composition also changed as a result of predation. After controlling for changes in group size, we found fewer reproductive females in groups during high predation (1.12 ± 0.05) than in low predation [1.28 ± 0.05 ; $F(1,119)=4.31$, $P=0.037$]. The average number of adult natal females present in groups was not significantly different during periods of high predation (0.32 ± 0.07) vs. low predation [0.41 ± 0.06 ; $F(1,119)=0.90$, $P=0.34$]. There was no significant difference between high (1.32 ± 0.06) and low predation (1.32 ± 0.05) for the number of potentially reproductive males [$F(1,119)=0.55$, $P=0.46$]. During high predation (0.40 ± 0.10) groups contained significantly fewer adult natal males than in periods of low predation [0.76 ± 0.09 ; $F(1,119)=7.12$, $P=0.009$].

Population density was significantly lower during periods of high predation (0.121 ± 0.002) than in low predation [0.109 ± 0.002 ; $F(1,119)=17.83$, $P<0.0001$]. The revised regression model of yearly home range size, including both predation and population density, was significant [$r^2=0.71$; $F(2,15)=18.37$, $P<0.0001$; Figure 3]. When used jointly, both predation (partial $r^2=0.37$) and population density (partial $r^2=0.34$) were significant predictors of home range size.

Discussion

Ecological constraints caused by group size and food availability are insufficient to explain the wide variation in home range size observed in golden lion

tamarin. In this study we have identified three sources of variation in tamarin home range size: 1) current group size, 2) male mate searching opportunities and/or enhanced group defense, and 3) future reproductive potential. We also document how all three can be affected by the interaction of predation and population density.

Ecological Constraints

Foraging competition between group members is thought to be a significant cost of group living in social animals (Wrangham 1980; Terborgh and Janson 1986; Dunbar 1993), and thus, increased travel distance in larger groups may be explained by depletion of food patches and avoidance of search field overlap among group members (Chapman and Chapman 2000b). In the present study, group size explained only 32% of the variation in home range size of golden lion tamarins. The results of the categorical group size analysis indicate that group size may affect ranging only in the largest groups. Very large golden lion tamarin groups (8+ individuals) had large home ranges, but at smaller group sizes, no effect of group size on ranging was found.

Habitat quality was not a significant predictor of home range size. Despite previous reports that swamp and dense forests contain more food resources than other habitats (Domingues et al. 1989; Dietz and Baker 1993; Dietz et al. 1997; Miller and Dietz 2005), it is possible that the percentage of these forest types in a home range is an inadequate measure of food availability, or that other resources, such as preferred sleeping sites (Hankerson et al. 2007), are also important in home range size and shape determination.

Male Breeding Opportunities and Territory Defense

Controlling for group size, tamarin home ranges were significantly larger in groups containing one or more adult natal males. Natal males are active participants in intergroup encounters at territorial boundaries, frequently fill breeding vacancies in adjacent groups, and do not breed in their natal groups (Baker and Dietz 1996; Baker et al. 2002; Kierulff et al. 2002). Home ranges were also larger in groups containing multiple potentially breeding males. Thus, home ranges may be larger because of enhanced defense capabilities (Peres 1989; Lehmann and Boesch 2003) and/or due to increased ranging related to male “prospecting” for breeding opportunities in adjacent groups. Further investigation into the role of natal males in defense and the timing of encounters with neighboring groups in relation to dispersal may allow for differentiation between these two explanations.

Future Reproductive Potential

Our finding of increased home range size in groups with two vs. one reproductive females and the lack of difference between groups with vs. without natal adult females, lends support to the reproductive potential explanation of home range size. Golden lion tamarin groups most frequently contain one breeding female and one breeding male and produce one or, occasionally, two litters of twins per year (Baker et al. 2002). However, reproductive potential is significantly greater in groups with multiple breeding females, in nearly all cases a mother and her daughter. It is not uncommon for groups with two reproductive females to give birth to 2-4 litters, with 5 or 6 surviving infants in a single year. Multiple breeding females are more common in groups containing an adult male unrelated to both reproductive females. Regardless

of the presence of an unrelated adult male, subordinate females that have not dispersed by 3 or 4 years of age are likely to breed (Dietz and Baker 1993; Dietz et al. 2000; Baker et al. 2002). As in the ecological constraints hypothesis, the presence of larger home ranges in groups with greater reproductive potential may be related to energetic demands. Rather than home ranges being constrained by current energetic demand (Clutton-Brock and Harvey 1977; Terborgh 1983; Chapman 1990; Wrangham et al. 1993), the increased range size appears to be related to future energetic needs. This explanation is consistent with other studies that predict a decrease in reproductive success if individuals are unable to expand home ranges as group sizes increase (Janson and van Schaik 1988; Isbell 1991; Janson and Goldsmith 1995).

The hypothesis that groups with high reproductive potential increase their range size in order to meet future energy needs assumes that the current range of the group would be insufficient to support a larger number of infants. We tested this assumption post hoc by examining tamarin productivity and infant survival in the smallest territories (i.e. those we expect to have the lowest total availability of food resources). We divided home ranges into size categories based on standard deviation: small (below 34.3 ha), medium (34.3-66.7 ha), and large (above 66.7 ha). We tested the differences among home range size categories using a one-way ANOVA, controlling for group size, group identity, and year effects. We found a significant relationship between home range size and number of infants born [$F(2, 126)=3.07$, $P=0.047$; Figure 4]. Small home ranges (0.04 ± 0.13) produced significantly fewer infants per year than large (0.70 ± 0.38 ; $t=2.01$, $P=0.048$) and medium sized home

ranges (0.60 ± 0.33 ; $t=2.15$, $P=0.034$). Medium sized home ranges were not significantly different from large home ranges ($t=0.32$, $P=0.74$). We also found a significant effect of home range size on number of litters produced annually [$F(2, 127)=4.06$, $P=0.02$; Figure 4]. Small home ranges (0.23 ± 0.12) produced significantly fewer litters than either medium (0.59 ± 0.16 ; $t=2.80$, $P=0.006$) or large home ranges (0.59 ± 0.22 ; $t=2.11$, $P=0.037$), with no significant difference found between medium and large home ranges ($t=0.03$, $P=0.98$). When including the number of infants born as a random covariate, there is no significant difference in the number of infants surviving in large, medium, and small home ranges per year as defined above [$F(2, 125)=0.68$, $P=0.51$].

Overall, small home ranges produced fewer litters and infants than did medium or large ranges. In fact, controlling for time since group formation, 15% of small-range years produced zero infants, while an additional 18% produced only one infant. This is compared to a 2% rate of zero births in medium-sized ranges and no instances of zero infants being born in large ranges. While infant survival was not significantly different between home range sizes, groups in the smallest home ranges may forego reproduction when infant survival is unlikely. It is unclear at what stage (mating, conception, pregnancy) in reproduction the process may be halted.

Predation and Population Density

Taken together, predation and population density explain 71% of the variation in lion tamarin home range size. However, research on the effect of increased predation pressure on movement patterns in other taxa has produced mixed results. Some studies found decreased movement in high pressure conditions (Norrdahl and

Korpimäki 1998) and decreased home range size (Borowski 1998; Nie and Liu 2005), while others reported no change in movement (Wolff and Davis-Born 1997; Hubbs and Boonstra 1998; Jonsson et al. 2000). The lack of a uniform effect on home range size may be explained by the species- or population-specific role predation plays in mediating changes in population density and demography.

Increased predation on lion tamarins resulted in decreased group size, fewer reproductive females and adult natal males in groups, and lower population density. As we have demonstrated, all of these factors are correlated with decreases in home range size, except population density. Overall, the effect of high levels of predation on home range size is negative. Home range size decreased from 52.6 ha during times of low predation to 45.3 ha during high predation. The decrease in home range size results from a predation-mediated change in group size, the number of reproductive females and the number of adult natal males in the group. The decrease in home range between groups with only one reproductive female vs. two reproductive females is 9.6 ha, while the decrease in range size in groups without vs. with natal adult males is 9.2 ha. Since the interaction between these two demographic variables on home range size was not significant, we would expect an additive effect of these factors and, therefore, a roughly 18.8 ha average decrease in home range size during times of high predation. The scale of this home range size decrease due to the loss of a reproductive female and all natal males is approximately equal to the observed 20.2 ha differential in home range size between small vs. large groups. However, the predator-mediated decrease in population density, correlated with an increase in home range size, offset some of the home range size decrease associated with smaller groups and the group

composition changes, resulting in an overall 7.3 ha decrease in home range size in times of intense predation.

The lack of a predation effect on the number of natal females in groups may be explained by emigration patterns observed in this population. Although the mean age of dispersal is approximately the same for natal males and females, a higher proportion of dispersing males move directly into potential breeding positions in adjacent groups (Baker et al. 2002). While high predation periods provided adult natal males with the opportunity to disperse into potential breeding positions, previous studies have shown that natal females typically leave their groups through forced evictions, regardless of changes caused by predation (Baker et al. 2002).

In conclusion, our results indicate that variation in predation mediates changes in several demographic factors, and it is these alterations in group composition and population density that explain the observed changes in home range size. Increased predation results in smaller lion tamarin home ranges because of the combined effects of decreased group size (i.e. decreased energetic constraints), fewer adult natal males in the group (i.e. diminished group defense and/or reduced need for “prospecting”), and fewer reproductive females in the group (i.e. less future reproductive potential). The effect of these factors is offset by lower population density during high predation, which results in range expansion due to reduced pressure from neighboring groups. The potential that lion tamarins are investing in real estate to provide resources for future offspring is unexpected, but not counterintuitive. The size of a golden lion tamarin group can double or triple in one year. Given that changes in home range size occur slowly relative to the potential increase in group size, natural selection should

favor individuals that expand their range size as a function of the group's future reproductive potential rather than its current energy requirement.

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Figure Legends

Figure 1. a) The regression of average group biomass (\pm SE) on average home range size (\pm SE), b) The regression of average group habitat quality on average home range size.

Figure 2. Home range size (ha) \pm SE when one vs. two reproductive females and one vs. more than one reproductive males were present in the group.

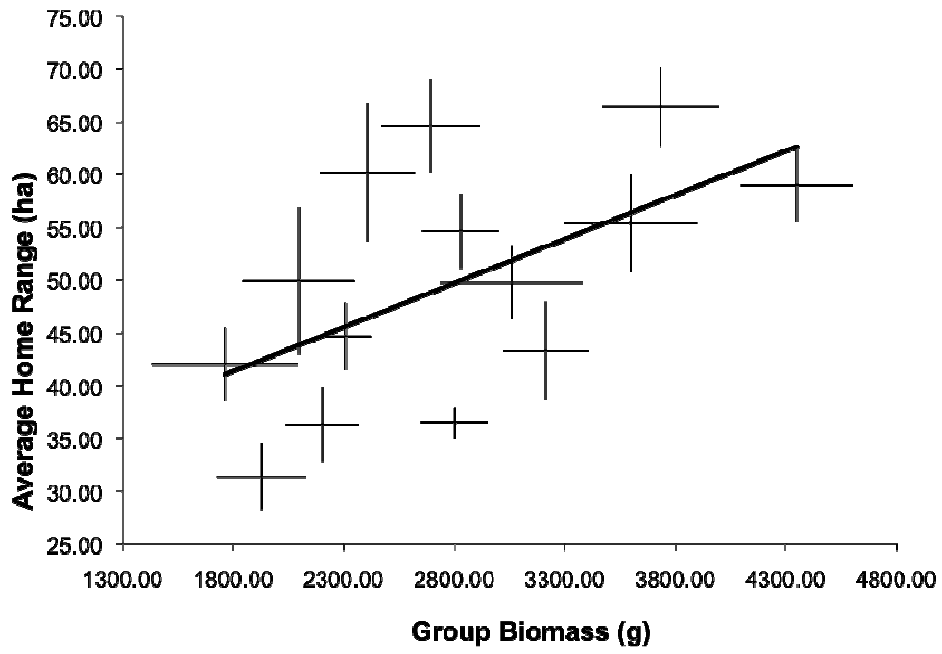
Figure 3. Regression of population density on average yearly home range size. Black squares represent the period of low predation (1987-May 1996, June 2004-2006). The white squares represent the period of high predation (June 1996-May 2004). The lines show the predicted regression line.

Figure 4. The average number of infants and litters born in small, medium, and large home range (HR) sizes \pm SE after controlling for group size.

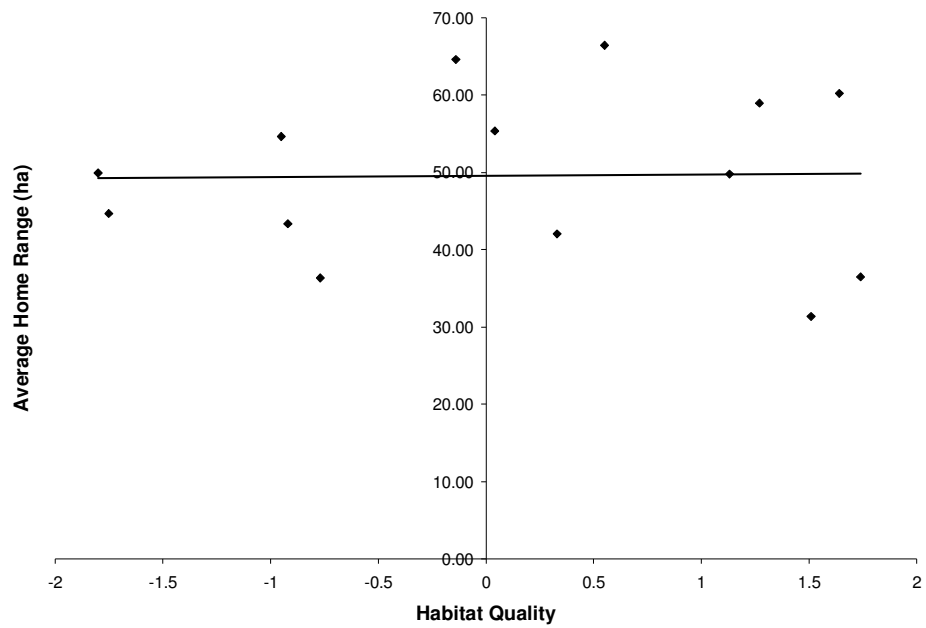
Figures

(Figure 1)

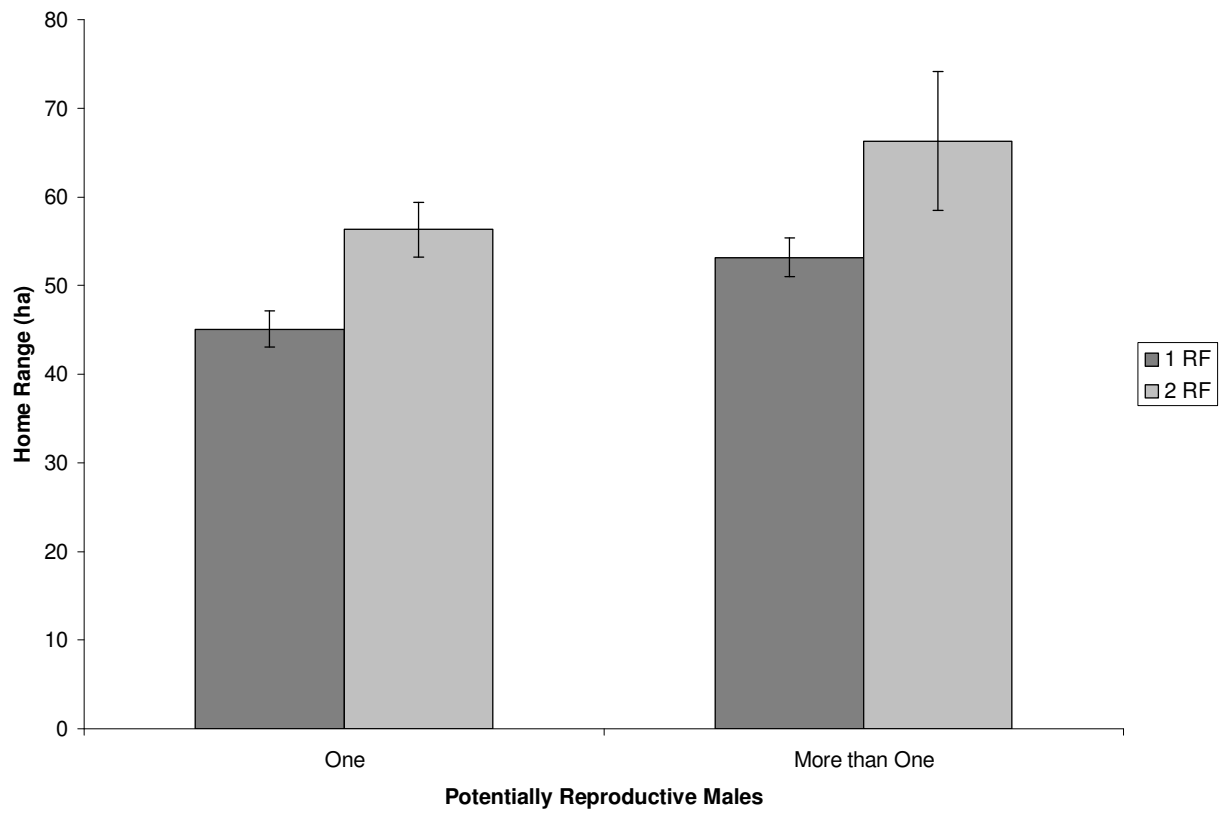
a)



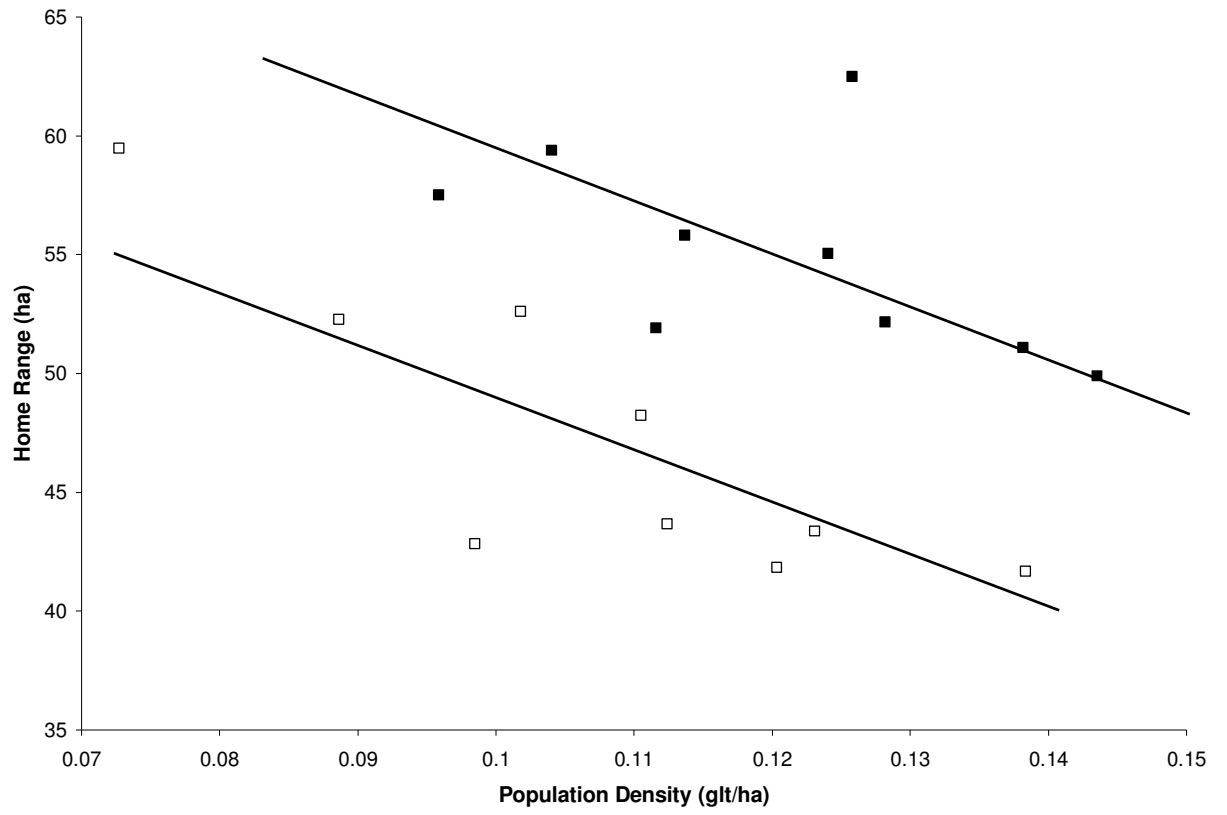
b)



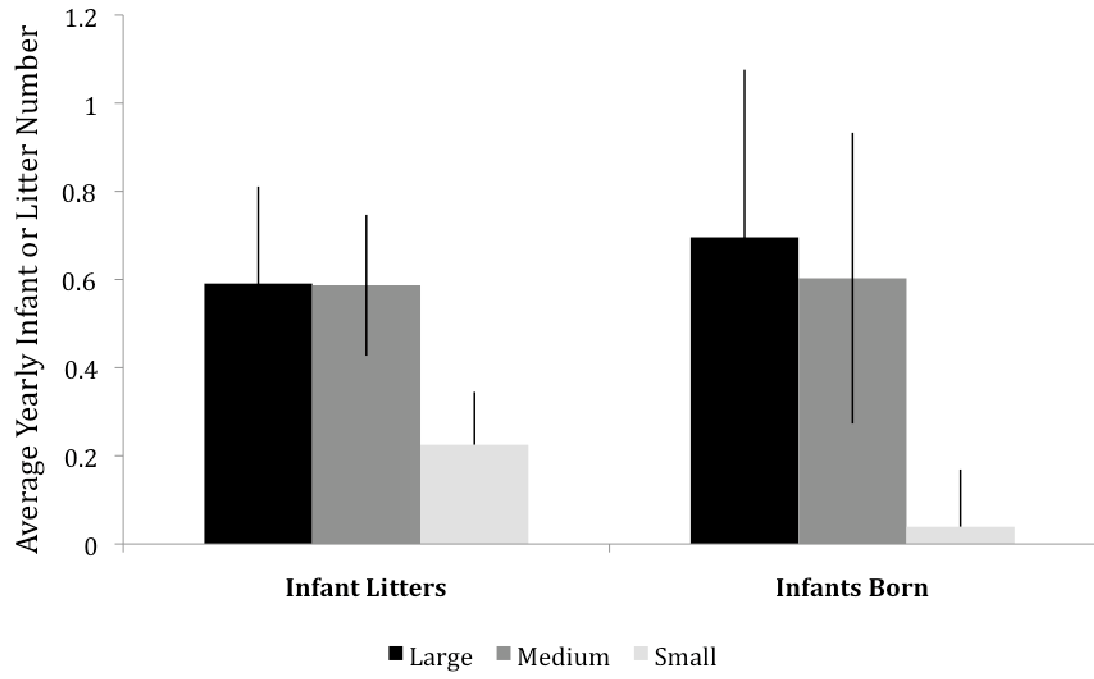
(Figure 2)



(Figure 3)



(Figure 4)



Appendix 1

Golden lion tamarin home range sizes from 1987-2006

Final home range and core area size for each group/year combination. N indicates the number of statistically independent data points used in the analysis. Group size, not including infants, is included for comparison.

Group	Year	h_{LSCV}	N	Home Range Size (ha)	Core Area Size (ha)	Polygons in home range	Polygons in core area	Group Size (no infants)
2F	19871988	52.03	44.45	8.63	1262	2	3	3
2F	19881989	51.52	50.05	8.94	895	1	4	5
2F	19891990	44.08	43.74	3.97	745	3	3	5
2F	19901991	41.7	43.96	7.21	456	1	3	5
2F	19911992	66.06	76.63	5.56	803	5	5	6
2F	19921993	56.95	59.97	4.27	566	2	3	8
2F	19931994	52.72	40.52	3.16	307	2	2	6
2F	19941995	58.27	56.44	6.71	282	1	5	4

Group	Year	h_{LSCV}	N	Home Range Size (ha)	Core Area Size (ha)	Polygons in home range	Polygons in core area	Group Size (no infants)
2F	19951996	42.1	47	6.56	602	3	3	4
2F	19961997	38.82	42.24	5.41	1036	1	3	4
2F	19971998	41.88	49.97	5.36	1205	1	4	5
2F	19981999	41.02	54.72	6.63	1333	2	3	5
2F	19992000	43.77	34	2.09	356	2	1	4
2M2	19911992	40.73	25.72	1.59	505	3	2	5
2M2	19921993	40.77	27.33	1.84	624	3	2	6
2M2	19931994	55.1	51.04	7.48	391	1	5	8
2M2	19941995	59.96	63.35	6.24	388	2	2	6
2M2	19951996	48.63	46.31	4.41	588	1	3	6
2M2	19961997	42.7	43.8	2.3	631	1	2	5
2M2	19971998	35.4	37.36	2.23	1172	1	1	5
2M2	19981999	36.8	32.8	1.78	848	2	1	4
2M3	19992000	54.62	82.83	6.62	821	2	2	4

Group	Year	h_{LSCV}	N	Home Range Size (ha)	Core Area Size (ha)	Polygons in home range	Polygons in core area	Group Size (no infants)
2M3	20002001	30.16	27.82	1.66	909	3	3	2
2M3	20012002	30.6	23.41	0.49	713	1	1	5
2M3	20022003	44.25	50.02	4.26	449	6	4	6
2M3	20032004	51.25	56.94	3.05	874	2	2	3
2M3	20042005	43.75	45.89	4.7	578	3	2	3
2M3	20052006	48.44	53.85	6.45	346	1	2	3
3M	19871988	51.85	76.38	8.49	1284	1	4	6
3M	19881989	45.96	66.12	4.89	1245	1	3	7
3M	19891990	53.17	82.17	5.44	1018	1	6	8
3M	19901991	59.41	65.54	13.08	406	2	4	8
3M	19911992	59.49	67.91	7.38	462	3	2	10
3M	19921993	57.81	69.98	6.49	570	2	2	7
3M	19931994	52.38	51.73	3.48	644	1	3	6
3M	19941995	48.86	44.76	11.39	515	2	2	7

Group	Year	h_{LSCV}	N	Home Range Size (ha)	Core Area Size (ha)	Polygons in home range	Polygons in core area	Group Size (no infants)
3M	19951996	51.24	57.24	2.95	687	1	2	5
3M	19961997	45.56	50.99	5.25	1056	2	4	5
3M	19971998	46.68	58.77	10.03	838	1	3	3
3M5	20012002	40.58	42.93	3.08	1428	4	2	4
3M5	20022003	44.16	48.51	2.47	1323	3	4	4
3M5	20032004	41.49	47.29	1.48	1282	3	3	3
3M5	20042005	62.24	32.66	2.14	301	5	1	1
AL	19981999	63.8	53.17	3.05	198	1	2	4
AL	20002001	50.37	67.52	2.91	766	1	3	6
AL	20012002	43.46	43.39	1.72	905	2	3	7
AL	20022003	47.22	63.49	9.98	1043	1	6	7
AL	20032004	48.61	56.99	8.88	685	2	5	5
AL	20042005	42.81	40.63	11.72	1147	2	2	3
AL	20052006	46.07	34.81	4.05	609	2	2	4

Group	Year	h_{LSCV}	N	Home Range Size (ha)	Core Area Size (ha)	Polygons in home range	Polygons in core area	Group Size (no infants)
BO	19891990	50.28	25.96	3.02	658	5	2	6
BO	19901991	81.73	69.1	6.95	449	1	2	6
BO	19911992	76.92	66.64	5.01	637	2	1	8
BO	19921993	70.45	61.04	7.25	601	2	3	8
BO	19931994	67.78	62.83	4.7	390	1	2	8
BO	19941995	77.39	80.33	9.62	714	1	4	9
BO	19951996	70.92	74.1	13.36	511	1	2	10
BO	19961997	67.15	69.44	10.1	1061	1	2	4
BO	19971998	60.15	49.16	4.54	1069	1	2	3
BO	19981999	52.73	45.26	2.8	1459	1	2	3
BO	19992000	57.67	43.84	3.36	1435	2	1	3
BO	20002001	53.42	36.54	2.07	976	4	2	4
BO	20012002	36.73	22.56	0.87	666	3	1	6
BO	20022003	43.07	44.84	1.88	1228	5	4	8

Group	Year	h_{LSCV}	N	Home Range Size (ha)	Core Area Size (ha)	Polygons in home range	Polygons in core area	Group Size (no infants)
BO	20032004	54.59	58.41	1.87	1678	4	2	8
BO	20042005	54.59	58.41	1.87	1067	4	2	9
BO	20052006	62.37	71.8	7.38	730	3	4	9
CJ	20002001	46.43	33.03	3.59	613	1	1	3
CJ	20012002	45.83	34.13	4.4	1022	2	4	3
CJ	20022003	44.45	26.79	2.11	1137	1	2	5
CJ	20032004	47.72	32.61	5.78	895	1	3	4
CJ	20042005	51.14	38.54	5.03	759	1	2	4
CJ	20052006	50.5	25.06	2.65	772	4	2	4
FA	19891990	45.88	44.05	5.03	431	1	3	2
FA	19901991	59.5	64.67	7.85	377	1	2	4
FA	19911992	66.22	49.88	11.56	115	1	3	5
FA	19921993	63.96	53.16	5.43	305	1	2	4
FA	19931994	63.09	66.14	15.16	505	2	5	4

Group	Year	h_{LSCV}	N	Home Range Size (ha)	Core Area Size (ha)	Polygons in home range	Polygons in core area	Group Size (no infants)
FA	19941995	76.94	47.88	6.21	241	2	2	5
FA	19951996	64.43	80.55	9.33	556	1	3	6
FA	19961997	61.62	81.26	7.97	855	1	4	7
FA	19971998	52.25	60.19	3.82	915	1	1	6
FA	19981999	55.29	89.14	12.93	1131	1	3	4
FA	19992000	50.06	77.28	8.51	1302	2	2	4
GC	19871988	55.42	74.58	6.77	1528	1	3	6
GC	19881989	76.1	104.82	17.33	730	1	2	6
GC	19891990	56.42	44.53	3.07	451	6	1	3
GC	19901991	46.42	39.36	3.23	456	1	2	3
GC	19911992	45.8	28.25	2.9	305	5	2	4
GC	19921993	34.74	23.32	3.17	282	1	4	4
GC	19931994	55.65	26.87	1.45	109	1	1	4
GC	19941995	54.58	43.55	5.52	171	1	3	6

Group	Year	h_{LSCV}	N	Home Range Size (ha)	Core Area Size (ha)	Polygons in home range	Polygons in core area	Group Size (no infants)
GF	19881989	45.33	38.22	4.2	953	1	2	4
GF	19891990	55.3	56.02	6.64	644	2	4	4
GF	19901991	54.95	36.87	1.8	418	6	1	5
GF	19911992	66.23	71.12	4.06	257	2	4	5
GF	19921993	58.08	36.52	6.04	261	3	2	4
GF	19931994	65.04	50.9	4.25	272	1	2	4
GF	19941995	49.31	26.19	3.67	340	1	2	2
GF	19951996	44.84	31.18	7.75	748	1	4	3
GF	19961997	32.9	30.38	3.45	1153	1	2	4
GF	19971998	37.31	28.23	0.91	1200	1	2	6
GF	19981999	48.04	49.36	1.13	1295	1	1	5
GF	19992000	51.46	52.77	1.31	1761	1	1	4
GF	20002001	50.5	53.57	2.17	1380	1	2	4
GF	20012002	53.42	57.5	2.01	792	2	1	3

Group	Year	h_{LSCV}	N	Home Range Size (ha)	Core Area Size (ha)	Polygons in home range	Polygons in core area	Group Size (no infants)
GF	20022003	36.3	31.61	4.24	1363	5	2	3
GF	20032004	35.41	30.85	1.72	1062	3	4	4
GF	20042005	21.28	60.02	5.18	945	4	4	5
GF	20052006	54.59	67.31	3.11	731	1	3	5
PA	20012002	55.35	59.86	5.43	852	2	3	4
PA	20022003	68.23	48.91	3.58	296	1	1	3
PA	20042005	47.21	60.08	5.64	781	3	1	5
PA	20052006	60.04	71.85	9.03	424	1	3	4
PP	19871988	35.37	32.55	3.52	1438	2	3	6
PP	19881989	35.04	32.91	9.11	1087	1	2	5
PP	19891990	39.5	31.13	6.11	787	1	4	5
PP	19901991	43.35	33.43	4.24	527	1	3	5
PP	19911992	47.89	41.03	6.47	496	4	1	6
PP	19921993	45.57	32.51	5.4	361	2	3	6

Group	Year	h_{LSCV}	N	Home Range Size (ha)	Core Area Size (ha)	Polygons in home range	Polygons in core area	Group Size (no infants)
PP	19931994	54.5	48.14	4.71	343	1	3	5
PP	19941995	47.16	35.44	3.33	385	2	4	5
PP	19951996	48.14	40.03	4.11	556	1	3	4
PP	19961997	35.71	32.77	2.07	928	1	3	4
PP	19971998	31.35	28.19	1.41	1116	4	1	3
PP2	19981999	32.2	30.34	5.31	933	2	3	2
PP2	19992000	33.44	37.89	7.65	1457	2	7	2
PP2	20002001	35.27	32.34	0.71	1138	1	1	2
PP2	20012002	37.27	35.96	4.88	738	3	2	4
PP2	20022003	34.12	32.85	2.93	1277	1	5	5
PP2	20032004	40.33	43.2	6.33	1014	1	6	4
PP2	20042005	35.87	27.46	2.61	831	3	4	4
PP2	20052006	25.44	16.87	2.47	766	2	3	4
SA	19871988	51.58	57.04	3.61	1595	1	2	9

Group	Year	h_{LSCV}	N	Home Range Size (ha)	Core Area Size (ha)	Polygons in home range	Polygons in core area	Group Size (no infants)
SA	19881989	58.66	70.56	5.78	1227	1	4	8
SA	19891990	61.53	57	2.98	867	1	1	10
SA	19901991	67.99	69.22	3.8	537	1	1	10
SA	19911992	59.56	70.03	6.1	654	1	1	9
SA	19921993	58.79	54.69	8.7	536	2	3	9
SA	19931994	54.81	45.91	4.56	419	2	1	6
SA	19941995	52.69	54.32	3.79	505	2	5	9
SA	19951996	47.31	45.22	3.78	586	1	2	7
SA	19961997	46.08	47.59	1.95	1222	1	1	6
SA	19971998	40.52	40.74	3.28	1027	2	1	7
SA	19981999	44.93	55.04	7.51	1243	2	6	6

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