

ABSTRACT

Title of dissertation: PROXIMATE MECHANISMS AND ULTIMATE CAUSES OF FEMALE REPRODUCTIVE SKEW IN COOPERATIVELY BREEDING GOLDEN LION TAMARINS, *LEONTOPITHECUS ROSALIA*

MaLinda Dawn Henry, Doctor of Philosophy, 2011

Dissertation directed by: Professor James M. Dietz
Behavior, Ecology, Evolution, & Systematics

Many cooperatively breeding species exhibit high reproductive skew. Delayed dispersal and cooperative breeding may have evolved as a consequence of the limits ecological constraints place on independent breeding. When simultaneous breeding by multiple females reduces the survival of the dominant's offspring, selection should favor dominants able to control subordinate reproduction. Monopolization of reproduction by dominant group members by means of suppression of subordinate reproduction has been documented in several taxa of cooperative breeders. In this dissertation I examine the proximate mechanisms and ultimate causes of reproductive skew in cooperatively breeding golden lion tamarins (*Leontopithecus rosalia*). In chapter one I combine data from phenological transects with hormonal evaluation of reproductive status to test whether caloric availability limits reproduction by female tamarins. Caloric availability

was sufficient to support not only pregnancy polygyny in 83% of tamarin groups, but also the additional group members resulting from multiple litters. The super abundance of calories and the timing of births suggested that competition for allocare rather than for food resources may be the selective force limiting reproduction by subordinate females. In my second chapter I combine hormonal and demographic data to explain reproductive skew in terms of the costs and benefits to subordinate fitness under existing social circumstances. Subordinate females older than 18 months of age ovulated while residing within their natal group, but conceptions were delayed one to two years following reproductive maturity. The likelihood of successful reproduction by a subordinate female doubled with each year of age of the dominant female. Conceptions under incestuous mating conditions were rare (7 of 37 pregnancies). My results provide support for the hypothesis that subordinate adult females under three years old exercise reproductive self-restraint. I speculate that the threat of being evicted from the group and inbreeding avoidance are sufficient to delay attempts at reproduction by young subordinates without the need for costly fighting with the dominant female. In my third chapter I test whether reproduction by subordinate adult female tamarins is limited by dominant females who have incomplete control (incomplete control model, ICM) or complete control (optimal skew model, OSM) over subordinate reproduction. I combine hormonal data with group demography and caloric availability to determine variables useful in predicting a successful pregnancy to a subordinate female. Whereas subordinate females younger than 2.5 years of age ovulated but did not conceive, all females older than 3.9 years of age became pregnant. Reproduction in subordinate adult females was not limited by hormonal suppression of ovulation or conception, but by the failure of 7 of 11

pregnancies to produce live offspring. The likelihood of reproductive success increased 1.7 times with each additional group member. My results suggest that when caloric availability is sufficient to support reproduction by two breeding females and the group members necessary to provide allocare for two litters, subordinate females do not abide by a social contract that would limit their reproduction (OSM). Instead, older subordinates compete with dominant females for reproduction and succeed in producing live young if the dominant female is at least 10 years old, if subordinates conceive while the dominant is heavily pregnant, and if they reside within larger groups (ICM).

PROXIMATE MECHANISMS AND ULTIMATE CAUSES OF FEMALE
REPRODUCTIVE SKEW IN COOPERATIVELY BREEDING GOLDEN LION
TAMARINS, *LEONTOPITHECUS ROSALIA*

by

MaLinda Dawn Henry

Dissertation submitted to the Faculty of the Graduate School of the
University of Maryland, College Park in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
2011

Advisory Committee:

Professor James M. Dietz, Chair
Assistant Professor Daniel Gruner
Professor David W. Inouye
Professor Mary Ann Ottinger
Dr. Katerina V. Thompson

© Copyright by

MaLinda Dawn Henry

2011

PREFACE

This dissertation contains an introduction section and three chapters. All chapters are presented in manuscript form, with abstract, introduction, methods, statistical analyses, results, discussion, and acknowledgements, followed by tables, figure legends, and figures. A single bibliography is provided at the end.

ACKNOWLEDGEMENTS

I would like to thank my committee for their guidance, support, and patience: James Dietz, Dan Gruner, David Inouye, Mary Ann Ottinger, and Kaci Thompson. I sincerely appreciate the substantial intellectual and editorial contributions made by Jim Dietz throughout the planning, execution, and writing of this dissertation. I also acknowledge the contributions made by the late Bob Denno to the ideas and methodologies contained within this dissertation. Jeff French has served as a second advisor providing invaluable advice and assistance with the endocrinological portions of this dissertation.

I thank the Brazilian Science Council (CNPq), Brazilian Institute for the Environment and Renewable Natural Resources (IBAMA), and the Golden Lion Tamarin Association (AMLD) for logistic support and permission to conduct this study. Funding for this project was provided by the American Society of Mammalogists, the Copenhagen Zoo Lion Tamarins of Brazil Fund, the University of Maryland Center for Biodiversity, a Darwin Fellowship from the University of Maryland BEES Program, and a Wylie Dissertation Fellowship from the University of Maryland Graduate School to M. Henry and by the National Science Foundation (SBR-9727687; BCS-0216096) to J. Dietz.

For assistance in the field, I thank Otávio Narciso, Synval de Melo, Jadir Ramos, and Andréia Martins. A special thanks to Ademilson de Oliveira who taught me to identify Brazilian plant species and helped me set up phenological transects. I thank Sarah Hankerson and Fabiano Godoy for creation of habitat maps. A special thanks to Sarah Hankerson for her invaluable statistical expertise and creative analytical mind. I thank Jennifer Siani for weekly tamarin weight data and Kimran Miller-Buckholz for

plant species identifications, dry weights, and caloric values. I thank Karen Bales for setting the precedent for endocrine work in this population of tamarins. Thanks to Tom Shirazi, Jeff Fite, and Kate Townley for assistance in endocrine analyses. I thank Lois Reid for making it possible for me to work in Brazil while remaining a doctoral student at the University of Maryland. Finally, I would like to thank my family for everything from sorting fecal samples to providing child care. Their unlimited love and support have made this possible.

TABLE OF CONTENTS

PREFACE.....	ii
ACKNOWLEDGEMENTS.....	iii
TABLE OF CONTENTS.....	v
LIST OF TABLES.....	ix
LIST OF FIGURES.....	x
INTRODUCTION.....	1
Chapter 1: Caloric availability does not limit reproduction in female golden lion tamarins (<i>Leontopithecus rosalia</i>).....	13
ABSTRACT.....	13
INTRODUCTION.....	14
Golden lion tamarin mating system.....	14
Food limitation hypothesis.....	15
Caloric availability affects ovulation and conception.....	17
Caloric availability affects reproductive success.....	19
Group size affects reproductive success.....	24
Timing affects reproductive success.....	25
Questions, hypotheses, predictions.....	26
METHODS.....	28
Study site.....	28
Study species.....	29
Individual identification and weighing.....	29
Behavioral observations.....	30
Fecal sample collection.....	31
Pregnanediol-3-glucuronide (PdG) and cortisol extraction from feces.....	32
PdG immunoassay.....	32
Cortisol immunoassay.....	34
Detection of ovulation, pregnancy, parturition, and abortion.....	35
PdG and cortisol averages by trimester.....	39
Interfemale interbirth intervals.....	40
Home range and habitat type quantification.....	40
Caloric availability.....	41
Minimum monthly caloric requirement.....	44
STATISTICAL ANALYSES.....	45
Hormonal changes associated with pregnancy.....	45
Hormonal profiles for successful versus non-successful pregnancies.....	46
Effect of caloric availability on reproductive success.....	48
Effect of group size and dominance on reproductive success.....	48
Timing of successful subordinate reproduction.....	49

RESULTS	49
Ovulation and conception	49
Hormonal changes associated with pregnancy	50
Hormonal profiles for successful versus non-successful pregnancies	52
Effect of caloric availability on reproductive success	53
Effect of group size and dominance on reproductive success	54
Timing of successful subordinate reproduction	54
DISCUSSION	55
Caloric abundance may promote pregnancy polygyny in GLTs	55
Caloric availability is not responsible for the alteration of hormonal profiles observed in failed pregnancies	58
Caloric availability is sufficient to support polygyny in large GLT groups	60
The availability of helpers rather than calories limits the timing of successful subordinate reproduction	61
ACKNOWLEDGEMENTS	63
TABLES	65
FIGURE LEGENDS	67
FIGURES	69

Chapter 2: Self-restraint limits reproduction by young adult subordinate female golden lion tamarins (<i>Leontopithecus rosalia</i>)	74
ABSTRACT	74
INTRODUCTION	75
Threat of eviction	81
Inbreeding avoidance	82
Hypotheses and predictions	85
METHODS	86
Study site	86
Study species	87
Individual identification and weighing	87
Behavioral observations	88
Fecal sample collection	89
Pregnanediol-3-glucuronide (PdG) and cortisol extraction from feces	90
Enzyme immunoassay (EIA) for PdG	90
Enzyme immunoassay (EIA) for cortisol	91
Detection of ovulation, pregnancy, parturition, and abortion	91
STATISTICAL ANALYSES	94
Threat of eviction and inbreeding avoidance	94
RESULTS	95
Subordinate ovulation without conception	95
Threat of eviction and inbreeding avoidance	96
DISCUSSION	97
Subordinate ovulation without conception	97
Threat of eviction and inbreeding avoidance	99
ACKNOWLEDGEMENTS	103
TABLES	104

FIGURE LEGENDS.....	105
FIGURES.....	106
Chapter 3: Incomplete control limits reproduction in older subordinate female golden lion tamarins (<i>Leontopithecus rosalia</i>).....	107
ABSTRACT.....	107
INTRODUCTION.....	109
Reproductive skew models.....	112
Hormonal control of subordinate reproduction.....	114
Behavioral control of subordinate reproduction.....	117
Stress in subordinate females.....	119
Age effects on subordinate reproduction.....	122
Timing of subordinate reproduction.....	127
Ecological constraints on subordinate reproduction.....	133
Hypotheses and predictions.....	136
METHODS.....	139
Study site.....	139
Study species.....	139
Individual identification and weighing.....	140
Behavioral observations.....	141
Fecal sample collection.....	142
Pregnanediol-3-glucuronide (PdG) and cortisol extraction from feces.....	142
Enzyme immunoassay (EIA) for PdG.....	143
Enzyme immunoassay (EIA) for cortisol.....	144
Detection of ovulation, pregnancy, parturition, and abortion.....	144
PdG and cortisol averages by trimester.....	147
Interfemale interbirth interval.....	147
Home range and habitat type quantification.....	148
Caloric availability.....	148
STATISTICAL ANALYSES.....	150
Stress in subordinate females.....	150
Effect of dominance, maternal age, and group size on reproduction.....	153
Effect of age of dominant female, timing of subordinate reproduction, and group size on reproduction.....	153
Effect of caloric availability on reproduction.....	154
RESULTS.....	154
Hormonal and behavioral control of subordinate reproduction.....	154
Stress in subordinate females.....	155
Effect of dominance, maternal age and group size on reproduction.....	156
Effect of age of dominant female, timing of subordinate reproduction, and group size on reproduction.....	157
Effect of caloric availability on reproduction.....	158
DISCUSSION.....	159
Hormonal control of subordinate reproduction.....	159
Behavioral control of subordinate reproduction.....	161
Stress in subordinate females.....	162

Age of the dominant female affects subordinate reproduction.....	164
Timing of subordinate reproduction	167
Ecological constraints on subordinate reproduction.....	169
ACKNOWLEDGEMENTS.....	171
TABLES	173
FIGURE LEGENDS.....	175
FIGURES.....	177
BIBLIOGRAPHY.....	180

LIST OF TABLES

CHAPTER 1

Table 1.1. Summary of the predictions generated by the food limitation hypothesis and empirical findings in golden lion tamarins. (Bold italics indicate predictions consistent with findings in golden lion tamarins. See text for explanations and additional details.)

Table 1.2. Reproductive summary for 21 GLT females from 7 free-ranging GLT groups sampled from March of 2004 through February of 2007.

CHAPTER 2

Table 2.1. Ovulatory status (O=ovulatory, N=non-ovulatory) and age at first conception for 21 GLT females from 7 free-ranging golden lion tamarin groups for which fecal samples were collected from March 2004 through February 2007.

CHAPTER 3

Table 3.1. Summary of reproductive and demographic data for 21 GLT females from 7 free-ranging GLT groups sampled from March of 2004 through February of 2007.

Table 3.2. Summary of the predictions generated by reproductive skew models and empirical findings in golden lion tamarins. (Bold italics indicate predictions consistent with findings in golden lion tamarins. See text for explanations and additional details.)

LIST OF FIGURES

CHAPTER 1

Figure 1.1. Mean (\pm standard error) fecal pregnanediol-3-glucuronide (PdG) and cortisol concentrations for adult females while non-pregnant (NP, n=179 samples, from 18 females) and during each trimester of pregnancy (1st trimester, I, n=65, 14; 2nd trimester, II, n=65, 14; 3rd trimester, III, n=58, 14). Statistically significant differences in means are indicated by different letters.

Figure 1.2. Mean (\pm standard error) fecal pregnanediol-3-glucuronide (PdG) and cortisol concentrations for successful vs. non-successful pregnancies just prior to conception (NP, n=32 pregnancies, 23 successful, 9 non-successful), during the 1st trimester (I, n=36, 26, 10), during the 2nd trimester (II, n=35, 25, 10), and during the 3rd trimester of pregnancy (III, n=31, 23, 8). Statistically significant differences in means are indicated by an asterisk.

Figure 1.3. Kilocalories from fruit and nectar contained within 7 GLT home ranges each month from March of 2004 through February of 2007 exceeded the 13,610 kcal/month requirement (blue horizontal line) for supporting the average group of GLTs and their reproduction.

Figure 1.4. Progesterone (PdG) profiles for a dominant mother (GLT720) and her subordinate daughter (GLT848) demonstrating that conceptions by the subordinate while the dominant female was heavily pregnant with her first litter of the year and prior to conception of the second litter by the dominant female were more likely to result in the birth of live infants. Green arrows indicate dates of conceptions resulting in the birth of live young (subsequent red arrow). Blue arrows indicate conceptions that resulted in

pregnancy loss. Red arrows indicate successful parturition dates. Note that the first two successful infant births by GLT848 (red arrows) occur between the birth of the first (red arrow in September) and second (red arrow in January or February) annual litters by GLT720, resulting in the staggering of successful births to the subordinate daughter between births to the dominant mother.

Figure 1.5. Progesterone (PdG) profiles for the eldest female in the study (GLT539) and her eldest daughter (GLT846). GLT539 was dominant until after the birth of her second litter in February of 2005 when GLT846 became dominant. While subordinate to her mother, GLT846 successfully reproduced when she conceived while her mother was heavily pregnant with her first litter of the year. Pregnancies by GLT539 that were conceived at the same time as those of her dominant daughter were lost at full term. Green arrows indicate dates of conceptions resulting in the birth of live young. Blue arrows indicate conceptions that resulted in pregnancy loss. Red arrows indicate successful parturition dates. Note that successful reproduction (red arrows) by two females during the same reproductive year occurred only when pregnancies were staggered.

CHAPTER 2

Figure 2.1. Ovulatory cycles as demonstrated by cyclical elevation in PdG concentrations in two subordinate adult females a) GLT 880 from 1.6-2.5 years of age and b) GLT 1227 from 1.5-2.9 years of age prior to first conception.

CHAPTER 3

Figure 3.1. Mean (\pm standard error) cortisol concentrations for successful vs. non-successful pregnancies just prior to conception (NP, n=32 pregnancies, 23 successful, 9

non-successful), during the 1st trimester (I, n=36, 26, 10), during the 2nd trimester (II, n=35, 25, 10), and during the 3rd trimester of pregnancy (III, n=31, 23, 8). Differences in means were not statistically significant according to linear mixed model analysis of variance.

Figure 3.2. Progesterone (PdG) profiles for a dominant mother (GLT720) and her subordinate daughter (GLT848) demonstrating that conceptions by the subordinate while the dominant female was heavily pregnant with her first litter of the year and prior to conception of the second litter by the dominant female were more likely to result in the birth of live infants. Green arrows indicate dates of conceptions resulting in the birth of live young (subsequent red arrow). Blue arrows indicate conceptions that resulted in pregnancy loss. Red arrows indicate successful parturition dates. Note that the first two successful infant births by GLT848 (red arrows) occur between the birth of the first (red arrow in September) and second (red arrow in January or February) annual litters by GLT720, resulting in the staggering of successful births to the subordinate daughter between births to the dominant mother.

Figure 3.3. Progesterone (PdG) profiles for the oldest female in the study (GLT539) and her eldest daughter (GLT846). GLT539 was dominant until after the birth of her second litter in February of 2005 when GLT846 became dominant. While subordinate to her mother, GLT846 conceived a successful litter while her mother was heavily pregnant with her first litter of the year. Pregnancies by GLT539 that were conceived at the same time as those of her dominant daughter were lost at full term. Green arrows indicate dates of conceptions resulting in the birth of live young. Blue arrows indicate conceptions that resulted in pregnancy loss. Red arrows indicate successful parturition

dates. Note that successful reproduction (red arrows) by two females during the same reproductive year occurred only when pregnancies were staggered.

INTRODUCTION

Cooperative breeding in which the young born to one or more breeding females are reared by non-reproductive helpers is rare among social mammals and is most highly developed in four taxa (Clutton-Brock, 2009): the marmosets and tamarins (*Callitrichidae*) (Goldizen, 1987a; Goldizen, 1987b; Tardif et al., 2002; Digby et al., 2007); the dogs (*Canidae*) (Moehlman, 1986; Creel & Creel, 2001); the diurnal mongooses (*Herpestidae*) (Rood, 1986; Creel & Waser, 1997; Clutton-Brock, 2006); and African mole-rats (*Bathyergidae*) (Bennett & Faulkes, 2000; Faulkes & Bennett, 2007). Across taxa, cooperative breeding is associated with high reproductive skew, defined as the monopolization of reproduction by one or a few group members (mammals: (Solomon & French, 1997a); birds: (Reyer et al., 1986; Mays et al., 1991; Schoech et al., 1991); fishes: (Fitzpatrick et al., 2008); and invertebrates: (Hamilton, 2004)). Limited opportunities for subordinate reproduction within the group combined with few options for successful dispersal and reproduction outside the group (Baker & Dietz, 1996; Goldizen et al., 1996; Clutton-Brock et al., 1998a; Clutton-Brock et al., 2001a; Baker et al., 2002; Clutton-Brock et al., 2006) may lead to the evolution of non-breeding helpers. Helpers improve growth and survival of the dominant's offspring (in birds: (Brown, 1987); coyotes (*Canis latrans*): (Bekoff & Wells, 1982); African wild dogs (*Lycaon pictus*): (Malcolm & Marten, 1982; Creel & Creel, 2001); blackbacked jackals (*Canis mesomelas*): (Moehlman, 1979); meerkats (*Suricata suricatta*): (Clutton-Brock et al., 2001b; Russell et al., 2003); dwarf mongooses (*Helogale parvula*): (Rood, 1990); badgers (*Meles meles*): (Kruuk, 1989); and marmosets and tamarins: (Dietz, 2004)). By helping to rear the young of related dominants (typically a mother or a sister),

subordinates with few options for their own reproduction benefit by increasing their own inclusive fitness (West-Eberhard, 1975; Sherman et al., 1995; Bourke, 1999; Ratnieks & Helanterä, 2009). Cooperative care reduces fitness costs associated with reproduction for the dominant female, increasing her rate of reproduction (Clutton-Brock et al., 1998b; Russell et al., 2003; Fite et al., 2005). Dominant females in cooperatively breeding species also have relatively long life spans (Arnold & Owens, 1998; Carey, 2001; Sherman & Jarvis, 2002), further augmenting the degree of reproductive skew (Hauber & Lacey, 2005; Clutton-Brock et al., 2006).

Golden lion tamarins (*Leontopithecus rosalia*) are cooperatively breeding callitrichid primates that display a high degree of reproductive skew. Golden lion tamarins (GLTs) reside in family groups of 2–11 individuals (Dietz & Baker, 1993; Dietz et al., 1994). Lion tamarin offspring typically delay dispersal and reproduction, and remain in their natal group to help with the care of infant siblings (Dietz & Baker, 1993). Cooperative care may be instrumental in the ability of callitrichids to meet the energetic needs associated with successfully rearing the litters of twins they are capable of producing either once or twice a year (Kleiman, 1977a; Sussman & Garber, 1987; Baker et al., 1993; Dietz & Baker, 1993). Dietz and Baker (1993) reported that reproduction was limited to a single dominant female (monogyny) in most GLT groups. Reproduction by two females in the same group (polygyny) occurred in only 10% of GLT groups. As long-term study continued, the incidence of rearing polygyny (more than one female rearing offspring to weaning) remained low (26.2% reported by Baker et al. (2002)), but pregnancy polygyny (more than one female confirmed as being pregnant within the same breeding season) was common (44.3% reported by Baker et al. (2002)). Polygyny has

been observed in an increasing number of callitrichid species (common marmosets (*Callithrix jacchus*): (Hubrecht, 1984; Digby & Ferrari, 1994; Digby, 1995b; Arruda et al., 2005); pygmy marmosets (*Cebuella pygmaea*): (Soini, 1982); cotton-top tamarins (*Saguinus oedipus*): (Savage et al., 1996a); saddle-back tamarins (*Saguinus fuscicollis*): (Goldizen et al., 1996); and moustached tamarins (*Saguinus mystax*): (Garber et al., 1984; Ramirez, 1984; Garber et al., 1993; Smith et al., 2001)). However, subordinate reproductive success remains lower than that of dominant females in both marmosets (Digby, 1995a; Arruda et al., 2005; Sousa et al., 2005; Saltzman et al., 2008; Saltzman et al., 2009) and tamarins (Price & McGrew, 1991; Goldizen et al., 1996; Savage et al., 1996a; Garber, 1997). The contradiction between high rates of pregnancy polygyny and low reproductive success by subordinate females encourages a re-examination of explanations for singular breeding in callitrichids.

Reports by Dietz and Baker (1993), Baker et al. (2002), French et al. (2003), and Hankerson (2008) point to ecological and social conditions leading to polygyny in GLT groups. Groups with two reproductive females were found more commonly within home ranges that contained more swamp forest (Dietz & Baker, 1993). Baker et al. (2002) suggested that polygyny may be more common on home ranges containing greater proportions of secondary and edge forest where food may be more abundant (Terborgh, 1983; Rylands, 1986; Rylands, 1987; Rylands & Faria, 1993). Larger home ranges contained more reproductive females (Hankerson, 2008). These studies provide indirect evidence in support of food limitation on GLT reproduction, but food resources were not directly quantified. French et al. (2003) suggested that polygyny was rare but did occur in some groups containing an old dominant female and at least one non-related male.

Based upon 16 years of demographic data, Dietz and Baker (unpublished data) found a significant positive relationship between the age category of the dominant female and the incidence of polygyny in GLT groups and concluded that older dominant females were no longer physically able to control reproduction by their subordinate daughters. Both studies were interpreted as providing support for the hypothesis of incomplete dominant control of subordinate reproduction, but could also provide support for the hypothesis that subordinate GLT females exercise reproductive self-restraint when they occupy groups with a young dominant female capable of evicting them from the natal group and when opportunities for non-incestuous matings do not exist within the group.

The goal of the current study is to examine the proximate mechanisms and ultimate causes of female reproductive skew in cooperatively breeding GLTs. My first chapter provides a test of the ecological constraints model. Ecological constraints limiting independent breeding may explain the evolution of delayed dispersal and cooperative breeding in birds (as reviewed in Hatchwell & Komdeur (2000)) and mammals (Kleiman, 1977b; Creel & Creel, 1991). Reproduction in cooperatively breeding callitrichid primates may be especially constrained by food availability (Leutenegger, 1980; Kirkwood & Underwood, 1984; Goldizen, 1987a; Price, 1992c; Tardif, 1994; Sánchez et al., 1999; Miller et al., 2006). Their small body size and minimal body fat storage (Power et al., 2001; Power et al., 2008) may not allow the buildup of energy reserves necessary to meet the unusually large (Leutenegger, 1973; Hearn, 1983; Kirkwood, 1985; Tardif et al., 1993; Ross & MacLarnon, 1995; Nievergelt & Martin, 1999; Tardif et al., 2001) energetic demand of producing and raising one or two litters of twins weighing in excess of 20% of maternal body weight each year

(Leutenegger, 1973; Ford, 1980; Leutenegger, 1980; Dietz & Baker, 1993; Dietz et al., 1994; Bales et al., 2001). Callitrichid females with greater food availability are in better physical condition and are more likely to ovulate, carry pregnancies to term, produce larger litters, and successfully rear litters (Kirkwood, 1983; Dietz & Baker, 1993; Tardif & Jaquish, 1994; Tardif & Jaquish, 1997; Bales et al., 2001; Tardif et al., 2001; Bales et al., 2002; De Vleeschouwer et al., 2003; Tardif & Bales, 2004; Tardif et al., 2004; Tardif et al., 2005). The food limitation hypothesis predicts increased reproductive success for females breeding when food is readily available (van Schaik & van Noordwijk, 1985; Di Bitetti & Janson, 2000). The objectives of the first chapter are to determine whether reproduction in wild GLT groups is limited to a single breeding female and whether the availability of calories limits reproduction in female GLTs.

Reproductive skew models consider how the availability of a variety of resources (including food, shelter, mates, and helpers) changes under different social and ecological contexts, and how these changes affect individual patterns of behavior to limit reproduction to only a few breeding individuals per group (Clutton-Brock, 2009). In my second chapter I explain reproductive skew in GLTs in terms of the costs and benefits to subordinate fitness under existing social circumstances. Under the hypothesis of subordinate restraint, subordinates forego reproduction when existing social and ecological conditions make a reproductive investment unlikely to succeed (Reyer et al., 1986; Hamilton, 2004; Young et al., 2008; Saltzman et al., 2009). Subordinate females able to exercise reproductive restraint when the likelihood of success is low may avoid or minimize their investments in failed reproductive attempts as well as increase their own chances of survival and future reproduction (Wasser & Barash, 1983; Jaquish et al., 1991;

Digby, 1995a; Abbott et al., 1997; Saltzman, 2003; Gilchrist, 2006a; Saltzman et al., 2009).

Given the large investment these small-bodied primates make in a single reproductive attempt (owing to long gestation periods (French et al., 2002) and high infant to maternal body mass ratios (Leutenegger, 1973)), selection should favor females able to detect conditions unfavorable for reproduction and restrain their own reproductive activity accordingly (Saltzman et al., 2009). One would also expect subordinates to exercise this restraint early on in the reproductive process, such as prior to conception, before appreciable costs have already accrued (Wasser & Barash, 1983). Therefore, one assumption of the subordinate restraint model is that subordinate females are capable of reproducing but they do not attempt to do so (Saltzman et al., 2009). Subordinate females may delay reproduction by avoiding matings (Rothe, 1975; Abbott, 1984) or delaying conceptions (Arruda et al., 2005; Sousa et al., 2005).

A second assumption of this model is that the threat of eviction from the natal group or of losing a costly reproductive investment is sufficient to restrain subordinates from attempting reproduction without the constant struggle and overt aggression assumed to take place under incomplete control models (Saltzman et al., 2009). By exercising self-restraint in response to social cues that serve as early indicators of unfavorable reproductive conditions, subordinates may also avoid the energetic costs and potential risks that may arise from conflict with the dominant female (including mounting a stress response, engaging in aggressive fights, eviction from the natal group and the risks associated with dispersal, pregnancy loss, and/or infanticide) (Saltzman et al., 2009). Subordinate restraint has been demonstrated in cooperatively breeding species when the

threat of infanticide on subordinate young is high (Digby, 1995a; Saltzman, 2003; Saltzman et al., 2008; Young et al., 2008; Abbott et al., 2009; Saltzman et al., 2009), when the threat of eviction from the natal group upon any attempt to reproduce is high (Johnstone & Cant, 1999; Hamilton, 2004; Buston et al., 2007), and when the risk of mating with close relatives and suffering the consequences of inbreeding depression is high (incest avoidance) (Mays et al., 1991; Clarke et al., 2001; Hamilton, 2004). The objective of my second chapter is to test the hypothesis that reproductive skew in female GLTs results from subordinates exercising reproductive self-restraint rather than dominant suppression of subordinate reproduction. I examine whether subordinates forego reproduction when the threat of eviction from the natal group and potential for inbreeding are high.

Clutton-Brock (2009) suggested an evolutionary pathway linking cooperative breeding with reproductive skew that relies upon the premise that reproduction by subordinates reduces the fitness of the dominant (Clutton-Brock et al., 2001b; Hodge, 2009); therefore, selection should favor dominants able to control subordinate reproduction. My third chapter examines the mechanisms and extent of dominant control over subordinate reproduction in female GLTs. Incomplete control models (ICM) of reproductive skew, also called tug of war models, presume that there is an ongoing contest or power struggle for successful reproduction between dominant and subordinate females (Johnstone, 2000; Beekman et al., 2003; Hager, 2003) in which both the dominant and the subordinate females will try to disrupt each other's reproductive attempts (Young & Clutton-Brock, 2006; Saltzman et al., 2009). Under ICM subordinate reproductive success is determined by the physical condition, size, or strength of each

contender (Reeve & Sherman, 1991; Clarke & Faulkes, 1997; Bernasconi & Strassmann, 1999; Hodge et al., 2008). Dominant females are assumed to win most, but not all of these contests (Clutton-Brock, 1998; Reeve & Shen, 2006). Subordinate females are occasionally able to breed when dominants cannot prevent them from doing so (Clutton-Brock et al., 2001a; French et al., 2003; Clutton-Brock et al., 2008). The frequency of successful breeding by subordinates depends upon the costs and benefits accrued by dominants as a result of suppressing subordinate reproduction as well as the costs and benefits accrued by subordinates in attempting to breed (Emlen, 1995; Emlen et al., 1998; Reeve et al., 1998; Dietz, 2004; Clutton-Brock et al., 2008).

In optimal skew models (OSM), also called concessions models, it is assumed that dominant females have complete control over reproduction by subordinate females (Johnstone, 2000; Hager, 2003; Dietz, 2004; Buston et al., 2007). When it is of benefit to the dominant female, as when subordinate daughters in this cooperatively breeding species remain in their natal group and provide care for the offspring of the dominant mother (Bales et al., 2001; Dietz, 2004), she is predicted to share reproduction with her daughter as a concession to entice subordinates to remain in the group (Emlen, 1982; Clutton-Brock, 1998; Reeve et al., 1998; Reeve & Shen, 2006). Under OSM dominant females weigh the costs and benefits to themselves of each potential mating by a subordinate female under the current set of demographic and ecological conditions, and either allow or deny reproductive opportunities to subordinate females within their group according to what would be most likely to increase their own inclusive fitness (Emlen et al., 1998; Johnstone, 2000; Hager, 2003; Dietz, 2004). In contrast to ICM, OSM assumes that subordinate females only succeed in reproducing when allowed to do so by the

dominant female (Clutton-Brock, 1998; Reeve et al., 1998; Johnstone, 2000; Hager, 2003; Buston et al., 2007). The purpose of the third chapter is to determine whether reproduction by subordinate female GLTs is limited by dominant females who have incomplete control or complete control over subordinate reproduction. I test the ICM prediction that subordinate females ovulate and conceive, but only those subordinates capable of winning fights with the dominant female give birth to live young. I test the OSM prediction that ovulation, conception and successful reproduction is allowed only by subordinate females providing inclusive fitness benefits to the dominant female.

These three chapters make significant contributions to our understanding of the endocrinological mechanisms and selective forces responsible for maintaining reproductive skew in free-ranging callitrichid primates. As reproductive skew is common among cooperatively breeding species (Solomon & French, 1997b) and has been proposed as an integral component to the evolution of cooperative care (Clutton-Brock, 2009), the results from this study also provide an indication of the ecological and social conditions under which cooperative breeding may have evolved. The evolution of monogyny and cooperative care in the Callitrichidae have been attributed to energetic constraints on small-bodied females that may require infant allocare (Kleiman, 1977b; Ford, 1980; Leutenegger, 1980; Dietz & Baker, 1993; Tardif et al., 1993; Dietz et al., 1994; Tardif, 1994; Tardif, 1997). My first chapter presents evidence that caloric availability in GLT home ranges is more than sufficient to support multiple breeding females, thus does not limit GLT reproduction. However, in chapters one and three I demonstrate how group size limits GLT reproduction and the importance of additional group members for providing allocare in polygynous groups. I speculate that competition

for allocare rather than for food resources may be the selective force limiting reproduction by subordinate females.

Dominant control over subordinate reproduction by means of hormonal suppression of ovulation and sexual behavior has been shown to be the primary mechanism maintaining reproductive skew in captive (Rothe, 1975; Abbott, 1984; Saltzman et al., 1997c) and wild (Digby, 1999; Sousa et al., 2005) callitrichid groups. The only hormonal study of wild GLTs provided evidence that the majority of subordinate females remained anovulatory within their natal group (French et al., 2003). In chapters two and three I demonstrate the lack of hormonal suppression in subordinate adult GLT females in this free-ranging population and I provide evidence supporting the hypothesis of self-restraint of reproduction in subordinate adult females under three years of age. Subordinate adult females ovulate and appear to be endocrinologically capable of reproduction beginning at 18 months of age, but conceptions are delayed one to two years in response to the greater threat of eviction presented by a young dominant female and to the lack of non-incestuous mating opportunities.

In chapter three I argue that subordinate females older than three years of age no longer restrain their own reproduction and that incomplete dominant control as opposed to optimal skew limits reproduction by older subordinate females. My argument is based upon the observation that all females younger than 2.5 years of age ovulated but did not conceive, whereas all females older than 3.9 years of age became pregnant. However, seven of eleven subordinate pregnancies did not produce live young. Results from logistical regression analyses suggest that older subordinates compete with dominant females for reproduction and succeed in producing live young if the dominant female is

at least 10 years old, if subordinates conceive while the dominant is heavily pregnant, and if they reside within larger groups (ICM).

Dominant aggression has been implicated in reducing post-conceptive reproductive success in subordinates (Arabian babblers (*Turdoides squamiceps*): (Zahavi, 1990); meerkats: (Clutton-Brock et al., 1998a; Clutton-Brock et al., 2001a; Kutsukake & Clutton-Brock, 2006; Young et al., 2006; Clutton-Brock et al., 2008); dingos (*Canis familiaris dingo*): (Corbett, 1988); African wild dogs: (Creel et al., 1997); dwarf mongooses: (Creel & Waser, 1991; Rasa, 1994; Creel & Waser, 1997); banded mongooses (*Mungos mungo*): (Gilchrist, 2006a; Cant et al., 2010); naked mole-rats (*Heterocephalus glaber*): (Faulkes & Abbott, 1997); prairie dogs (*Cynomys ludovicianus*): (Hoogland, 1985); Mongolian gerbils (*Meriones unguiculatus*): (Saltzman et al., 2006a); and in GLTs: (Kleiman, 1979; Inglett et al., 1989; French et al., 2002)). In chapter three I present results from enzyme immunoassay for the stress hormone cortisol that refute the role of dominant aggression and chronic social stress in limiting reproduction by subordinate female GLTs.

In addition to these contributions made to basic science, my results contribute to the conservation of this endangered species. The conditions found here to favor polygyny, thus increasing reproductive output, can be used in formulating management plans. My study on caloric availability quantifies the resource base necessary to support polygyny in wild GLT groups and may be used as a guide when selecting potential sites for relocation of tamarin groups and the usability of forest corridors and surrounding matrix. Results from this dissertation may also be used to increase reproductive output in

captive populations or increase the likelihood of successful reproduction by pairs whose genes are underrepresented in the current population.

Future population viability assessments for this endangered species may use results from my study. In chapter one I report that 83% of GLT groups contained two reproductive females, doubling the number of polygynous groups previously reported (Baker et al., 2002). In contrast with results from French et al. (2003) indicating that the majority of subordinate females over 18 months of age remained anovulatory, in chapter two of this dissertation I demonstrate ovulation in subordinate females beginning at 18 months of age. I also report a mean age at first reproduction of 3.1 years as opposed to the previous estimate of 3.6 years (Bales et al., 2001). Whereas reproductive senescence has been demonstrated in elderly captive callitrichids (Tardif, 1985; Tardif & Ziegler, 1992; Caro et al., 1995), the results I present in chapter three agree with those of Bales et al. (2001) and demonstrate that elderly females remain capable of reproduction. Together, my results suggest that the reproductive potential of this population may be higher than previously estimated.

Chapter 1: Caloric availability does not limit reproduction in female golden lion tamarins (*Leontopithecus rosalia*)

ABSTRACT

Delayed dispersal and cooperative breeding may have evolved as a consequence of the limits ecological constraints place on independent breeding. Reproduction in cooperatively breeding callitrichid primates may be especially constrained by food availability. Their small body size and minimal body fat may not allow sufficient energy stores to meet the unusually large energetic requirement necessary to produce one or two litters of twins weighing over 20% of maternal body weight each year. In the current study I examine whether the availability of calories from fruit and nectar species limited reproduction in female golden lion tamarins (*Leontopithecus rosalia*). I collected three years of data from seven free-ranging groups of tamarins in Poço das Antas Biological Reserve, Rio de Janeiro, Brazil. I used hormonal (progesterone and cortisol) profiles obtained through non-invasive immunoassay of feces to detect ovulation in subordinates. I also used changes in body mass, bi-annual physical examinations, and behavioral observations to diagnose pregnancies. I used circulating cortisol concentrations during early pregnancy as a measure of metabolic stress and both progesterone and cortisol during late pregnancy as indicators of fetal and placental growth. I defined reproductive success as pregnancies that resulted in the birth of live infants. I recorded group compositions daily, and performed phenological surveys to quantify average monthly caloric availability. I compared hormonal profiles of successful vs. non-successful pregnancies using linear mixed model analysis of variance. I identified variables useful in predicting a successful pregnancy using logistic regression analyses. Caloric

availability did not limit reproduction in adult female tamarins. All home ranges contained calories in fruit and nectar that far exceeded the minimum required to support reproduction. Under these conditions of high caloric availability both dominant and subordinate adult females ovulated and became pregnant resulting in an 83% rate of pregnancy polygyny. Lower 3rd trimester progesterone and cortisol concentrations in non-successful pregnancies compared to successful pregnancies could not be attributed to insufficient caloric availability. The likelihood of a successful pregnancy increased 1.7 times with the addition of each group member, suggesting that calories were sufficient to support not only pregnancy by multiple breeding females, but also the additional group members resulting from multiple litters. The super abundance of calories and the timing of births suggested that competition for allocare rather than for food resources may be the selective force limiting reproduction by subordinate females.

INTRODUCTION

Golden lion tamarin mating system

Golden lion tamarins (*Leontopithecus rosalia*) are small, neotropical primates in the family Callitrichidae (marmosets and tamarins). Golden lion tamarins (GLTs) typically reside in family groups of 2–11 individuals (Dietz & Baker, 1993; Dietz et al., 1994). Dietz and Baker (1993) described the mating system in GLTs as monogyny with about a 10% incidence of polygyny. However, when examining groups containing more than one potentially reproductive female, 44.3% showed pregnancy polygyny (more than one female was confirmed as being pregnant within the same breeding season) and 26.2% showed rearing polygyny (more than one female reared offspring to weaning) (Dietz & Baker, 1993; Baker et al., 2002). Typically, a single male monopolizes copulations with

a single breeding female during her fertile period; however, about 40% of groups studied were potentially polyandrous, containing two or more potentially reproductive males (Baker et al., 1993; Baker et al., 2002). Lion tamarin offspring typically delay dispersal and reproduction, and remain in their natal group to help with the care of infant siblings (Dietz & Baker, 1993). Cooperative care has been suggested to be instrumental in the ability of callitrichids to meet the energetic needs associated with successfully rearing the litters of twins they are capable of producing either once or twice a year (Kleiman, 1977a; Sussman & Garber, 1987; Baker et al., 1993; Dietz & Baker, 1993).

Reports by Dietz and Baker (1993), Baker et al. (2002), and Hankerson (2008) point to ecological conditions leading to polygyny in GLT groups. Groups with two reproductive females were found more commonly within home ranges that contained more swamp forest (Dietz & Baker, 1993). Baker et al. (2002) suggest that polygyny may be more common on home ranges containing greater proportions of secondary and edge forest where food may be more abundant (Terborgh, 1983; Rylands, 1986; Rylands, 1987; Rylands & Faria, 1993). Larger home ranges contained more reproductive females (Hankerson, 2008). These studies provide indirect evidence in support of food limitation on GLT reproduction, but food resources were not directly quantified.

Food limitation hypothesis

According to the model of ecological constraints, food availability and its distribution through time and space affect almost every aspect of an organism's life history (Ross, 1991; Ross, 1992), including mating systems (Goldizen, 1987a; Dietz & Baker, 1993; Baker et al., 2002), reproductive timing (Altmann, 1980; van Schaik & van Noordwijk, 1985; Goldizen et al., 1988; Dietz et al., 1994; Di Bitetti & Janson, 2000),

and reproductive output (Dietz & Baker, 1993; Altmann & Alberts, 2003; Altmann & Alberts, 2005; Stewart et al., 2005). Ecological constraints limiting independent breeding may explain the evolution of delayed dispersal and cooperative breeding in birds (as reviewed in Hatchwell & Komdeur (2000)) and mammals (Kleiman, 1977b; Creel & Creel, 1991). Reproduction in cooperatively breeding callitrichid primates may be especially constrained by food availability (Leutenegger, 1980; Kirkwood & Underwood, 1984; Goldizen, 1987a; Price, 1992c; Tardif, 1994; Sánchez et al., 1999; Miller et al., 2006). Their small body size (non-pregnant adult female GLTs weigh 598 g on average (Dietz et al., 1994)) and minimal body fat storage (Power et al., 2001; Power et al., 2008) may not allow the buildup of energy reserves necessary to meet the unusually large (for primates) (Leutenegger, 1973; Hearn, 1983; Kirkwood, 1985; Tardif et al., 1993; Ross & MacLarnon, 1995; Nievergelt & Martin, 1999; Tardif et al., 2001) energetic demand of producing and raising one or two litters of twins weighing in excess of 20% of maternal body weight each year (Leutenegger, 1973; Ford, 1980; Leutenegger, 1980; Dietz & Baker, 1993; Dietz et al., 1994; Bales et al., 2001). This heavy energetic burden placed upon small-bodied callitrichid females may require the participation of group members as infant allocaregivers, thus leading to the evolution of a monogynous mating system and cooperative infant care in the Callitrichidae (Kleiman, 1977b; Ford, 1980; Leutenegger, 1980; Dietz & Baker, 1993; Tardif et al., 1993; Dietz et al., 1994; Tardif, 1994; Tardif, 1997). In addition, a continuous food supply may be required to support callitrichid body maintenance and reproduction (Tardif et al., 2004; Tardif et al., 2005). Where food resources are limited or when energetic costs are high, GLTs have been observed to reduce the amount of time they spend in energetically expensive activities such as travel,

foraging, and play (Miller et al., 2006; Sales Coelho et al., 2008). Nievergelt & Martin (1999) suggested that captive common marmosets (*Callithrix jacchus*) meet the increased energetic demands of pregnancy by reducing time spent in energetically expensive behaviors. During late pregnancy, when energy costs were high, captive female cotton-top tamarins (*Saguinus oedipus*) fed *ad libitum* reduced locomotion (Price, 1992b). Free-ranging GLTs in Poço das Antas Biological Reserve (PDA) reduced time spent in foraging for insect prey during late pregnancy (Siani, 2009) and spent more time sleeping or remaining stationary (Miller et al., 2006). The suite of energy-conserving behaviors that have evolved in the Callitrichidae suggest an energetic tradeoff among daily activities, thermoregulation, and reproduction in this species (Thompson et al., 1994). Thompson et al. (1994) also found that GLTs had moderately low energetic requirements relative to other mammals and primates their size, a finding inconsistent with their high reproductive output and indicative of constraints on energy availability. Based upon this body of evidence, I hypothesized that reproduction in wild adult GLT females is limited by food availability.

Caloric availability affects ovulation and conception

Females under conditions of abundant food resources may be more likely to meet the energetic requirements necessary not only to support their own metabolism, but also to maintain normal reproductive cycles of estrus, mating, conception, pregnancy, birth, lactation, and the resumption of estrus (Takahashi, 2002); a cycle physiologically controlled by hormones. Studies on the effects of dietary restriction on reproduction originally focused on gonadotropins (follicle stimulating hormone (FSH) and luteinizing hormone (LH)) as responsible for anovulation (Bronson, 1989; Downing & Scaramuzzi,

1991), since these hormones are primarily responsible for follicle growth, ovulation, and the production of estrogen and progesterone by the ovary (Ojeda & Griffin, 1996). Conversely, ewes fed enriched diets exhibit increased ovulation rates without a corresponding change in FSH or LH. Instead, the metabolic hormone insulin increases with food quality (Downing & Scaramuzzi, 1991). When food is scarce or energetic demands are high, reproduction may be halted by metabolic hormones such as leptin, insulin, and corticotropin-releasing hormone (CRH). Though the exact mechanism is unknown, these metabolic hormones exert some influence on the hypothalamic-pituitary-gonadal axis, most likely on the ovary directly, to control the production of progesterone and estrogen (Nelson, 2005). In turn, progesterone produced by the *corpus luteum* is involved in the negative feedback mechanisms controlling cyclical follicular development in the ovary leading to ovulation and maintaining the uterine lining for successful implantation after conception (Ojeda, 1996).

When food is abundant, females of many species are more likely to ovulate and conceive (Dailey & Neill, 1981; Frisch, 1982; Lee, 1987; Kirkwood et al., 1987; Downing & Scaramuzzi, 1991). An abundance of literature has linked the lowering of the average age of menarche with improvements in nutrition and body condition in women (Tanner, 1962; Brown, 1966; Dreizen et al., 1967; Baanders-Van Halewin & de Ward, 1968; Bojilen & Bentzoin, 1968; Wolanski, 1968; Kennedy, 1969; Frisch & Revelle, 1971; Weir et al., 1971; Stein & Susser, 1975; Frisch, 1982; Frisch, 1984). Asian Hanuman langurs (*Presbytis entellus*) (Koenig et al., 1997), Japanese macaques (*Macaca fuscata fuscata*) (Takahashi, 2002), and Sumatran long-tailed macaques (*Macaca fascicularis*)(van Schaik & van Noordwijk, 1985) are more likely to ovulate and

conceive at a time of year when food resources are most abundant and females are in their best physical condition. Wild female GLTs at PDA increase the amount of time spent foraging during the cool, dry months just prior to pregnancy and lactation, perhaps improving body condition for reproduction (Miller et al., 2006). Captive GLTs fed *ad libitum* begin to show normal ovarian cyclicity at around 18 months of age (French et al., 2002), whereas wild females often remain anovulatory until well after 24 months of age (French et al., 2003). Mating and conceptions in wild GLT populations may also be delayed even after normal ovarian cyclicity has been established, resulting in average ages of primiparous subordinate females well over the 18-24 months associated with puberty (Bales et al., 2001; Baker et al., 2002) (Chapter 2, this dissertation). In addition, the number of ova released at ovulation increases with food availability and maternal weight in sheep (Downing & Scaramuzzi, 1991), common marmosets (Tardif & Jaquish, 1997), and cotton-top tamarins (Kirkwood, 1983).

Caloric availability affects reproductive success

Caloric availability may also affect success rates of existing pregnancies through a hormonal feedback loop (Knott, 2001; Tardif et al., 2004; Tardif et al., 2005; Jansson & Powell, 2006; Rutherford & Tardif, 2008; Rutherford, 2009). It has been suggested that the placenta serves as a nutrient sensor that calibrates fetal growth to maternal condition through the use of hormones (Jansson & Powell, 2006; Rutherford & Tardif, 2008; Rutherford, 2009). Though the *corpus luteum* produces progesterone during very early pregnancy, the placenta is responsible for the significant rise in circulating maternal progesterone concentrations as pregnancy progresses (Carr, 1996; Nelson, 2005). Progesterone functions in maintaining pregnancies by inhibiting uterine contractions,

inhibiting prostaglandin (thereby inhibiting parturition), and blocking the cellular immune response that would otherwise attack the fetus residing within the uterus as a foreign body (Carr, 1996).

Under conditions of low caloric availability, the placenta may respond by reducing the amount of progesterone it produces (Bronson, 1989), leading to premature delivery or preterm abortion. When the calories available to pregnant females are not restricted, progesterone levels increase as the fetus develops and the placenta increases in size (Tardif et al., 2004; Tardif et al., 2005). Carbohydrate intake and metabolism may also increase with progesterone (Czaja & Goy, 1975; Pliner & Fleming, 1983). During pregnancy, as progesterone concentrations continue to rise, the resulting increase in food consumption helps support the developing fetus as well as provide energy reserves for lactation (Nelson, 2005).

If food resources are limited, an “energy save” mode of metabolism may be required to provide the energy necessary for reproduction (Kirkwood & Underwood, 1984; Dietz et al., 1994; Thompson et al., 1994; Bales, 2000; Bales et al., 2001; Tardif et al., 2001; Miller et al., 2006). Cortisol, a glucocorticoid hormone, is responsible for the mobilization of energy reserves from protein and fat into useable glucose during food deprivation or periods of stress (Nelson, 2005). In well-fed animals, cortisol levels are typically low. As food intake decreases, cortisol levels increase to meet energetic demand (Schneider & Wade, 1999). Thus, cortisol can be used as an indicator of relative energetic demand and metabolic stress in non-pregnant and early pregnant female GLTs. This technique has been used to measure the relative energetic demands of mating and

readiness for reproduction in female muriquis (*Brachyteles arachnoides hypoxanthus*) (Strier et al., 2003).

Connections between cortisol and maternal energetic demand must be made with caution during late pregnancy as cortisol levels increase significantly during the 3rd trimester of pregnancy in callitrichids (Ziegler et al., 1995; Smith & French, 1997b; Albuquerque et al., 2001; Ziegler et al., 2004; Bales et al., 2005; Tardif et al., 2005). As the fetus matures, placental CRH stimulates production of adrenocorticotrophic hormone (ACTH) by the fetal pituitary gland. Together, placental CRH and fetal pituitary ACTH stimulate the fetal adrenal gland to produce cortisol and dehydroepiandrosterone sulfate (DHEAS) (Coulter & Jaffe, 1998; Smith et al., 1998). Cortisol and DHEAS drive placental CRH production. Thus, a positive feedback loop linking the placenta, fetal pituitary gland, and fetal adrenal gland results in greater concentrations of circulating maternal cortisol (Goland et al., 1994; Coulter & Jaffe, 1998; Smith et al., 1998; Smith et al., 1999; Challis et al., 2000; Umezaki et al., 2001; Mastorakos & Ilias, 2003). Rather than an indication of lower food intake, increased metabolic demand, or stress in heavily pregnant females, sustained peaks in cortisol concentrations during late pregnancy are the result of the normal increase in placental activity and fetal development associated with a pregnancy that has advanced into the 3rd trimester (Bales et al., 2005; Tardif et al., 2005; Power et al., 2006).

The food limitation hypothesis predicts increased reproductive success for females breeding when food is readily available. Females that conceive too early or too late in the breeding season may be unable to find adequate food resources to support reproduction (Di Bitetti & Janson, 2000; Strier, 2000). On the other hand, females

reproducing under conditions of higher food availability are more likely to carry their pregnancies to term (Tardif et al., 2004; Tardif et al., 2005) and produce sufficient quantity and quality of milk (Altmann, 1980; Tardif et al., 2001; Dunbar et al., 2002; Power et al., 2008). Their offspring may experience higher growth rates both pre- (Li et al., 1998; Tardif & Bales, 2004) and post-partum (Dietz et al., 1994; Tardif et al., 2001; Tardif & Bales, 2004) as well as lower infant mortality (Altmann, 1980; Small & Smith, 1986). The selective advantage conferred on individuals able to time reproduction with maximum food availability has led to distinct patterns of birth seasonality among primates occupying seasonal environments (van Schaik & van Noordwijk, 1985; Di Bitetti & Janson, 2000). The high energetic costs of primate reproduction (Dufour & Sauther, 2002), including the energetic demands of lactation that may double caloric intake (Altmann, 1980; Kirkwood & Underwood, 1984; Martin, 1984; Crockett & Rudran, 1987; Goldizen, 1987a; Gittleman & Thompson, 1988; Savage, 1995; Koenig et al., 1997; Nievergelt & Martin, 1999; Tardif et al., 2001) and the need for readily available foods at weaning (Martin, 1973; Charles-Dominique, 1977; Petter, 1978; Altmann, 1980; Chivers & Raemaekers, 1980; Nash, 1983; Martin, 1984; Goldizen et al., 1988), have selected for individuals that are able to time lactation and weaning to occur during periods of abundant food resources (Nash, 1983; Boinski, 1987; Lee, 1987; Goldizen et al., 1988; Strier, 1991; Lee & Hauser, 1998; Di Bitetti & Janson, 2000).

Reproductive timing in GLTs also appears to conform to predictions derived from the food limitation hypothesis. GLTs exhibit two distinct birth peaks within the wet season: the largest peak occurring from September through November (Dietz et al., 1994; French et al., 1996; De Vleeschouwer et al., 2003); the second peak from January

through February (Dietz et al., 1994; De Vleeschouwer et al., 2003). In a study designed to test the predictions derived from the food limitation hypothesis, Dietz et al. (1994) suggested that GLT reproduction was indeed limited by food availability. The observed seasonal pattern of reproduction placed parturition, lactation and weaning within the seven month wet season when resources were presumed to be most abundant.

Several studies show that primates with greater food availability are in better physical condition and have greater reproductive output. Amboseli baboons (*Papio cynocephalus*) supplemented with food out of a tourist lodge garbage dump are heavier and show greater reproductive success than non-provisioned individuals (Altmann & Alberts, 2003; Altmann & Alberts, 2005). Fruit and insect availability at Cocha Cashu Biological Station, Manu National Park, southeast Peru, was lower during a four-month dry season (May-September). During that period saddle-back tamarins (*Saguinus fuscicollis*) lost an average of 5% of their body mass and no births occurred between mid-March and mid-August (Goldizen et al., 1988). Marmosets and tamarins fed *ad libitum* in captivity frequently have two litters per year and may produce triplets (Wolfe et al., 1975; Gengozian et al., 1978; Kirkwood, 1983; Tardif & Jaquish, 1997; Strier, 2001; De Vleeschouwer et al., 2003; Tardif et al., 2003), whereas their wild counterparts often produce only one litter of twins or singletons per year (Goldizen et al., 1988; Dietz & Baker, 1993; Dietz et al., 1994; Bales et al., 2001). Golden-headed lion tamarin (*Leontopithecus chrysomelas*) groups residing within *cabruca* agroforest where the invasive jackfruit (*Artocarpus heterophyllum*) provides a super-abundant and concentrated food resource year round have greater reproductive success (producing twins in every reproductive season) than do their counterparts occupying primary forest

(Oliveira, 2010). Female GLTs at PDA are heavier during the wet season when food is most abundant than they are at the end of the dry season when food is less abundant (Dietz et al., 1994). Wild GLT females that are provisioned weigh more than their non-provisioned counterparts (Bales et al., 2002). Heavier GLT females gave birth to more live young at PDA (Bales et al., 2001). Typically, marmosets and tamarins that receive more food are in better physical condition (weigh more) (Epple, 1970; Kirkwood, 1983; Bales et al., 2002; Tardif et al., 2004). Females in better physical condition are more likely to ovulate, carry pregnancies to term, produce larger litter sizes, and successfully rear litters (Kirkwood, 1983; Dietz & Baker, 1993; Tardif & Jaquish, 1994; Tardif & Jaquish, 1997; Bales et al., 2001; Tardif et al., 2001; Bales et al., 2002; De Vleeschouwer et al., 2003; Tardif & Bales, 2004; Tardif et al., 2004; Tardif et al., 2005).

Group size affects reproductive success

If pregnancies by multiple breeding females are to be successful, caloric availability within the home range must be high enough to support not only two pregnant females, but also up to four infants and the group members providing allocare for these infants (Goldizen, 1987a; Goldizen et al., 1988; Dietz & Baker, 1993; Goldizen et al., 1996; Baker et al., 2002; Clutton-Brock et al., 2008). If reproduction is limited by available food, as the number of individuals occupying the home range increases the number of calories available within the home range must increase in order to meet the daily nutritional requirements of each additional group member (Dawson, 1979; Terborgh, 1983; Terborgh & Stern, 1987; Chapman, 1988; Peres, 1994; Dietz et al., 1997; Ganas & Robbins, 2005; Wiczowski, 2005; Miller & Dietz, 2006). If increased daily travel to obtain additional resources to support a larger group is not possible or does

not provide sufficient resources, food intake per individual may decline (Foster, 1982), which may in turn lead to reduced reproductive success (Janson & van Schaik, 1988; Isbell, 1991; Janson & Goldsmith, 1995; Koenig, 2002). Under conditions of reduced caloric availability, group members may reduce food sharing with pregnant females or dependent infants in order to increase their own intake (Rapaport & Ruiz-Miranda, 2006). Conversely, under conditions of high food availability the caloric requirements of all group members are more likely to be met and pregnancies may be more likely to succeed.

When group sizes are small the calories available within the home range are divided among fewer individuals. If receiving a larger share of calories results in heavier females (Epple, 1970; Kirkwood, 1983; Bales et al., 2002; Tardif et al., 2004), and heavier females have higher reproductive success (Kirkwood, 1983; Dietz & Baker, 1993; Tardif & Jaquish, 1994; Tardif & Jaquish, 1997; Bales et al., 2001; Tardif et al., 2001; Bales et al., 2002; De Vleeschouwer et al., 2003; Tardif & Bales, 2004; Tardif et al., 2004; Tardif et al., 2005), then pregnancies by GLT females should be more likely to succeed when these females reside in groups containing fewer individuals.

Timing affects reproductive success

If caloric availability is insufficient to support simultaneous reproduction by multiple females residing within the same home range, then pregnancies by multiple breeding females that are timed such that infant arrivals are staggered should be more likely to succeed (Digby, 1995a; Clutton-Brock et al., 2008). Staggering infant births reduces the length of time when the caloric demands of two pregnant females, two lactating females, and potentially four dependent infants must be met at the same time. GLT females giving birth twice a year typically give birth to their first litter in late

September or early October and to their second litter in mid-February. Females giving birth to only a single litter annually typically give birth in November. The two annual peaks in infant births, one from October through November and another in February (Dietz et al., 1994) may reflect the staggering of births among GLT females. When there is overlap in infant dependency periods, those infants arriving first will have exclusive access to maternal milk and allocaregivers until the arrival of the second litter (Digby, 1995a). The length of time that first-born infants benefit from exclusive access to resources depends upon the interval between births by multiple breeding females residing within the same home range (interfemale interbirth interval, IFIBI).

Questions, hypotheses, predictions

The goal of this study was to determine whether the availability of calories from fruit and nectar species limits reproduction in female GLTs. The following questions were addressed in this study: 1) Is reproduction in wild golden lion tamarin groups limited to a single breeding female? 2) Is reproduction by wild female GLTs limited by caloric availability? In answering these questions I hope to understand better the ecological conditions that have an impact on reproductive output in this cooperatively breeding species. I collected the following data on seven groups of GLTs over three reproductive years: caloric availability, group demography, female reproductive status and metabolic stress levels as determined through non-invasive hormonal assays for progesterone and cortisol, and reproductive success defined as pregnancies that resulted in the birth of live offspring. I tested the following predictions derived from the hypothesis that reproduction by wild adult female GLTs is limited by caloric availability

to support pregnancy, to support simultaneous breeding by two females, and/or to support a large group (Table 1.1):

Prediction 1: If caloric availability is consistently above the minimum required for reproduction, then all adult females will ovulate and conceive.

Prediction 2: Pregnancies that are successful will have lower cortisol concentrations during the non-pregnant period just prior to conception and during the 1st trimester of pregnancy, indicating that the mother is not under metabolic stress as a result of caloric insufficiency.

Prediction 3: Pregnancies that are successful will have higher progesterone and cortisol concentrations during the 3rd trimester, indicating that fetal and placental growth is not limited by insufficient calories.

Prediction 4: Pregnancies will be more likely to succeed when caloric availability is high.

Prediction 5: Pregnancies will be more likely to succeed when females reside within a group containing fewer individuals (with which she must divide limited calories).

Prediction 6: Pregnancies will be more likely to succeed when the interfemale interbirth interval is longer (placing litter arrivals further apart and reducing the length of time when infant dependency periods overlap).

Prediction 7: Pregnancies will be more likely to succeed when they are conceived before another pregnancy in the same reproductive season (reducing overlap in infant births and giving the female pregnant first and her infants prior access to limited food resources).

METHODS

Study site

Data were collected within the 6300 ha Poço das Antas Biological Reserve (PDA), Rio de Janeiro State, Brazil (22° 30' - 33' S, 42° 15' - 19' W) (Miller & Dietz, 2006). The reserve is predominantly secondary forest consisting of a patchwork of habitat types resulting from the various stages of secondary succession following human occupation (Dietz et al., 1997). The areas of secondary forest used by GLTs include hillside, lowland transitional, and swamp.

PDA has a wet (October through April (Dietz et al., 1994; Hankerson, 2008)) and a dry season (June through August (Dietz & Baker, 1993; Hankerson, 2008)) each year. During the three years of this study, PDA received an average of 2135.6 ± 184.1 (standard error) mm of precipitation each year, with 1821.4 ± 250.8 mm of rain falling over all wet months of each year, and 314.3 ± 72.2 mm of rain falling over all dry months each year (unpublished data). An average of 260.2 ± 18.9 mm of rain fell during each wet month as compared to an average of 62.9 ± 7.4 mm of rain during each dry month (unpublished data). Average temperatures ranged from 21.7 ± 0.1 ° C minimum to 27.6 ± 0.2 ° C maximum during the wet season, and from 18.2 ± 0.1 ° C minimum to 25.0 ± 0.2 ° C maximum during the dry season (unpublished data). Day length varied from 12 hours 38 minutes during the wet season to 11 hours 22 minutes during the dry season (Observatório Nacional, 2004; Observatório Nacional, 2005; Observatório Nacional, 2006; Observatório Nacional, 2007).

Study species

Golden lion tamarins once occupied much of the Atlantic Coastal Forest of Rio de Janeiro State, Brazil. Today, primarily as a result of habitat loss, fragmentation, and forest degradation and with the exception of a few small coastal populations, GLTs are found only in small patches of remnant forest centered around the São João river basin (Rylands et al., 2002; Ruiz-Miranda et al., 2008). GLTs were ranked as “critically endangered” from 1963 to 2002 due to low numbers, narrow distribution, and threat of continued habitat loss (Hilton-Taylor, 2000; Rylands et al., 2002). Due to successful local, national, and international conservation efforts, GLTs were reclassified as “endangered” in 2003 (IUCN, 2010). Still, only an estimated 1500 GLTs remain in the wild (Ruiz-Miranda et al., 2008); PDA holds the largest remaining population (Rylands et al., 2002; Ruiz-Miranda et al., 2008). Currently, an estimated 350 GLTs exist within the secondary forests protected by the reserve (Rylands et al., 2002; Ruiz-Miranda et al., 2008).

The GLT diet includes fruits, seeds, flowers, nectar, gum, insects, and small vertebrate prey (Dietz et al., 1997; Miller, 2002; Procópio de Oliveira, 2002; Miller & Dietz, 2006; Procópio de Oliveira et al., 2008a). In this study, I focused only on the calories provided from fruit and nectar species occurring within GLT home ranges.

Individual identification and weighing

The animals under study at PDA are native and unmanipulated except for bi-annual live captures necessary for replacing radio collars to facilitate group location. During these routine captures, usually in May or early June and again in December or January, individuals are given identifiable markings (hair dye and tattoos), weighed, and

evaluated for growth and body condition including notes regarding female nipple length (reflecting parity), lactation, and pregnancy (Dietz & Baker, 1993; Dietz et al., 1994). During the current study weights were also obtained weekly from August through December of each year using baited scales in the field (Bales, 2000; Bales et al., 2002; Siani, 2009).

Behavioral observations

I collected data on 7 groups of wild GLTs at PDA, each containing 2 to 13 individuals and 1 to 3 adult females. All individuals were habituated to the presence of human observers. I collected data over three reproductive years: 2004-2005, 2005-2006, and 2006-2007. A reproductive year was defined as the 1st of March through the 28th of February in order to encompass the mating period, pregnancy, and the first annual peak in infant births (October through November (Dietz et al., 1994)) as well as post-partum ovulation, mating, and pregnancy that lead to the second annual peak in infant births (February (Dietz et al., 1994)). Six of these groups were observed from March 2004 through February 2007. Another group was added to the study in June of 2005, and was observed until the end of the study in February of 2007. Group sizes fluctuated but losses typically were filled by colonizers. Field assistants performed randomly alternated daily behavioral observations on these seven study groups. Focal observations included observed reproductive behavior; food species consumed; time spent eating each species; and time spent in travel, foraging, rest, encounters with neighboring groups, and infant care. Group scans recorded position, habitat type, and activity every 20 minutes. Group composition was recorded daily including all births, deaths, emigrations, and immigrations.

The ages of individuals born within study groups are known from long-term demographic data or estimated to year based upon weight, the eruption of permanent teeth, and degree of tooth wear and discoloration noted at semi-annual captures (Dietz et al., 1994; Bales et al., 2001; French et al., 2003). Adults were defined as individuals older than 18 months of age (Dietz & Baker, 1993), corresponding to the average age of sexual maturation (French & Stribley, 1987; French et al., 1989; Dietz et al., 1994; French et al., 2002).

Each group contained one adult female who was behaviorally dominant to other females in the group. Dominance was assigned to the predominant aggressor based upon archwalks, mounts, and chases and winner of fights (Dietz & Baker, 1993; Bales et al., 2005).

Fecal sample collection

I collected 1176 fecal samples from individually identified female GLTs in seven free-ranging social groups from March 2004 through February 2007. Feces were collected from a total of 21 GLT females including 14 adults, 4 females that passed from subadult to adult, 1 from juvenile to adult, 1 from juvenile to subadult, and 1 from infant to subadult (Table 1.2). I collected samples year-round during reproductive and non-reproductive months of the year. I collected fecal samples from each female once or twice per week as they left their sleeping locations or during subsequent observations. I attempted to restrict fecal collection to the morning hours to reduce diurnal variation in concentrations of fecal progesterone metabolites (Sousa & Ziegler, 1998; French et al., 2003). As a result, 28% of samples were collected before 0900h, and 83% by 1200h. No more than 10 hours passed between fecal sample collection and storage in a freezer.

Samples remained frozen until analysis at the Callitrichid Research Center, University of Nebraska at Omaha.

Pregnanediol-3-glucuronide (PdG) and cortisol extraction from feces

Pregnanediol-3-glucuronide (PdG) is a metabolite of progesterone excreted in the feces and has been validated as a reliable indicator of circulating progesterone concentrations (Bales, 2000; French et al., 2003). Cortisol is excreted directly into the feces. PdG and cortisol were extracted simultaneously from fecal samples. Fecal samples were allowed to thaw at room temperature and I then removed large seeds, leafy material and undigested insect parts. Fecal samples were dried in a drying oven at 37 ° C prior to weighing for hormonal extraction. Hormonal extraction was performed by briefly vortexing and then shaking 0.125 g of dried fecal matter in 2.5 ml of solubilizing extraction buffer (40% methanol (MeOH):60% phosphate buffered saline (PBS)) for 12-16 hours on a shaker rack. Samples were then briefly vortexed to remove residue along the tube walls and centrifuged for 15 min at 2000 rpm at 6 ° C. The supernatant was decanted into a clean test tube and refrozen for storage until further diluted for assay.

PdG immunoassay

PdG was measured using an assay previously described (Bales, 2000; French et al., 2003). Extracted fecal samples were diluted 1:5 in PBS prior to assay to place sample PdG concentrations within the range of the standard curve. PdG standards ranged from 10,000 to 78 pg/well and were prepared using halving dilutions in 1:5 extraction buffer:PBS. Controls were 1:5 extraction buffer:PBS. Internal quality control pools consisted of female Geoffroy's marmoset (*Callithrix geoffroyi*) urine since a more recent and extensive assay history existed for comparison. They were run at high concentrations

(1:80 in 1:5 extraction buffer:PBS) and low concentrations (1:640 in 1:5 extraction buffer:PBS). PdG concentrations were determined through standardized enzyme immunoassay techniques (EIA) and calculations resulting from a four-parameter sigmoidal curve-fitting function. The intra- and inter-assay coefficients of variation for high and low concentrations of a urine quality control pool for the PdG assay were 9.1% and 19.9% (high), and 7.4% and 26.7% (low), respectively. This EIA assay for PdG has been previously validated against circulating hormone levels by noting the production of parallel displacement curves when PdG standards were assayed together with serial dilutions of extracted feces collected from females at different times during pregnancy (Bales, 2000; French et al., 2003). The accuracy of the assay was also previously tested by spiking fecal sample supernatant with 2000 pg of PdG standard and measuring the recovery of that PdG standard as $108.6\% \pm 5.9\%$ (n=6) (French et al., 2003).

Hormone concentrations that were within 10% above and below the standard curve (11,000 pg/well through 70.2 pg/well) were accepted and used at face value in calculations to arrive at ng PdG/g feces. Concentrations above (n=28) or below (n=167) the 10% cut off were assigned values of 11,000 and 70.2 pg/well, respectively. The large number of samples with very low PdG concentrations was expected due to the number of young females from which feces was collected, but could not be avoided since dilution of fecal extracts by less than 1:5 or bringing more fecal extract to the EIA well would have caused interference in the assay due to the increase in methanol concentrations. As such, the risk of false positive pregnancy diagnoses based on PdG concentrations was minimal since overestimation was limited to very low PdG values and very high PdG values were conservatively underestimated.

Cortisol immunoassay

Fecal cortisol was measured using an assay previously described (Bales, 2000; Bales et al., 2005). Extracted fecal samples were diluted 1:10 in PBS prior to assay to place sample cortisol concentrations within the range of the standard curve. Cortisol standards ranged from 1,000 to 7.8 pg/well and were prepared using halving dilutions in 1:10 extraction buffer:PBS. Controls were 1:10 extraction buffer:PBS. Internal quality control pools consisted of female Geoffroy's marmoset urine since a more recent and extensive assay history existed for comparison. They were run at high concentrations (1:2560 in 1:10 extraction buffer:PBS) and low concentrations (1:20,480 in 1:10 extraction buffer:PBS). Cortisol concentrations were determined through standardized EIA techniques and calculations resulting from a four-parameter sigmoidal curve-fitting function. The intra- and inter-assay coefficients of variation for high and low concentrations of a urine quality control pool for the cortisol assay were 3.9% and 11.4% (high), and 3.9% and 20.7% (low), respectively. This EIA assay for fecal cortisol has been previously validated against circulating hormone levels by noting the production of parallel displacement curves when cortisol standards were assayed together with serial dilutions of extracted feces collected from females at different times during pregnancy (Bales, 2000; Bales et al., 2005). The accuracy of the assay was also tested by Bales (2000, 2005) by spiking fecal sample supernatant with 100 pg of cortisol standard and measuring the recovery of that cortisol standard as $101\% \pm 2.0\%$ (n=6).

Samples that were more than 10% above the highest standard were re-assayed after further dilution. A small number of samples produced results that were below the lowest standard value by 10% or more (15 cases distributed over 10 females with no

female having more than 3 samples with low values). These samples were assigned the value corresponding to 10% below the lowest standard (7.02 pg/well) that was used to calculate ng cortisol/g feces.

Detection of ovulation, pregnancy, parturition, and abortion

I plotted PdG and cortisol concentrations over time to help visualize reproductive patterns for individual GLT females. Variation in progesterone levels corresponds to ovulation, the formation of the *corpus luteum*, and placental development (Ojeda, 1996; Nelson, 2005) and has been used to trace ovarian cycles and pregnancy in GLTs (French & Stribley, 1985; French & Stribley, 1987; Bales, 2000; French et al., 2002; French et al., 2003). I examined progesterone profiles of subordinate adult GLT females from 18 months of age until conception of their first pregnancy. Subordinate adult females were considered ovulatory if non-pregnant progesterone profiles showed cyclical elevation in PdG concentrations averaging 20 days in periodicity (French et al., 2002).

Pregnancy was diagnosed primarily by the prolonged elevation of PdG concentrations (Bales, 2000; French et al., 2002; French et al., 2003). Cortisol, a glucocorticoid responsible for mobilizing fat and protein reserves for use by the body in times of food deprivation or stress (Nelson, 2005), also shows a significant increase in concentration during the 3rd trimester of GLT pregnancy (Bales, 2000; Bales et al., 2005), so can be used as a late pregnancy diagnostic. In addition, pregnant GLT females demonstrate steady and considerable weight gain beginning in their 2nd trimester of pregnancy and continuing throughout gestation (Bales et al., 2001; Hankerson, 2008). Parturition was diagnosed by a sudden drop in PdG concentrations to baseline levels (Bales, 2000; French et al., 2002; French et al., 2003) accompanied by a rapid and large

amount of weight loss (mean=112.7 g; range 73 to 142 g; n=12 full term pregnancies for which immediate pre- and post-partum weights were available (Siani, 2009)). I defined successful pregnancies as those that were carried to full term and that resulted in observations of new infants carried and nursed during the first week after birth by the female I identified as the mother. Birth dates were recorded within one or two days of parturition for most infants and within one week for all observed infants born during this study. To establish a calendar for each successful pregnancy I divided the 125-day gestation period (French et al., 2002) into trimesters. Trimesters were assigned by counting back from known parturition dates: 84-125 days (3rd trimester), 42-83 days (2nd), and 0-41 days (1st) (French & Stribley, 1985; French et al., 2002). Because hormone profiles are highly individualized, for each reproductive female I calculated average PdG concentrations during each trimester of pregnancy and during non-pregnant periods to provide “typical” values for successful pregnancies. These trimester averages were used as a guide in diagnosing suspected pregnancies for which infants were not observed and to determine the probable trimester in which pregnancies were aborted.

Pregnancy diagnoses and assignment of trimesters when no infants were observed were made consulting multiple sources of information on a case by case basis. I consulted average trimester PdG values for successful pregnancies. Females that produced offspring showed mean PdG concentrations of 1500 ng PdG/g feces when they were not pregnant. Their mean PdG concentrations rose to 3500 ng PdG/g feces during the 1st trimester of pregnancy. Mean PdG concentrations above 5000 ng PdG/g feces were considered indicative of a pregnancy that had progressed into the 2nd trimester. Concentrations averaging 10,000 ng PdG/g feces or higher were considered indicative of

3rd trimester pregnancy. Consistently high levels of PdG that suddenly dropped to titer levels indicated pregnancy loss or parturition depending on when concentrations returned to baseline values (Bales, 2000; French et al., 2002; French et al., 2003).

Results from cortisol assays were also used as a cross-check when diagnosing pregnancy. A large and consistent rise in cortisol reaching a mean of 15,000 ng cortisol/g feces was used to diagnose pregnancies that had proceeded into the middle to late 3rd trimester. Short rises in PdG concentrations that were not accompanied by weight gain often coincided with temporary increases in cortisol concentrations and potentially stressful events such as bi-annual captures, immigration of new individuals into social groups, and increased group encounter frequencies. Extremes in nutrition and stress can affect any assay using a metabolite (PdG) rather than measuring the hormone of interest (progesterone) directly (Griffin, 1996). Thus, cortisol was also used as a cross-check to prevent false positive early pregnancy diagnoses based upon elevated PdG concentrations resulting from stress.

I consulted records on weekly weight gain or loss in the GLT females. Since no significant weight gain occurs during the 1st trimester of GLT pregnancy (Bales et al., 2001; Hankerson, 2008; Siani, 2009), I did not attempt to use weight to diagnose pregnancies that did not progress past the 1st trimester. However, I used patterns of weight gain in females in the current study to establish general guidelines for diagnosing pregnancy from the 2nd trimester onward. Females gaining 5-10% of their non-pregnant average weight in a consistently rising pattern were diagnosed as being in their 2nd trimester of pregnancy. Steady weight gain in excess of 10% of a female's non-pregnant body weight was used as an indicator of a 3rd trimester pregnancy. Females that gained

approximately 20% of their body mass were considered to have reached full term, since neonatal weight for *Leontopithecus* is on average 20% of maternal body weight (Tardif et al., 1993). Average weight loss for 12 births during the current study for which immediate pre- and post-partum weights were available was 18.6% of the females' post-partum weight (Siani, 2009). Rapid weight loss was considered indicative of parturition or the loss of a 2nd or 3rd trimester pregnancy. Using weight gain or loss based upon percentages of normative body weight allowed me to account for individual differences in non-pregnant body mass (Dietz et al., 1994; Siani, 2009) while remaining consistent with the average patterns of weight gain throughout pregnancy for our study population. All females were adults when suspected pregnancies occurred; therefore, observed weight gains were not due to those gains associated with maturation (Dietz et al., 1994; Hankerson, 2008). Siani (2009) found that females gained weight during the wet season (October through April) when females were typically pregnant, but these gains were small (on the order of 15-20 g) when compared to those of 2nd and 3rd trimester pregnancy, thus did not interfere with pregnancy diagnosis.

I consulted bi-annual capture records from 2004 through 2007 for each female suspected of being pregnant. These records included each female's weight (considered together with the weights obtained without capture as described above), nipple length (parous females having nipple lengths >3 mm in length), whether a female was lactating or not (indicative of a recent pregnancy carried through parturition whether infants were observed or not), and the results of uterus palpation for pregnancy and trimester diagnosis at the time of capture (Dietz & Baker, 1993; Dietz et al., 1994). These physical examinations provided data points during early pregnancy in late May or June when field

weights were not available and pregnancy diagnoses were not often possible given hormonal concentrations that remain low during this early stage.

Ad libitum field observations regarding female appearance and behavioral changes were consulted for additional confirmation, though were not considered diagnostic. Heavily pregnant GLTs have distended and rounded abdomens. They also travel with a characteristic pelvic girdle swing. In contrast with non-pregnant females that typically obtain their own prey, visibly pregnant females are often provisioned with prey items by the dominant male in the group or aggressively steal prized food items such as small vertebrate prey from other group members. Once at the head of territorial encounters with neighboring GLT groups, females in late pregnancy tend to remain at the rear of such potentially dangerous interactions without becoming involved in displays and chases. Finally, a few days prior to parturition gravid females were described as lethargic, and their daily travel lengths were greatly reduced. These observations are consistent with data from captive cotton-top tamarins indicating a significant reduction in locomotion during late pregnancy (Price, 1992b).

PdG and cortisol averages by trimester

I divided pregnancies that did not result in the observation of live infants, thus did not have known dates of parturition, into trimesters using the guidelines established above and counting either forward or backward from an established trimester to obtain surrounding trimester cut off dates as well as probable conception and projected parturition dates. I then calculated average PdG and cortisol concentrations for each trimester for all pregnancies, successful and non-successful, as well as for non-pregnant adult females.

Interfemale interbirth intervals

I defined interfemale interbirth interval (IFIBI) as the number of days between consecutive known or calculated parturition dates by different females within the same group that were pregnant at the same time during the same reproductive season whether both pregnancies were carried through to parturition or not.

Home range and habitat type quantification

I defined a home range as the area within which a group of GLTs could be found 95% of the time (Kernohan et al., 2001). I used ArcView 3.2 with fixed kernel density to map ranges based on GLT group locations collected at 20 min intervals during daily follows. Home ranges were calculated separately for each reproductive year. Once I had mapped the home ranges for each reproductive year, I categorized the habitats contained within each home range as either hillside (see definitions of hilltop and hillside forest in Dietz et al. (1997)), lowland transitional (see definition of corridor in Dietz et al. (1997)), or swamp forest (see definitions of swamp forest and gingers in Dietz et al. (1997)). I distinguished these habitat types based upon their topography, vegetation structure and composition, degree of moisture, and soil properties (James & Shugart Jr., 1970; Peres, 1994; Dietz et al., 1997; Brugiére et al., 2002; Procópio de Oliveira, 2002; Raboy et al., 2004; Procópio de Oliveira et al., 2008b). I mapped the location of each habitat type within each annual home range by dividing the range into 50 x 50 m grid cells with x and y axes corresponding to GPS coordinates. I used a handheld GPS to arrive at the location corresponding to each of the grid cells on the range map where I then evaluated the habitat type occurring there. The few grid cells which I did not visit were assigned a habitat type based upon knowledge of the area and by considering the habitat type

recorded for neighboring grid cells. By layering the habitat map on top of annual home ranges in ArcView 3.2, I was able to quantify the area of each GLT home range occupied by hill, lowland transitional, and swamp habitat for each reproductive year.

Caloric availability

To quantify monthly caloric availability from fruit and nectar within GLT home ranges, I established in each of six ranges three transects (one of each habitat type), each 195 m in length and 10 m wide. At monthly intervals I evaluated all individuals of plant species that were identified as being eaten by GLTs occurring within these transects for the presence of edible fruit and nectar-producing flowers. I ranked the quantities of flowers, unripe fruit, and ripe fruit present in each monitored tree on a scale from 0 (absence) to 4 (100%) based on the percentage of the tree crown covered in flowers, unripe fruit, and/or ripe fruit (Peres, 1994). I then counted the number of edible unripe fruits, ripe fruits, and nectar-producing flowers present in GLT food trees within three imaginary 1 m³ boxes at random locations within the fruit-bearing region of each tree crown. I estimated fruit-bearing tree crown volume by using a volume formula corresponding to the shape of the portion of the tree crown that contained fruit (Miller & Dietz, 2004). Values for the two horizontal radii in these formulas were obtained by calculating the average horizontal distance from the trunk of the tree to the furthest point in the crown where fruit was present in each of the four compass directions (N, S, E and W). Where fruit was not present on all sides of the tree, horizontal radii measured only in those compass directions where fruit could be found were included in mean radius calculations and volume formulas were modified to reflect the true shape of the fruit-bearing region of the crown. The height used in calculating fruit-bearing crown volume

was obtained using a tangent height gauge to measure the highest and lowest points within the tree crown where fruit occurred. The distance between these points was divided by two to serve as the third, vertical radius in volume formulas. I multiplied the average of the three counts of ripe fruits per unit volume times estimated fruit-bearing tree crown volume to estimate total fruits available in the tree (NRC, 1981; Chapman et al., 1992; Miller & Dietz, 2004). I performed similar calculations for unripe fruit and nectar-producing flowers for each tree.

I quantified the number of edible fruits and nectar-producing flowers of each species present within sampled transects each month using the fruit counts performed on individual trees and extrapolations from standard curves for those trees that were given rankings but fruits were not counted. Specifically, I assigned each of the species that produced edible fruit or flowers during phenological sampling to one of nine species groups. I categorized species groups based upon similarities of life form, fruit size, and fruiting arrangement such that all members of a given group with a similar ordinal fruit and flower ranking also had similar quantities of fruit or flowers present in their crowns. My goal was to establish a reliable relationship between fruit rank and fruit number. Combining data from individuals of multiple species was necessary to produce more robust curves including data from more individual trees. I produced a separate standard curve for each of the nine species groups by plotting ordinal rankings (0-4) on the x axis and their corresponding fruit and flower counts on the y axis for all individuals within the same species group for which both pieces of information were available. I used nonlinear regression to fit a power curve to the data. A power function was chosen since its shape best represented the nature of how fruit quantity increased with ranking ($R^2 = 0.8256-$

0.9966 for all nine curves) (Motulsky & Christopoulos, 2003). I estimated the number of edible fruits and nectar-producing flowers present within trees that were given only rankings by extrapolating from the appropriate standard curve.

I then converted estimates of edible fruits and nectar-producing flowers into estimates of edible calories. For edible fruits I multiplied the number of fruits of each species present during each phenological sample by the dry weight of a single fruit of that species (obtained from Miller & Dietz (2004) and Miller (unpublished data)). I multiplied that product by the number of calories per gram of dry matter of that species (obtained from Miller (2002), Miller & Dietz (2006), and Miller (unpublished data)).

I estimated calories available from *Symphonia globulifera* nectar, the only species of nectar that I saw GLTs consume, by multiplying the calories from nectar present in each flower by the quantity of *S. globulifera* flowers present in each sampled transect. I used methods reported by Kearns & Inouye (1993) and Dafni et al. (2005) to estimate cal/flower based upon the following information. Gill Jr et al. (1998) reported that each flower contained a median amount of 66.5 μ l of nectar with a mean total sugar concentration of 10%. Dafni et al. (2005) reported an energetic value of 4 cal/mg of sugar (sucrose) in nectar.

For those species within transects that produced edible fruit during the course of this study, but for which dry weights or caloric values were not available (n=11 species), I substituted values of those fruits most similar to the unknown in terms of size, consistency, taste, portion eaten, and typically within the same genera. Where commonalities with a fruit species of known dry weight and caloric content did not exist (n=2 species), I substituted the average dry weight and caloric content for all members of

the species group to which the unknown was previously assigned. These calculations provided an estimate of the average number of calories from fruit and nectar per hectare available within each habitat type during each month of the reproductive year for 2004-2005, 2005-2006, and 2006-2007. I extrapolated to estimate the available calories from fruit and nectar each month in each home range during the three reproductive years.

Minimum monthly caloric requirement

I estimated the minimum number of calories required to support the average group of GLTs and their reproduction based upon published values for daily energetic intake and expenditure for pregnant female common marmosets (Tardif et al., 2004), adult male and adult pregnant female cotton-top tamarins (Kirkwood & Underwood, 1984; Savage, 1995), and adult reproductive female GLTs (Miller et al., 2006). Daily energetic requirements ranged from 83.4 - 94.5 kcal/individual/day when applied to an average adult GLT body weight of 600g (Dietz et al., 1994; Hankerson, 2008). I calculated a range that encompassed the energetic requirements of adult pregnant females, non-pregnant females, and males. I did so by multiplying both the 83.4 kcal/individual/day and the 94.5 kcal/individual/day intake by the average group size for the seven groups studied, which was 5.1 individuals per group. Doing so, I estimated between 425.3 and 482.0 kcal were required to support the average GLT group for a single day. The monthly caloric requirement based upon 30 days was estimated at between 12,759 and 14,460 kcal/group/month. Taking the average of these two figures, I estimated that if the home range contained at least 13,610 kcal per month, the minimum caloric requirement to support a group of GLTs and their reproduction would be met for that month.

STATISTICAL ANALYSES

Hormonal changes associated with pregnancy

I performed a linear mixed model analysis of variance (ANOVA) using the GLIMMIX procedure in SAS 9.2 (SAS Institute, Cary, North Carolina) to determine whether PdG and cortisol concentrations changed significantly as females became pregnant and as pregnancy proceeded from one trimester to another. To avoid hormonal variation due to differences in reproductive maturity (French & Stribley, 1987; French et al., 1989; French et al., 2002; French et al., 2003), only data for adult females were included in analyses. The dataset tested consisted of 367 monthly hormonal averages from 18 adult females from 7 GLT groups (n=18 females contributing 179 samples while non-pregnant, n=14 females contributing 65 samples during their 1st trimester of pregnancy, n=14 females contributing 65 samples during their 2nd trimester of pregnancy, and n=14 females contributing 58 samples during their 3rd trimester of pregnancy). Samples from both successful and non-successful pregnancies were included. GLIMMIX allows for the assignment of both random and repeated effects, such as individual female identity, thus addressing the problem of pseudoreplication that occurs when multiple observations are drawn from a single female or from multiple females occupying a single home range by accounting for correlations within the data (Diggle et al., 1999; Bales et al., 2001; Bales et al., 2002). The home range occupied by each female (HR) was included as a random variable, and I controlled for individual female identity (FEMID) as the subject within home range (HR(FEMID)). I included the identity of each pregnancy (PREGID) as a repeated variable with female identity as the subject (PREGID(FEMID)) to account for the fact that there were multiple pregnancies

per female, but controlling for the identity of each female across the pregnancies. The data were log transformed to meet the assumptions of normality prior to analysis.

Pairwise comparisons were performed on least squared means using a Tukey-Kramer adjustment for multiple comparisons.

Hormonal profiles for successful versus non-successful pregnancies

I used logistic regression analyses to test for a statistical relationship between circulating maternal PdG and cortisol concentrations (during the non-pregnant period just prior to pregnancy, the 1st trimester of pregnancy, the 2nd trimester of pregnancy, and/or the 3rd trimester of pregnancy) and the likelihood that the pregnancy would result in live infants. Using PdG concentrations at each of the four stages of reproduction as potential predictor variables, I performed backward selection eliminating non-significant variables (those with the largest $p\text{-value} > 0.05$) one at a time. I repeated this analysis using average cortisol levels associated with each of the four reproductive stages for each pregnancy as potential predictors of a successful pregnancy. The full dataset of 37 pregnancies was reduced to 25 pregnancies (20 successful and 5 non-successful) for which hormonal averages were available for all four states of pregnancy. I controlled for multiple pregnancies by some females by including FEMID as a covariate in the model. The backward selection process resulted in models that contained only non-significant predictor variables and which neither met the assumptions required for a logistic regression model nor provided a good fit to the data. Therefore, I used the Score Chi-Square to select a reduced number of hormonal explanatory variables that were more likely to predict a successful pregnancy. I chose a model with the smallest number of variables explaining the largest amount of variation between successful and non-

successful pregnancies. To predict successful pregnancies based upon PdG, I chose a model including only the 3rd trimester PdG averages as the explanatory variable and FEMID as a covariate. Thirty-one pregnancies (23 successful and 8 non-successful) for which 3rd trimester PdG averages were available were included in these analyses. To predict successful pregnancies based upon cortisol, I chose a model including the 1st, 2nd, and 3rd trimester cortisol averages as explanatory variables and FEMID as a covariate. Thirty pregnancies (23 successful and 7 non-successful) for which cortisol averages for all three trimesters were available were included in the analyses. I performed the logistic regression procedure again using the two reduced models to determine whether a successful pregnancy could be predicted based upon 3rd trimester PdG levels and/or 1st, 2nd, and 3rd trimester cortisol levels. Using this alternate method all assumptions were met for both models.

To determine whether hormonal profiles differed for successful vs. non-successful pregnancies I performed a series of linear mixed model ANOVAs (GLIMMIX procedure in SAS 9.2), one for each stage of pregnancy (non-pregnant, 1st, 2nd, and 3rd trimester), focusing on one hormone at a time. I included 32 pregnancies (23 successful and 9 non-successful) for which PdG and cortisol data were collected just prior to the pregnancy in question, 36 pregnancies (26 successful and 10 non-successful) for which hormonal data were collected during the 1st trimester, 35 pregnancies (25 successful and 10 non-successful) for which hormonal data were collected during the 2nd trimester, and 31 pregnancies (23 successful and 8 non-successful) for which hormonal data were collected during the 3rd trimester. FEMID was included as the subject within the random HR effect as a covariate in the model. HR(FEMID) was removed as a covariate if the covariance

parameter associated with it was 0 thereby treating each reproductive attempt for a given female within a given home range as independent (Bales et al., 2001; Bales et al., 2002). I controlled for individual non-pregnant baseline differences in PdG and cortisol among females in this analysis by including baseline PdG (AVG_NP_PDG) and cortisol (AVG_NP_CORT) concentrations in the model when testing for differences between successful and non-successful pregnancies during the three trimesters of pregnancy, but not during non-pregnant periods. I defined the baseline PdG or cortisol concentrations for each adult female as the average PdG or cortisol concentration of all samples collected from that female while she was non-pregnant. Where necessary I used a log transformation to meet normality requirements prior to analysis.

Effect of caloric availability on reproductive success

I used logistic regression analyses to test for a statistical relationship between average number of calories per month of pregnancy in the home range and the likelihood that the pregnancy would result in live infants. I also tested for a relationship between season (wet or dry) of parturition and the likelihood of success. I included calories and season as potential explanatory variables in the original model and removed non-significant effects by backward selection as described above. All 37 pregnancies detected during the course of the study were included in this analysis including 26 successful and 11 non-successful pregnancies to 14 dominant and subordinate females. I included FEMID as a covariate in the model. All assumptions were met for this model.

Effect of group size and dominance on reproductive success

I used logistic regression analyses to test for a statistical relationship between group size during a given pregnancy and the likelihood that the pregnancy would result in

live infants. I also included the dominance status of the pregnant female in the model to test whether a pregnancy by a dominant or a subordinate female had a greater likelihood of success. Non-significant variables were removed by backward selection as described above. The full dataset of 37 pregnancies was used in this analysis. FEMID was included in the model as a covariate. The final model was accepted when every variable remaining in the model was significant, the model as a whole was significant, and all assumptions for the model were met.

Timing of successful subordinate reproduction

To identify variables useful in predicting a successful pregnancy to a subordinate female pregnant at the same time as the dominant female in her group I used the logistic regression procedure with backward selection of non-significant effects as described above. Explanatory variables included group size, interfemale interbirth interval (IFIBI), whether the dominant or subordinate female became pregnant first, and the age of the dominant female. The dataset consisted of 11 cases of simultaneous pregnancies in 2 females within the same group (4 cases where both the dominant and subordinate females were successful and 7 cases in which only the dominant female was successful). FEMID was included in the model, but removed when the effect was non-significant so that each reproductive attempt by the same female was treated as an independent observation (Bales et al., 2001; Bales et al., 2002). All assumptions were met for this model.

RESULTS

Ovulation and conception

Female GLTs reached puberty at approximately 18 months of age as demonstrated by non-pregnant PdG concentrations that rose from an average of 426.08

ng PdG/g feces in sub-adults to 1093.10 ng PdG/g feces in adults. GLT females between 18 months of age and the conception of their first pregnancy showed cyclical elevation in PdG concentrations from less than 500 ng PdG/g feces to an average of 1000 ng PdG/g feces with 15-30 day periodicity consistent with ovulatory patterns observed in adult GLTs (Chapter 2, this dissertation). Age of first conception ranged from 2.5 to 3.9 (mean=3.1 ± 0.2 standard error) years for 8 GLT females conceiving for the first time during this study (Table 1.2). All adult females over 3.9 years of age became pregnant. Fourteen adult GLT females conceived 37 pregnancies. Ten females gave birth to 48 infants as the result of 26 successful pregnancies. Seven females conceived 11 non-successful pregnancies. Of the 21 GLT females sampled, only 5 females did not conceive after reaching adulthood. Four of the five were younger than three years of age but did show cyclical elevations in PdG concentrations. The fifth female was of unknown age and remained within a habituated study group for just three months during which time she did not become pregnant.

Six of the seven GLT groups studied contained more than one adult (post-pubertal) female, thus were potentially polygynous. Five of these six groups (83%) exhibited pregnancy polygyny. Four pregnancies by two subordinate adult females in two groups resulted in the birth of live young

Hormonal changes associated with pregnancy

The patterns of change in PdG and cortisol concentrations associated with each stage of pregnancy were consistent with those previously published for GLTs (Bales, 2000; French et al., 2003; Bales et al., 2005) and other callitrichids (Ziegler et al., 1995; Smith & French, 1997b; Ziegler & Sousa, 2002; Ziegler et al., 2004). Consistency

between the trimester based hormone profiles in this study and previous studies of successful callitrichid pregnancies provides support for my pregnancy diagnoses and assignment of dated samples to trimesters based upon hormonal concentrations, changes in maternal body mass, and field observations for pregnancies without known parturition dates.

Both PdG (F-value=50.34, ddf=342, $p < 0.0001$) and cortisol (F-value=41.95, ddf=342, $p < 0.0001$) concentrations were significantly affected by stage of pregnancy (Figure 1.1). Mean PdG concentrations increased significantly following conception (from 1633.15 ± 390.11 (mean \pm standard error) ng PdG/g feces when non-pregnant to 3615.69 ± 606.96 ng PdG/g feces during the 1st trimester; t-value=5.86, df=342, adjusted $p < 0.0001$). PdG levels did not increase significantly from the 1st to the 2nd trimester (4162.51 ± 608.81 ng PdG/g feces in the 2nd trimester; t-value=0.44, df=342, adjusted $p = 0.9711$). Another significant increase in PdG occurred from the 2nd trimester to the 3rd trimester of pregnancy (9668.11 ± 638.09 ng PdG/g feces in the 3rd trimester; t-value=4.85, df=342, adjusted $p = 0.0001$). Cortisol did not increase significantly following conception (from 1599.31 ± 656.85 ng cortisol/g feces while non-pregnant to 2029.61 ± 1029.28 ng cortisol/g feces during the 1st trimester; t-value=0.04, df=342, adjusted $p = 1.000$). However, cortisol increased significantly as females moved from the 1st to the 2nd trimester of pregnancy (2609.53 ± 1032.27 ng cortisol/g feces during the 2nd trimester; t-value=2.67, df=342, adjusted $p = 0.0395$). The largest increase was from the 2nd to the 3rd trimester of pregnancy (12807.00 ± 1082.87 ng cortisol/g feces during the 3rd trimester; t-value=6.58, df=342, adjusted $p < 0.0001$).

Hormonal profiles for successful versus non-successful pregnancies

A logistic regression model including average PdG levels during the 3rd trimester of pregnancy and controlling for FEMID just missed statistical significance (Likelihood Ratio Chi-Square=5.67, df=2, p=0.0587). Average PdG levels during the 3rd trimester of pregnancy alone was a marginally significant predictor of a successful pregnancy by a female GLT (Wald Chi-Square=3.42, df=1, p=0.0645). Given the average 3rd trimester PdG levels of a pregnant female, the model predicts that I can correctly classify a pregnancy that will be successful in producing live offspring 77.2 % of the time.

According to the linear mixed model ANOVA, successful GLT pregnancies had significantly higher PdG levels during the 3rd trimester of pregnancy (mean=11390.00 ± 1348.75 ng PdG/g feces) than did non-successful pregnancies (mean=6072.36 ± 2286.92 ng PdG/g feces) (F-value=4.30, ddf=28, p=0.0475) (Figure 1.2). PdG levels during the non-pregnant period, the 1st, and 2nd trimester of successful pregnancies were not statistically different than the corresponding PdG levels in non-successful pregnancies.

A logistic regression model including average cortisol levels during all three trimesters of pregnancy and controlling for FEMID was also marginally significant (Likelihood Ratio Chi-Square=8.73, df=4, p=0.0681). By knowing the average 1st, 2nd and 3rd trimester cortisol concentrations of a pregnant female, I could correctly predict a successful pregnancy 81.4% of the time. My analyses indicated that lower cortisol levels during the 1st trimester of pregnancy and higher cortisol levels during the 2nd and 3rd trimesters were loosely associated with successful pregnancies. Though cortisol levels during a single trimester alone were each non-significant predictors of successful pregnancies (1st trimester Wald Chi-Square=0.47, df=1, p=0.4914; 2nd trimester Wald

Chi-Square=0.63, df=1, p=0.4274), higher cortisol levels during the 3rd trimester alone were the most useful in predicting pregnancy success when data for all three trimesters were not available (Wald Chi-Square=2.31, df=1, p=0.1284).

In concordance with my logistic regression analyses, the linear mixed model ANOVA indicated a non-significant trend toward higher levels of cortisol for successful pregnancies when compared to non-successful pregnancies during both the 2nd (successful mean=3310.31 ± 616.89 vs. non-successful mean=1429.67 ± 977.01 ng cortisol/g feces; F-value=2.68, ddf=32, p=0.1113) and 3rd trimester (successful mean=18688.00 ± 5121.92 vs. non-successful mean=9652.59 ± 5923.39 ng cortisol/g feces; F-value=2.59, ddf=16, p=0.1269) of pregnancy (Figure 1.2). Cortisol levels during the 2nd and 3rd trimesters of successful pregnancies were approximately double those of non-successful pregnancies.

Effect of caloric availability on reproductive success

All 7 GLT home ranges contained more than the 13,610 kcal/month required to support reproduction by a group of GLTs during all months of each of the 3 reproductive years (Figure 1.3).

Neither average monthly caloric availability (Wald Chi-Square=1.14, df=1, p=0.2866) nor the season of parturition (Wald Chi-Square=1.25, df=1, p=0.2635) were significant predictors of a successful pregnancy, and the logistic regression model containing these two non-significant explanatory variables and controlling for FEMID was non-significant (Likelihood Ratio Chi-Square=0.11, df=1, p=0.7446).

Effect of group size and dominance on reproductive success

Both dominance status of the pregnant female (Wald Chi-Square=7.69, df=1, p=0.0055) and the number of individuals in her group (Wald Chi-Square=4.52, df=1, p=0.0335) were significant predictors of a successful pregnancy according to a significant logistic regression model that also controlled for FEMID (Likelihood Ratio Chi-Square=15.37, df=3, p=0.0015). A pregnant female holding dominant status in her group during her pregnancy was 40.4 (95% confidence limits=3.0-552.1) times as likely to give birth to live young as a pregnant female holding a subordinate ranking. Pregnant females residing in larger groups also had a higher likelihood of having a successful pregnancy. For every additional group member, pregnant females increased their chances of success by 1.7 (95% confidence limits=1.0–2.9) times. Given information on the dominance status of the pregnant female and the number of individuals residing within her group, I was able to classify a pregnancy correctly as successful 88.5% of the time.

Timing of successful subordinate reproduction

A logistic regression model including both the age of the dominant female (Wald Chi-Square=1.32, df=1, p=0.2499) and whether the dominant or subordinate female was pregnant first (Wald Chi-Square=2.23, df=1, p=0.1353) as predictors of reproductive success to a subordinate female whose pregnancy overlapped with that of a dominant female was marginally significant (Likelihood Ratio Chi-Square=4.98, df=2, p=0.0829). Though neither of these pieces of information was a significant predictor of subordinate success, knowing both of these pieces of information provided an 85.7% likelihood of correctly predicting a successful pregnancy to a subordinate female. Pregnancies by subordinates were 0.06 times as likely to be successful (95% confidence interval was

0.001-2.4) if the subordinate female was pregnant before the dominant female. However, all four successful pregnancies by subordinate females were conceived prior to overlapping pregnancies of the dominant female (Figures 1.4 and 1.5). Three successful subordinate pregnancies were conceived prior to the conception of the second annual litter by the dominant female. One successful subordinate pregnancy was conceived just three days prior to the conception of the dominant female's first litter of the year. Interfemale interbirth interval (Wald Chi-Square=0.24, df=1, p=0.6275) and group size (Wald Chi-Square=0.79, df=1, p=0.3755) were removed from the model as non-significant predictor variables in the order stated. Continuing past this point with backward selection of non-significant terms resulted in a non-significant model (Likelihood Ratio Chi-Square=2.28, df=1, p=0.1307) without any statistically significant predictor variables.

DISCUSSION

Caloric abundance may promote pregnancy polygyny in GLTs

The availability of calories did not limit reproduction among either dominant or subordinate GLT females. Instead, caloric availability was sufficient to allow reproduction by two females within the majority of groups studied. The seven GLT home ranges included in this study each contained calories in fruit and nectar that far exceeded the minimum required to support GLT reproduction (Figure 1.3), even in the smallest and poorest of territories. As predicted under these conditions of high caloric availability, subordinate adult female GLTs ovulated while still in their natal group. These findings are contrary to those reported in the only other study to monitor reproductive endocrinology in this wild population (French et al., 2003), but corroborate

studies in captivity that point to the lack of ovarian suppression in subordinate females in the genus *Leontopithecus* after 18 months under conditions of abundant food availability (French, 1987; French & Stribley, 1987; French et al., 1989; Inglett, 1993; Monfort et al., 1996; French et al., 2002).

In the current study all females over 3.9 years of age became pregnant regardless of whether they were still residing in their natal group. Under conditions of high caloric availability, pregnancy was more common in this GLT population than previously reported (Baker and Dietz, 1993; Dietz et al. 1994; Baker et al. 2002; French et al., 2003). Subordinate females were pregnant at the same time as dominant females 11 times during 3 reproductive years. The 83% rate of pregnancy polygyny observed in this study represents an almost doubling of the 44.3% rate reported by Baker et al. (2002). Baker et al. (2002) included data collected over 141 group breeding seasons including long periods of low population turnover. Study groups at that time were very stable and dominant females tended to be older resulting in a set of circumstances that have been shown to promote polygyny in GLTs (Dietz & Baker, 1993; Baker et al., 2002; French et al., 2003; Dietz, 2004). The current study consisted of observations from only 21 group breeding seasons (7 GLT groups over 3 reproductive years) when predation levels were low, population turnover was again relatively low, and older dominant females remained longer within groups. With most if not all breeding positions occupied by tenured females, eldest subordinate daughters attempted reproduction within their natal groups leading to high rates of pregnancy polygyny. In addition, the use of non-invasive hormonal assays and weekly weighings allowed detection of pregnancies that previously went unobserved.

Having more than enough calories available to meet the increased energetic demands of pregnancy during all months of each reproductive year, it is not surprising that neither caloric availability, nor the season in which parturition occurred were significant predictors of a pregnancy resulting in live birth among the females included in this study. It is possible that GLT reproduction may not be limited by carbohydrate resources, but instead by the availability of protein (Kohrs et al., 1976; Kirkwood, 1983; Downing & Scaramuzzi, 1991). Home ranges containing larger areas of swamp habitat where microforaging sites containing insect prey occur at higher densities (Dietz et al., 1997) are more likely to support polygynous groups (Dietz & Baker, 1993). Insects are a major source of fat and protein in the GLT diet (Peres, 1986; Dietz et al., 1997; Kierulff et al., 2002) and consumption of some minimum quantity of insects may be required to provide the baseline level of body fat and protein necessary for the steroid hormones involved in reproduction to function normally (Ojeda, 1996; Takahashi, 2002).

For one particular GLT group energetic limitations on reproduction are likely to have been responsible for the three successive pregnancy losses experienced by the one adult female residing within the group. The group PP3 produced no infants during the 2005-2006 and 2006-2007 reproductive years though the adult female in that group was pregnant three times during these two reproductive years. Pregnancy loss in this group coincided with an extreme loss of territory to neighboring groups. PP3 was forced out of a swamp basin that provided a reliable source of food (unpublished data) and backed up onto a hillside bordered by non-utilizable pasture. PP3 contained the lowest caloric availability of all groups studied (Figure 1.3). Though my estimates of caloric availability in the PP3 range exceeded daily caloric requirements, the time spent in

energetically expensive encounters and competition for those resources with encroaching neighbors may have both increased energetic need as well as limited actual consumption of the resources falling within PP3's range. In addition, the apparent super-abundance of carbohydrate resources may not have been utilizable in its entirety due to ephemeral fruiting booms of hillside species such as *Miconia cinnamomifolia* and *Miconia lepidota*.

Caloric availability is not responsible for the alteration of hormonal profiles observed in failed pregnancies

Hormonal profiles during pregnancy followed the general pattern predicted by the food limitation hypothesis (Figure 1.1). Females whose pregnancies resulted in live births had low cortisol concentrations during early pregnancy and elevated concentrations of cortisol and progesterone during late pregnancy (Figure 1.2) typical of a successful pregnancy in callitrichids (Ziegler et al., 1995; Smith & French, 1997b; Bales, 2000; French et al., 2002; Ziegler & Sousa, 2002; French et al., 2003; Ziegler et al., 2004; Bales et al., 2005) and fitting the pattern predicted under conditions of adequate food availability. Hormone profiles during pregnancies that failed had significantly lower 3rd trimester progesterone concentrations than profiles during successful pregnancies. The lack of a 3rd trimester peak in progesterone was a reliable predictor of subsequent pregnancy loss in GLTs. Females whose pregnancies failed also had 3rd trimester cortisol concentrations that were approximately half those of females during successful pregnancies (though this difference was not statistically significant). Lower 3rd trimester progesterone and cortisol were predicted if insufficient calories limited fetal growth and perhaps led to placental dysfunction and fetal demise (Tardif et al., 2004; Tardif et al., 2005).

Insufficient caloric availability was not responsible for the hormonal differences between successful and non-successful pregnancies. I performed a series of *post hoc* analyses to test the effect of monthly caloric availability on monthly average PdG and cortisol concentrations while non-pregnant and during each of the three trimesters of pregnancy. I used a linear mixed model ANOVA (GLIMMIX). The dataset consisted of monthly average PdG and cortisol concentrations for 18 females while non-pregnant (n=178) and 14 females during each trimester of pregnancy (1st trimester n=65, 2nd trimester n=65, 3rd trimester n=58). The home range occupied by each female was included as a random variable, and I controlled for individual female identity as the subject within home range (HR(FEMID)). I included the identity of each pregnancy as a repeated variable with female identity as the subject (PREGID(FEMID)) to account for the fact that there were multiple pregnancies per female, but controlling for the identity of each female across the pregnancies. HR(FEMID) was removed as a covariate if the covariance parameter associated with it was 0 thereby treating each reproductive attempt for a given female within a given home range as independent (Bales et al., 2001; Bales et al., 2002). Individual differences in baseline hormonal concentrations were also controlled by including AVG_NP_PDG and AVG_NP_CORT in the model when testing for effects during the three trimesters of pregnancy, but not during non-pregnant periods. A log transformation was performed as necessary to meet normality requirements prior to analysis. I found that caloric availability had a non-significant effect on PdG levels either in non-pregnant females or in pregnant females during any trimester. Likewise, caloric availability did not significantly affect cortisol concentrations while non-pregnant or in the 1st trimester of pregnancy. Low cortisol concentrations in pregnant females during

both the 2nd and 3rd trimesters of pregnancy (the condition existing in pregnancies that failed) were significantly associated with higher rather than lower caloric availability (2nd trimester F-value=6.36, ddf=45.97, p=0.0152; 3rd trimester F-value=5.34, ddf=51.99, p=0.0249). Lower 3rd trimester progesterone and cortisol concentrations in pregnancies that failed to produce live young could not be attributed to insufficient caloric availability.

Caloric availability is sufficient to support polygyny in large GLT groups

Females in larger groups had an increased likelihood of carrying a pregnancy to term and giving birth to live young, suggesting that calories were sufficient to support not only pregnancy by multiple breeding females, but also the additional group members resulting from multiple litters. In contrast with predictions of the food limitation hypothesis the likelihood of a successful pregnancy by either a dominant or a subordinate female increased 1.7 times with the addition of each group member. The only subordinate female to reproduce successfully within her natal group for more than a single reproductive season resided within the largest GLT group studied (mean of 9.3 individuals compared to a mean of 4.3 individuals for all other groups). Home ranges containing abundant food resources like those occupied by the GLTs at PDA should support larger groups (Dawson, 1979; Terborgh, 1983; Terborgh & Stern, 1987; Chapman, 1988; Peres, 1994; Dietz et al., 1997; Ganas & Robbins, 2005; Wiczowski, 2005; Miller & Dietz, 2006) without a corresponding reduction in individual caloric intake (Foster, 1982). With ample calories available to all group members, reproduction should not be limited to a single breeding female. An abundant food supply should lead to high rates of pregnancy polygyny (Goldizen, 1987a; Goldizen et al., 1988; Dietz &

Baker, 1993; Goldizen et al., 1996; Baker et al., 2002; Clutton-Brock et al., 2008) and greater reproductive success (Kirkwood, 1983; Janson & van Schaik, 1988; Isbell, 1991; Dietz & Baker, 1993; Tardif & Jaquish, 1994; Janson & Goldsmith, 1995; Tardif & Jaquish, 1997; Bales et al., 2001; Tardif et al., 2001; Bales et al., 2002; Koenig, 2002; De Vleeschouwer et al., 2003; Tardif & Bales, 2004; Tardif et al., 2004; Tardif et al., 2005). Additionally, in cooperatively breeding species larger group sizes and the resulting increase in allocare provided to dependent young should increase reproductive success (in birds: reviewed by (Brown, 1987); greater ani cuckoo (*Crotophaga major*): (Riehl, 2010); coyotes (*Canis latrans*): (Bekoff & Wells, 1982); lions (*Panthera leo*): (Bygott et al., 1979); African wild dogs (*Lycaon pictus*): (Malcolm & Marten, 1982); blackbacked jackals (*Canis mesomelas*): (Moehlman, 1979); dwarf mongooses (*Helogale parvula*): (Rood, 1990); meerkats (*Suricata suricatta*): (Hodge et al., 2008); badgers (*Meles meles*): (Kruuk, 1989); common marmosets: (Koenig, 1995), moustached tamarins (*Saguinus mystax*): (Garber et al., 1984; Sussman & Garber, 1987); cotton-top tamarins: (Price, 1992a; Savage et al., 1996b); saddle-back tamarins: (Terborgh & Goldizen, 1985); and GLTs: (Dietz & Baker, 1993; Bales et al., 2001; Siani, 2009)). Higher reproductive success increases group size. Therefore, as pointed out by Dietz and Baker (1993), large group size may be either a cause or an effect of polygyny.

The availability of helpers rather than calories limits the timing of successful subordinate reproduction

Births of live infants to subordinate females were staggered between successive births by dominant females such that periods of intense infant dependency on allocare did not overlap (Figures 1.4 and 1.5). When both dominant and subordinate females were

pregnant during the same reproductive season, the likelihood of the subordinate female giving birth to live young increased if the subordinate conceived her pregnancy prior to the dominant female as predicted under the food limitation hypothesis. However, calories were more than sufficient to support simultaneous reproduction by two breeding females. All four successful pregnancies by subordinate females were conceived prior to overlapping pregnancies of the dominant mother. In all four of these cases the dominant mother in the group gave birth to two litters per reproductive year, typically one in September and another in late January or early February. Three of four successful pregnancies by subordinate daughters were conceived prior to conception of the second litter of the year by the dominant female. The infants of these subordinate females were born 17, 17, and 35 days (IFIBIs) prior to the infants of the second litter of the dominant female. Infants of the subordinate female born at this time avoid competition for allocare for at least the first two to five weeks of life. The previous litter by the dominant mother has already been weaned and as juveniles they are largely independent in terms of nutrition and locomotion (Baker, 1991; Ruiz-Miranda et al., 1999; Tardif et al., 2002; Siani, 2009). The subsequent litter by the dominant mother will not arrive for at least another two weeks and will be cared for almost entirely by their mother for the first three weeks of their life (Hoage, 1978; Baker, 1991; Santos et al., 1997; Tardif et al., 2002). The availability of helpers during these first few weeks may be particularly important to subordinate females that tend to be younger and less experienced (Epple, 1975; Hoage, 1978; Kirkwood et al., 1983; Tardif et al., 1984; Johnson et al., 1991; French et al., 1996; Bardi et al., 2001). The only successful pregnancy by a subordinate female that was not staggered between pregnancies of the dominant female was the third successful

pregnancy within the natal group by that particular subordinate daughter. This subordinate female still conceived prior to the dominant female, but did so just three days prior to conception of her mother's first pregnancy of the year. Thus, the subordinate female's litter arrived just three days (IFIBI) prior to the dominant female's litter in September. The observation that this subordinate female alone provided the majority of care for this litter (Siani, 2009) lends support to the idea that when multiple litters arrive less than two weeks apart subordinate females may forego allocare for their infants. My results combined with those of Digby (1995a) and Goldizen et al. (1996) suggest that competition for allocare rather than for food resources may be the selective force limiting reproduction by subordinate females.

ACKNOWLEDGEMENTS

Funding for this project was provided by the American Society of Mammalogists, the Copenhagen Zoo Lion Tamarins of Brazil Fund, the University of Maryland Center for Biodiversity, a Darwin Fellowship from the University of Maryland BEES Program, and a Wylie Dissertation Fellowship from the University of Maryland Graduate School to M. Henry and by the National Science Foundation (SBR-9727687; BCS-0216096) to J. Dietz. I thank the Brazilian Science Council (CNPq), Brazilian Institute for the Environment and Renewable Natural Resources (IBAMA), and Golden Lion Tamarin Association (AMLD) for logistic support and permission to conduct this study. This research complies with the guidelines of the University of Maryland Animal Care and Use Committee and all applicable Brazilian laws. Importation of fecal samples into the U.S. was conducted under the auspices of CITES, USDA, and CDC. Special thanks to Jim Dietz and Jeff French for their guidance and support throughout this project. I thank

Ecología research assistants Otávio Narciso, Synval de Melo, Jadir Ramos, and Andréia Martins for help with data collection in the field. A special thanks to Ademilson de Oliveira who taught me to identify Brazilian plant species and helped me set up phenological transects. I thank Jeff Fite, Kate Townley, and Tom Shirazi for assistance with endocrine analyses. Thanks to Jennifer Siani for tamarin weights and Kimran Miller-Buckholz for plant species identifications, dry weights, and caloric values. I sincerely appreciate the work done by Sarah Hankerson mapping habitat data and performing statistical analyses. I thank Karen Bales for setting the precedent for endocrine work in this population of tamarins.

TABLES

Table 1.1. Summary of the predictions generated by the food limitation hypothesis and empirical findings in golden lion tamarins. (Bold italics indicate predictions consistent with findings in golden lion tamarins. See text for explanations and additional details.)

Predictions	Food limitation hypothesis	Findings in golden lion tamarins
Subordinates females ovulate.	<i>yes</i>	yes
Subordinates females conceive.	<i>yes</i>	yes
Pregnancies with lower cortisol levels just prior to conception and during the 1 st trimester are more likely to succeed.	<i>yes</i>	yes, lower 1 st trimester cortisol predicts success
Pregnancies with higher progesterone and cortisol during the 3 rd trimester are more likely to succeed.	<i>yes</i>	yes
Pregnancies under higher caloric availability are more likely to succeed.	yes	no
Pregnancies in smaller groups are more likely to succeed.	yes	no, larger
Pregnancies with longer interfemale interbirth intervals are more likely to succeed.	yes	no
Pregnancies conceived first are more likely to succeed.	<i>yes</i>	yes

Table 1.2. Reproductive summary for 21 GLT females from 7 free-ranging GLT groups sampled from March of 2004 through February of 2007.

Group	Group exhibits polygyny	Female ID	Age category (years)	Age (years) at first conception if during study	Successful pregnancies	Infants born	Non-successful pregnancies	Fecal samples
3M5	N	782	Adult (4.5-6.7)		0	0	1	32
AL	Y	539	Adult (10.6-13.3)		2	2	2	97
AL	Y	846	Adult (2.8-5.3)	2.9	3	6	0	78
AL	Y	1267	Infant to subadult (0.2-1.3)	Did not conceive	0	0	0	21
BO2	Y	720	Adult (9.4-12.3)		6	11	0	125
BO2	Y	848	Adult (2.4-5.3)	2.5	3	6	2	136
BO2/POR	Y/N	880	Subadult to adult (1.4-4.1)	2.8	3	6	0	88
BO2/POR	Y/N	899	Subadult to adult (1.1-2.4)	Did not conceive	0	0	0	39
BO2/POR	Y/N	1227	Subadult to adult (0.7-2.9)	Did not conceive	0	0	0	68
BO2/POR	Y/N	1241	Subadult to adult (0.8-2.0)	Did not conceive	0	0	0	52
GF	Y	766	Adult (5.6-6.9)		2	4	0	35
GF	Y	889	Adult (1.6-3.0)	2.5	0	0	1	18
GF	N	1266	Adult (2.9-4.0)	3.4	1	1	0	32
PA	Y	869	Adult (4.7-7.3)		4	8	0	98
PA	Y	884	Adult (1.7-3.3)	2.7	0	0	1	60
PA	Y	1271	Juvenile to subadult (0.4-1.4)	Did not conceive	0	0	0	32
PP3	N	750	Adult (8.7-10.5)		1	2	3	77
PP3	N	1238	Juvenile to adult (0.3-1.9)	Did not conceive	0	0	0	56
PP3	Y	1264	Adult (4.0-4.3)	3.9	1	2	0	12
PP3	Y	1265	Adult (3.3-4.2)	3.9	0	0	1	10
PP3	N	T0PP3	Adult (Unknown)	Did not conceive	0	0	0	10
				$\bar{x} = 3.1 \pm 0.2$	$\Sigma = 26$	$\Sigma = 48$	$\Sigma = 11$	$\Sigma = 1176$

FIGURE LEGENDS

Figure 1.1. Mean (\pm standard error) fecal pregnanediol-3-glucuronide (PdG) and cortisol concentrations for adult females while non-pregnant (NP, n=179 samples, from 18 females) and during each trimester of pregnancy (1st trimester, I, n=65, 14; 2nd trimester, II, n=65, 14; 3rd trimester, III, n=58, 14). Statistically significant differences in means are indicated by different letters.

Figure 1.2. Mean (\pm standard error) fecal pregnanediol-3-glucuronide (PdG) and cortisol concentrations for successful vs. non-successful pregnancies just prior to conception (NP, n=32 pregnancies, 23 successful, 9 non-successful), during the 1st trimester (I, n=36, 26, 10), during the 2nd trimester (II, n=35, 25, 10), and during the 3rd trimester of pregnancy (III, n=31, 23, 8). Statistically significant differences in means are indicated by an asterisk.

Figure 1.3. Kilocalories from fruit and nectar contained within 7 GLT home ranges each month from March of 2004 through February of 2007 exceeded the 13,610 kcal/month requirement (blue horizontal line) for supporting the average group of GLTs and their reproduction.

Figure 1.4. Progesterone (PdG) profiles for a dominant mother (GLT720) and her subordinate daughter (GLT848) demonstrating that conceptions by the subordinate while the dominant female was heavily pregnant with her first litter of the year and prior to conception of the second litter by the dominant female were more likely to result in the birth of live infants. Green arrows indicate dates of conceptions resulting in the birth of live young (subsequent red arrow). Blue arrows indicate conceptions that resulted in pregnancy loss. Red arrows indicate successful parturition dates. Note that the first two

successful infant births by GLT848 (red arrows) occur between the birth of the first (red arrow in September) and second (red arrow in January or February) annual litters by GLT720, resulting in the staggering of successful births to the subordinate daughter between births to the dominant mother.

Figure 1.5. Progesterone (PdG) profiles for the eldest female in the study (GLT539) and her eldest daughter (GLT846). GLT539 was dominant until after the birth of her second litter in February of 2005 when GLT846 became dominant. While subordinate to her mother, GLT846 successfully reproduced when she conceived while her mother was heavily pregnant with her first litter of the year. Pregnancies by GLT539 that were conceived at the same time as those of her dominant daughter were lost at full term. Green arrows indicate dates of conceptions resulting in the birth of live young. Blue arrows indicate conceptions that resulted in pregnancy loss. Red arrows indicate successful parturition dates. Note that successful reproduction (red arrows) by two females during the same reproductive year occurred only when pregnancies were staggered.

FIGURES

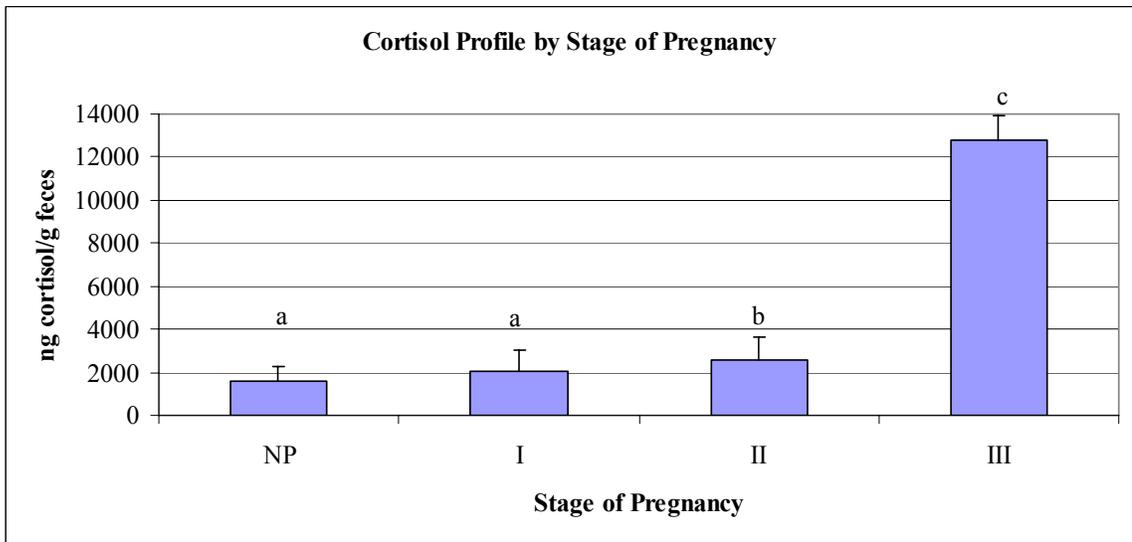
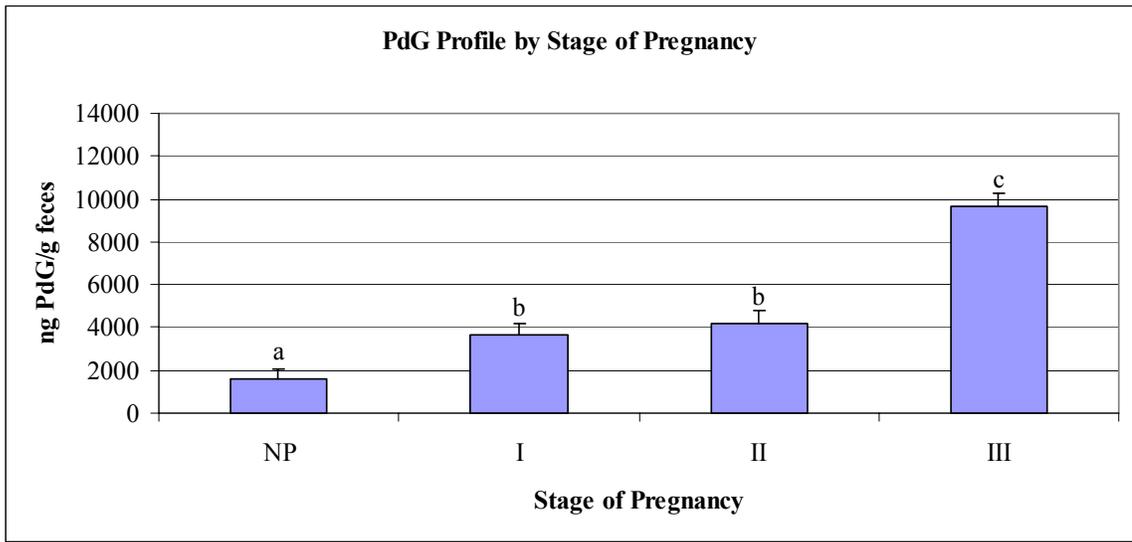


Figure 1.1.

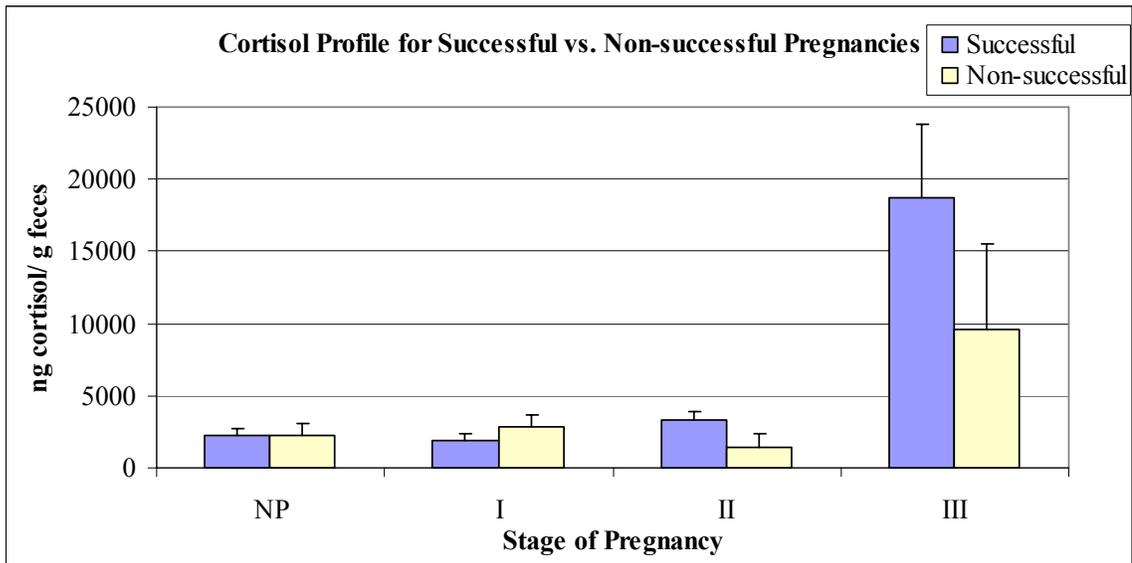
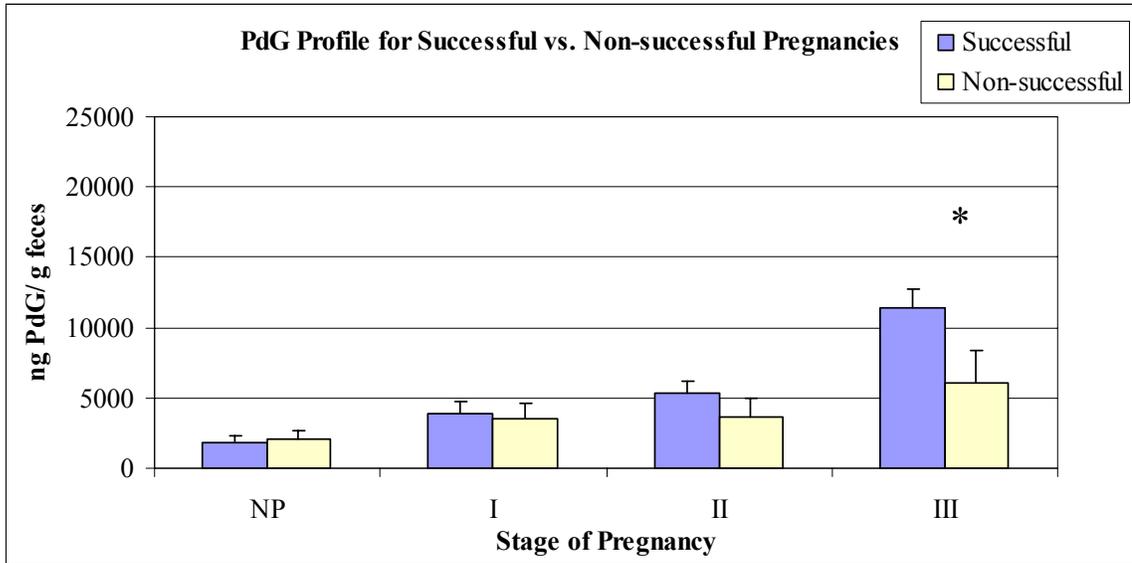


Figure 1.2.

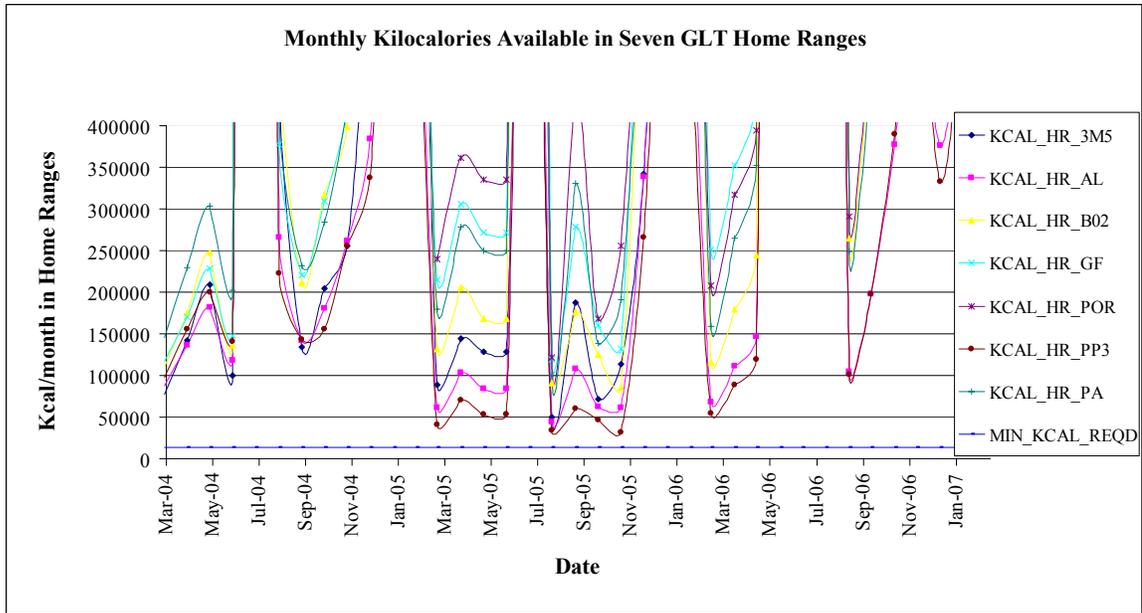


Figure 1.3.

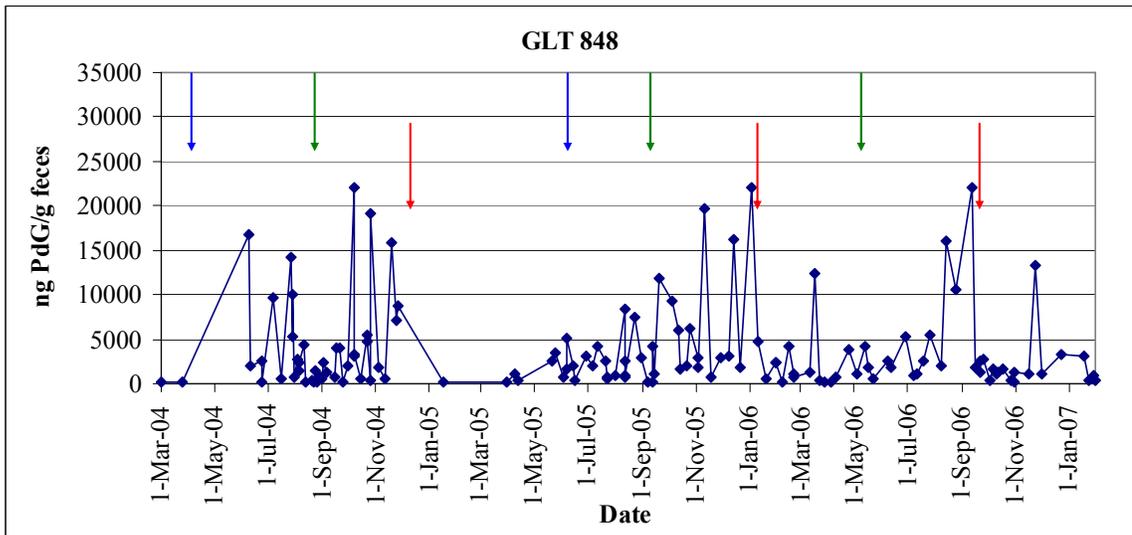
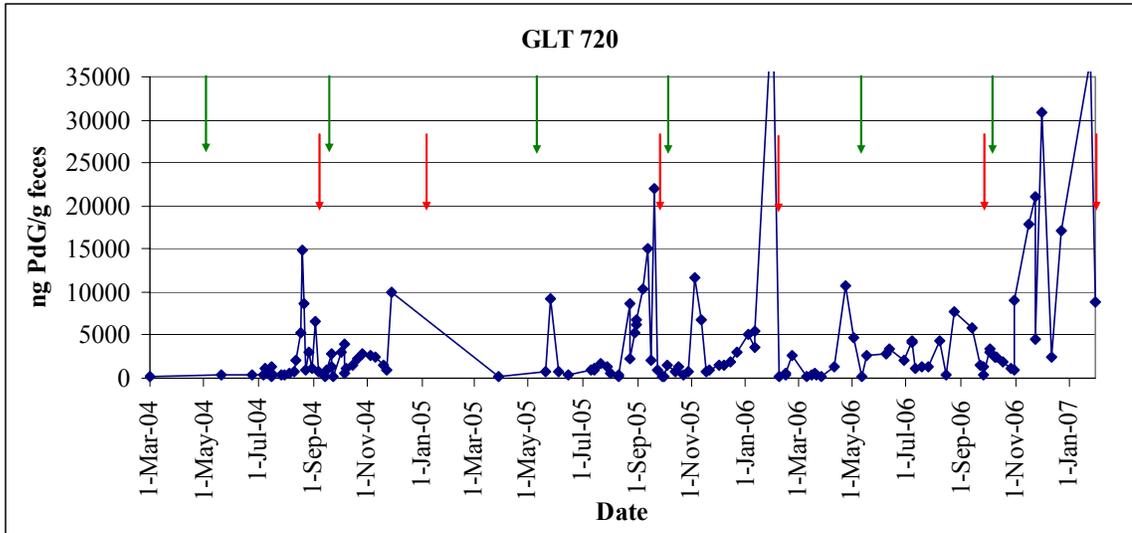


Figure 1.4.

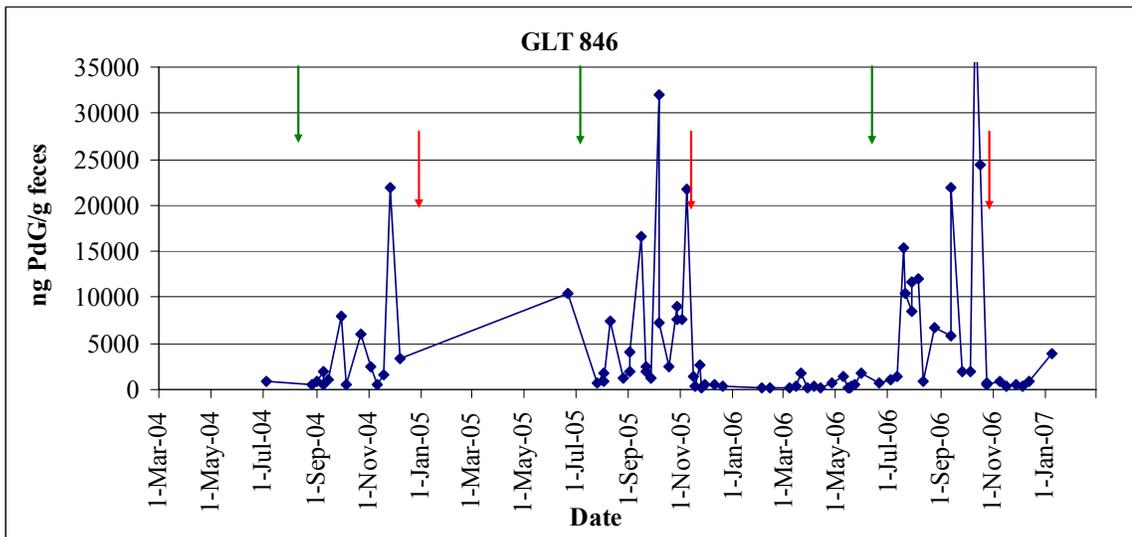
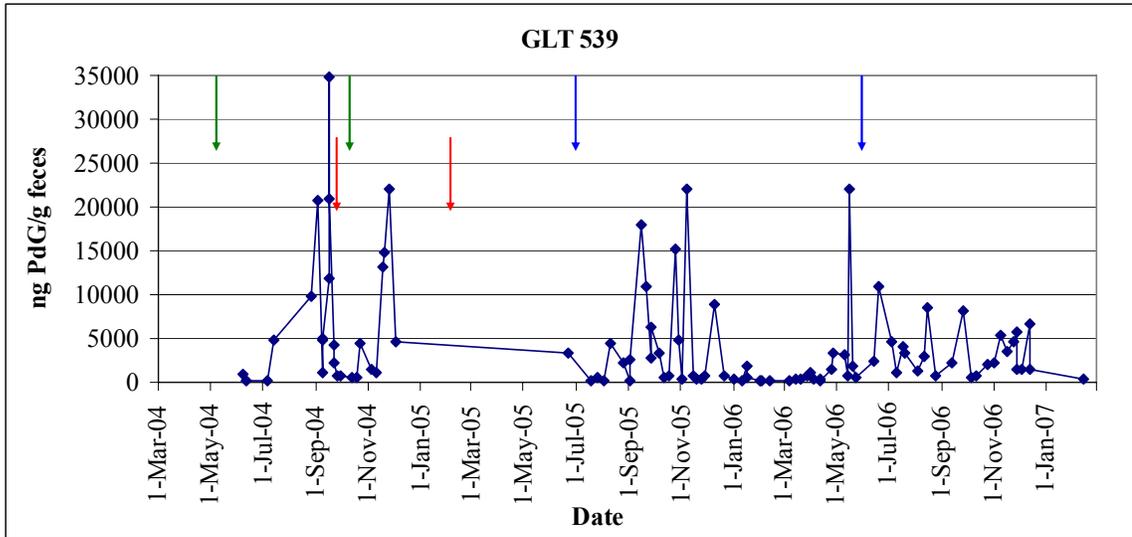


Figure 1.5.

Chapter 2: Self-restraint limits reproduction by young adult subordinate female golden lion tamarins (*Leontopithecus rosalia*)

ABSTRACT

The monopolization of reproduction by dominant group members in cooperatively breeding species has been explained in terms of the reduction in dominant fitness that occurs when subordinates are allowed to breed. In the current study I explain reproductive skew in cooperatively breeding golden lion tamarins (*Leontopithecus rosalia*) in terms of the costs and benefits to subordinate fitness under existing social circumstances. I tested the hypothesis that subordinate females exercise reproductive self-restraint when conditions are unfavorable for successful breeding. I collected three years of data from seven free-ranging tamarin groups in Poço das Antas Biological Reserve, Rio de Janeiro, Brazil, recording group compositions daily. I used hormonal (progesterone and cortisol) profiles obtained through non-invasive immunoassay of feces to detect ovulation in subordinates. I also used changes in body mass, bi-annual physical examinations, and behavioral observations to diagnose pregnancies of both dominant and subordinate females. I defined reproductive success as pregnancies that resulted in the birth of live infants. I performed logistic regression analyses comparing pregnancies that resulted in the birth of live infants to those that did not to identify variables useful in predicting a successful pregnancy to a subordinate female. Subordinate females older than 18 months of age ovulated while residing within their natal group, but conceptions were delayed one to two years following reproductive maturity as predicted if young subordinate females were exercising reproductive self-restraint. The likelihood of successful reproduction by a subordinate female doubled with each year of age of the

dominant female as predicted if the ability of dominant females to interfere in subordinate reproduction by evicting subordinates from the group decreased with age.

Conceptions under incestuous mating conditions were rare (7 of 37 pregnancies) demonstrating inbreeding avoidance. However, my data did not provide evidence in support of inbreeding depression as the selective force behind incest avoidance since the likelihood of giving birth to live young did not differ between pregnancies conceived under incestuous versus non-incestuous mating conditions. My data provide support for the hypothesis that young subordinate adult females exercise reproductive self-restraint by delaying conception while in groups containing a young dominant female and no unrelated male. I speculate that the threat of being evicted from the group and inbreeding avoidance are sufficient to delay attempts at reproduction by young subordinates without the need for costly fighting with the dominant female.

INTRODUCTION

For social organisms, the resources available to individuals are dependent upon current group dynamics. Reproductive skew models consider how the availability of a variety of resources (including food, shelter, mates, and helpers) changes under different social and ecological contexts, and how these changes affect individual patterns of behavior to limit reproduction to only a few breeding individuals per group (reproductive skew) (Clutton-Brock, 2009). Thus, asymmetrical patterns of breeding and reproduction are explained in terms of individual fitness costs and benefits that accrue under existing ecological and demographic circumstances. Monopolization of reproduction by dominant group members by means of social suppression of subordinate reproduction has been documented in several taxa of cooperative breeders including mammals (Solomon

& French, 1997a), birds (Reyer et al., 1986; Mays et al., 1991; Schoech et al., 1991), fishes (Fitzpatrick et al., 2008), and invertebrates (Hamilton, 2004). The goal of the current study was to identify the mechanisms responsible for maintaining reproductive skew in the cooperatively breeding golden lion tamarin (*Leontopithecus rosalia*).

Golden lion tamarins (GLTs) are small, neotropical primates in the family Callitrichidae. GLTs typically reside in family groups of 2–11 individuals (Dietz & Baker, 1993; Dietz et al., 1994). Lion tamarin offspring typically delay dispersal and reproduction, and remain in their natal group to help with the care of infant siblings (Dietz & Baker, 1993). Cooperative care has been suggested to be instrumental in the ability of callitrichids to meet the energetic needs associated with successfully rearing the litters of twins they are capable of producing once or twice a year (Kleiman, 1977a; Sussman & Garber, 1987; Baker et al., 1993; Dietz & Baker, 1993). Dietz and Baker (1993) described the mating system in GLTs as monogyny with about a 10% incidence of polygyny; successful reproduction is most commonly limited to a single dominant female. More recent investigations have suggested that the incidence of pregnancy polygyny (more than one female confirmed as being pregnant within the same breeding season) may be much higher (Chapter 1, this dissertation), but rearing polygyny (more than one female reared offspring to weaning) remains low (Baker et al., 2002). Dietz and Baker (1993), Baker et al. (2002), and Hankerson (2008) provided indirect support for the hypothesis that reproduction by multiple breeding females was limited by food availability, but a more recent study quantifying caloric availability within GLT home ranges found that home ranges contained sufficient calories to support polygyny (Chapter 1, this dissertation). French et al. (2003) suggested that polygyny was rare but did occur

in some groups containing an old dominant female and at least one non-related male. Based upon 16 years of demographic data, Dietz and Baker (unpublished data) found a significant positive relationship between the age category of the dominant female and the incidence of polygyny in GLT groups and concluded that older dominant females were no longer physically able to control reproduction by their subordinate daughters. Both studies were interpreted as providing support for the hypothesis of incomplete dominant control of subordinate reproduction, but could also provide support for the hypothesis that subordinate GLT females exercise reproductive self-restraint when they occupy groups with a young dominant female capable of evicting them from the natal group and when opportunities for non-incestuous matings do not exist within the group.

Under the hypothesis of subordinate restraint, subordinates forego reproduction when existing social and ecological conditions make a reproductive investment unlikely to succeed (Reyer et al., 1986; Hamilton, 2004; Young et al., 2008; Saltzman et al., 2009). Subordinate females able to exercise reproductive restraint when the likelihood of success is low may avoid or minimize their investments in failed reproductive attempts as well as increase their own chances of survival and future reproduction (Wasser & Barash, 1983; Jaquish et al., 1991; Digby, 1995a; Abbott et al., 1997; Saltzman, 2003; Gilchrist, 2006a; Saltzman et al., 2009). Given the large investment these small-bodied primates make in a single reproductive attempt (owing to long gestation periods (French et al., 2002) and high infant to maternal body mass ratios (Leutenegger, 1973)), selection should favor females able to detect conditions unfavorable for reproduction and restrain their own reproductive activity accordingly (Saltzman et al., 2009). One would also expect subordinates to exercise this restraint early on in the reproductive process, such as

prior to conception, before appreciable costs have already accrued (Wasser & Barash, 1983). Therefore, one assumption of the subordinate restraint model is that subordinate females are capable of reproducing but they do not attempt to do so (Saltzman et al., 2009). Subordinate females may delay reproduction by avoiding matings (Rothe, 1975; Abbott, 1984) or delaying conceptions (Arruda et al., 2005; Sousa et al., 2005).

A second assumption of this model is that the threat of eviction from the natal group or of losing a costly reproductive investment is sufficient to restrain subordinates from attempting reproduction without the constant struggle and overt aggression assumed to take place under incomplete control models (Saltzman et al., 2009). By exercising self-restraint in response to social cues that serve as early indicators of unfavorable reproductive conditions, subordinates may also avoid the energetic costs and potential risks that may arise from conflict with the dominant female (including mounting a stress response, engaging in aggressive fights, eviction from the natal group and the risks associated with dispersal, pregnancy loss, and/or infanticide) (Saltzman et al., 2009). Subordinate restraint has been demonstrated in cooperatively breeding species when the threat of infanticide on subordinate young is high (Digby, 1995a; Saltzman, 2003; Saltzman et al., 2008; Young et al., 2008; Abbott et al., 2009; Saltzman et al., 2009), when the threat of eviction from the natal group upon any attempt to reproduce is high (Johnstone & Cant, 1999; Hamilton, 2004; Buston et al., 2007), and when the risk of mating with close relatives and suffering the consequences of inbreeding depression is high (incest avoidance) (Mays et al., 1991; Clarke et al., 2001; Hamilton, 2004).

In a review of the literature for both captive and wild groups of common marmosets (*Callithrix jacchus*), Saltzman et al. (2009) concluded that reproduction by

subordinate females is self-restrained rather than impeded by dominant females. Adult subordinate female common marmosets undergo both suppression of ovulation as well as inhibition of sexual behavior in captivity (Rothe, 1975; Abbott, 1984; Saltzman et al., 1997c) and in the wild (Digby, 1999; Sousa et al., 2005). Reproductive suppression in this species is rapidly reversible in response to changes in group composition (Saltzman et al., 2009). Subordinate females begin to ovulate shortly after removal of the subordinate female from her natal group or the removal of the dominant female from the group (Evans & Hodges, 1984; Abbott et al., 1988; Abbott & George, 1991). Upon introduction of a non-natal male into the group, subordinate females began to engage in sexual behavior (Anzenberger, 1985; Hubrecht, 1989; Kirkpatrick-Tanner et al., 1996; Saltzman et al., 1997b; Saltzman et al., 1997c; Saltzman et al., 2004). Anovulation and the lack of socio-sexual behavior on the part of these subordinate females does not appear to be stress induced or imposed upon subordinates by dominant females (Saltzman et al., 2009), since subordinate marmoset females receive little or no aggression from dominant females (Epple, 1967; Abbott, 1984; Saltzman et al., 1994; Digby, 1995b; Saltzman et al., 1997c; Sousa et al., 2005), subordinates rarely attempt to mate within their natal group (Rothe, 1975; Abbott, 1984), and interference in the few matings engaged in by subordinate females is rare (Kirkpatrick-Tanner et al., 1996; Lazaro-Perea et al., 2000). In addition, concentrations of the stress hormone cortisol are no higher in subordinate marmoset females than in dominant females (Abbott et al., 1981; Saltzman et al., 1994; Johnson et al., 1996; Saltzman et al., 1998; Ziegler & Sousa, 2002; Sousa et al., 2005; Saltzman et al., 2006b; Saltzman et al., 2006c) in contrast with what would be expected if subordinates suffered from chronic stress as the result of receiving constant harassment

by the dominant female (Abbott et al., 2003). The threat of infanticide by the dominant female was proposed as the ultimate cause for subordinate reproductive restraint in this species (Saltzman et al., 2009).

Unlike marmosets, captive subordinate adult GLT females undergo normal ovulatory cycles while residing within their natal groups (French, 1987; French & Stribley, 1987; French et al., 1989; Inglett, 1993; Monfort et al., 1996; French et al., 2002). Singular breeding by a dominant female in captive GLT groups has been attributed to female-female aggression and incest avoidance (Kleiman, 1979; Inglett et al., 1989; French et al., 2002). In contrast with studies of captive GLTs and in agreement with patterns found in both captive and wild common marmosets, the only hormonal study of wild GLTs provided evidence that the majority of subordinate females remained anovulatory within their natal group (French et al., 2003). However, the presence of an elderly dominant female or the entry of an unrelated male into the natal group led to the onset of ovulation and conceptions in some subordinate daughters. Aggression levels have been shown to be mild and infrequent within established GLT groups in the wild (Baker, 1991; Dietz & Baker, 1993; Baker et al., 2002). Cortisol concentrations did not differ between anovulatory subordinates, ovulatory subordinates, and ovulatory dominant females (Bales et al., 2005). These findings suggest that adult subordinate GLT females residing in their natal groups are physiologically capable of reproduction, but reproductive restraint is self-imposed rather than imposed upon them through stressful aggressive interactions with the dominant female.

Threat of eviction

If subordinates attempting reproduction risk eviction from the group, selection may favor subordinate females that delay conceptions until the risk is lower (Johnstone & Cant, 1999; Hamilton, 2004; Buston et al., 2007). Evictions from the natal group are more common after subordinates reach sexual maturity (Baker, 1991; Baker et al., 2002; Clutton-Brock et al., 2008), indicative of dominant females that may not tolerate reproductive competition (Clutton-Brock et al., 1998a; Young et al., 2006; Clutton-Brock et al., 2008). Young dominant females may pose a greater threat of eviction to their subordinate daughters since they are more likely to be in good physical condition (weigh more (Dietz et al., 1994) and have longer canine teeth (Dietz, unpublished data)) and physically able to mount persistent and successful attacks on subordinates (Hodge et al., 2008). In established groups of GLTs, high levels of aggression have been observed a few days before and after eviction of a group member (Baker, 1991; Dietz & Baker, 1993; Baker et al., 2002; Bales et al., 2005). The evicted individual is often chased and aggressively attacked by the dominant female and other same-sex group members (Baker et al., 2002). The costs associated with eviction from the natal group are especially high in females because they spend significantly longer periods of time outside of protective social groups as they face severe and often hostile competition for limited reproductive openings elsewhere (Baker & Dietz, 1996; Goldizen et al., 1996; Baker et al., 2002). Individuals roaming independently outside of social groups face increased risk of predation (Coimbra-Filho, 1977; Caine, 1987), attack by neighboring groups (Baker & Dietz, 1996), and hypothermia (Bartholomew & Rainey, 1971; Contreras, 1984; Ligon et al., 1988; Thompson et al., 1994). Rates of successful female dispersal are low in many

cooperatively breeding mammals exhibiting high reproductive skew (Clutton-Brock, 2009) including tamarins and lion tamarins (Goldizen et al., 1996; Baker et al., 2002). Isolation from the group may result in high levels of social stress (Johnson et al., 1996; Smith & French, 1997a; Smith & French, 1997b), that can inhibit energy investment in reproduction (Sapolsky, 2000; Sapolsky, 2002). Eviction from the group may culminate in the stress-induced loss of a pregnancy that was conceived while within the group (Gilchrist, 2006a; Young et al., 2006). The combination of increased risks and high energetic costs incurred by subordinate females that are evicted from the natal group may reduce a female's chance of survival and reproduction such that selection favors subordinate females that exercise reproductive restraint while residing within a group containing a young dominant female.

Inbreeding avoidance

When the deleterious effects of inbreeding lead to reduced survival of offspring conceived from incestuous matings, selection may favor subordinate females that exercise reproductive self-restraint in response to the lack of breeding opportunities with non-related males (Mays et al., 1991; Clarke et al., 2001; Hamilton, 2004). Subordinate reproduction should be rare when subordinates lack access to unrelated males (so that the benefits of attempting to breed are relatively low) (Clutton-Brock et al., 2008). A number of studies in mammals and birds have found a correlation between the physiological inhibition of reproduction and relatedness of potential mates in the group (Reyer et al., 1986; Mays et al., 1991; Carter & Roberts, 1997; French, 1997; Carlson et al., 2004). Subordinate meerkat (*Suricata suricatta*) females in groups containing only related males have lower luteinizing hormone and estradiol concentrations than

subordinates occupying groups containing an unrelated male (Carlson et al., 2004) making subordinate meerkat females less likely to ovulate and conceive under incestuous mating conditions. Incest may also be avoided through behavioral mechanisms. Subordinate common marmoset daughters do not mate with their fathers or conceive while residing within an intact natal group (Saltzman et al., 2004). Fully mature subordinate females often fail to breed for one to two years while remaining within their natal group (Arruda et al., 2005; Sousa et al., 2005). However, upon introduction of an unrelated male to the group, subordinate females readily mate with the non-natal male and may become pregnant (Anzenberger, 1985; Hubrecht, 1989; Kirkpatrick-Tanner et al., 1996; Saltzman et al., 1997b; Saltzman et al., 1997c; Saltzman et al., 2004). A similar delay in mating behavior and conceptions has been documented for subordinate female GLTs remaining within their natal group. The mean age at first reproduction for wild subordinate female GLTs is 3.6 years (Bales et al., 2001), well over the 16-18 months of age associated with the onset of normal ovarian cyclicity (French & Stribley, 1987; French et al., 1989; French et al., 2002). In the only other study using hormonal profiles to diagnose pregnancy in wild GLTs the presence of a male not related to the subordinate female was a key factor in determining whether a subordinate female ovulated and became pregnant within her natal group (French et al., 2003). Incest avoidance has been suggested as one possible reason for delays in reproductive activity by subordinate female marmosets and tamarins remaining within their natal group (Dietz et al., 2000; Baker et al., 2002; French et al., 2002). The occurrence of polygyny in captive common marmoset groups is often associated with the introduction of an unrelated male (Rothe & Koenig, 1991). The presence of an unrelated male within the

group also had a significant positive effect on the incidence of polygyny in wild saddle-back tamarin (*Saguinus fuscicollis*) groups (Goldizen et al., 1996), captive and wild cotton-top tamarin (*Saguinus oedipus*) groups (Price & McGrew, 1991; Savage et al., 1996a), as well as wild GLT groups (Baker et al., 2002).

In order for incest avoidance to function as a selective pressure for subordinate reproductive restraint, there must be a reduction in profitability that occurs when subordinates engage in incestuous matings (Hamilton, 2004). A major cost of inbreeding is the reduced survival of inbred young. Inbred young of 11 out of 12 small mammal species (including 9 families in 3 orders) experienced higher juvenile mortality rates than non-inbred young (Ralls & Ballou, 1982a). When comparing rates of infant survival among 14 species of captive primates, infant mortality was higher for inbred offspring in 15 out of 16 colonies studied (Ralls & Ballou, 1982b). In a more comprehensive study of 38 mammalian species in captivity, mortality was at least 33% higher in offspring from parent-offspring or full sibling matings than in offspring of unrelated parents (Ralls et al., 1988). Without the benefit of molecular-genetic techniques to assess whether offspring are indeed inbred, it is difficult to assess accurately the costs of inbreeding in wild populations where paternity must be assumed based upon group composition (Moore, 1993; Dietz et al., 2000). That concern notwithstanding, Dietz et al. (2000) found that inbreeding depression caused by assumed father/daughter matings may limit successful reproduction by subordinate females by causing higher rates of infant mortality. In that study, paternity was estimated based upon behavioral observations. Dietz and Baker (1993) examined first pregnancies for 19 females (primiparous females) and found 14 of those to be father (or brother)/daughter matings (paternity estimated by group

composition at time of conception). None of those presumed incestuous offspring survived to weaning; whereas one or more infants from 86% of the non-incestuous matings survived to weaning. In addition, the survivorship of presumed inbred tamarins remained lower than that of non-inbred tamarins for at least the first two years of life (Dietz et al., 2000). Younger subordinate females mating within their natal group run a greater risk of mating with their father or brother and perhaps losing a costly reproductive investment due to inbreeding depression. These females may not conceive under incestuous conditions in favor of delaying their investment until a non-natal male joins the group (French et al., 2003) or they are able to secure non-incestuous matings from males outside the group, perhaps during encounters with neighboring groups (Digby, 1999; Baker et al., 2002; Young et al., 2007).

Hypotheses and predictions

The goal of this study was to determine whether subordinate adult female GLTs are capable of reproducing (ovulate) but limit their own reproduction by not conceiving when the probability of reproductive success is low. Alternatively, dominant suppression of ovulation and/or dominant aggression may render subordinate females incapable of reproducing. To test the hypothesis of subordinate self-restraint I collected three years of data from seven groups of GLTs. I used data on group demography, reproductive status as diagnosed through non-invasive hormonal assays for progesterone and cortisol, and reproductive success defined as pregnancies that resulted in the birth of live offspring. I tested four predictions derived from the hypothesis that subordinate adult female GLTs limit their own reproduction in response to cues by a young dominant female and in the absence of a non-related male within the group.

Prediction 1: Subordinate adult females will ovulate, but will not conceive while there is a young dominant female present in the group (in response to the threat of eviction).

Prediction 2: Pregnancies by subordinate females will be more likely to succeed as the age of the dominant female increases (potentially avoiding the negative consequences of eviction).

Prediction 3: Subordinate adult females will ovulate, but will not conceive while there is no non-related male present in the group (inbreeding avoidance).

Prediction 4: Pregnancies by subordinate females will be more likely to succeed when a non-related male is present within the group at the time of conception (potentially avoiding the negative consequences of inbreeding depression).

METHODS

Study site

Data were collected within the 6300 ha Poço das Antas Biological Reserve (PDA), Rio de Janeiro State, Brazil (22° 30' - 33' S, 42° 15' - 19' W) (Miller & Dietz, 2006). The reserve is predominantly secondary forest consisting of a patchwork of habitat types resulting from the various stages of secondary succession following human occupation (Dietz et al., 1997). The areas of secondary forest used by GLTs include hillside, lowland transitional, and swamp (refer to definitions of hilltop/hillside forest, corridor, and swamp forest/gingers in Dietz et al. (1997)).

PDA has a wet (October through April (Dietz et al., 1994; Hankerson, 2008)) and a dry season (June through August (Dietz & Baker, 1993; Hankerson, 2008)) each year. During the three years of this study, PDA received an average of 2135.6 ± 184.1

(standard error) mm of precipitation each year (unpublished data). An average of 260.2 ± 18.9 mm of rain fell during each wet month as compared to an average of 62.9 ± 7.4 mm of rain during each dry month (unpublished data). Average maximum temperatures were 27.6 ± 0.2 ° C during the wet season and 25.0 ± 0.2 ° C during the dry season (unpublished data).

Study species

Golden lion tamarins once occupied much of the Atlantic Coastal Forest of Rio de Janeiro State, Brazil. Today, primarily as a result of habitat loss, fragmentation, and forest degradation and with the exception of a few small coastal populations, GLTs are found only in small patches of remnant forest centered around the São João river basin (Rylands et al., 2002; Ruiz-Miranda et al., 2008). GLTs were ranked as “critically endangered” from 1963 to 2002 due to low numbers, narrow distribution, and threat of continued habitat loss (Hilton-Taylor, 2000; Rylands et al., 2002). Due to successful local, national, and international conservation efforts, GLTs were reclassified as “endangered” in 2003 (IUCN, 2010). Still, only an estimated 1500 GLTs remain in the wild (Ruiz-Miranda et al., 2008); PDA holds the largest remaining population (Rylands et al., 2002; Ruiz-Miranda et al., 2008). Currently, an estimated 350 GLTs exist within the secondary forests protected by the reserve (Rylands et al., 2002; Ruiz-Miranda et al., 2008).

Individual identification and weighing

The animals under study at PDA are native and unmanipulated except for bi-annual live captures necessary for replacing radio collars to facilitate group location. During these routine captures, usually in May or early June and again in December or

January, individuals are given identifiable markings (hair dye and tattoos), weighed, and evaluated for growth and body condition including notes regarding female nipple length (reflecting parity), lactation, and pregnancy (Dietz & Baker, 1993; Dietz et al., 1994). During the current study weights were also obtained weekly from August through December of each year using baited scales in the field (Bales, 2000; Bales et al., 2002; Siani, 2009).

Behavioral observations

I collected data on 7 groups of wild GLTs at PDA, each containing 2 to 13 individuals and 1 to 3 adult females. All individuals were habituated to the presence of human observers. Six of these groups were observed from March 2004 through February 2007. Another group was added to the study in June of 2005, and was observed until the end of the study in February of 2007. Group sizes fluctuated but losses typically were filled by colonizers. Field assistants performed randomly alternated daily behavioral observations on these seven study groups. Focal observations included observed reproductive behavior, fights, and encounters with neighboring groups. Group scans recorded activity every 20 minutes. Group composition was recorded daily including all births, deaths, emigrations, and immigrations. These data were entered into a genealogical database program (SPARKS 1.53, ISIS, Apple Valley, Minnesota) used to track relatedness of group members and reproductive output.

The ages of individuals born within study groups are known from long-term demographic data or estimated to year based upon weight, the eruption of permanent teeth, and degree of tooth wear and discoloration noted at semi-annual captures (Dietz et al., 1994; Bales et al., 2001; French et al., 2003). Adults were defined as individuals

older than 18 months of age (Dietz & Baker, 1993) corresponding to the average age of sexual maturation (French & Stribley, 1987; French et al., 1989; Dietz et al., 1994; French et al., 2002). The average life span for captive tamarins is nine years of age (Dyke et al., 1993).

Each group contained one adult female who was behaviorally dominant to other females in the group. Dominance was assigned to the predominant aggressor based upon archwalks, mounts, and chases and winner of fights (Dietz & Baker, 1993; Bales et al., 2005).

Fecal sample collection

I collected 1176 fecal samples from individually identified female GLTs in 7 free-ranging social groups from March 2004 through February 2007. Feces were collected from a total of 21 GLT females including 14 adults, 4 females that passed from subadult to adult, 1 from juvenile to adult, 1 from juvenile to subadult, and 1 from infant to subadult (Table 2.1). I collected samples year-round during reproductive and non-reproductive months of the year. I collected fecal samples from each female once or twice per week as they left their sleeping locations or during subsequent observations. I attempted to restrict fecal collection to the morning hours to reduce diurnal variation in concentrations of fecal progesterone metabolites (Sousa & Ziegler, 1998; French et al., 2003). As a result, 28% of samples were collected before 0900h, and 83% by 1200h. No more than 10 hours passed between fecal sample collection and storage in a freezer. Samples remained frozen until analysis at the Callitrichid Research Center, University of Nebraska at Omaha.

Pregnanediol-3-glucuronide (PdG) and cortisol extraction from feces

Pregnanediol-3-glucuronide (PdG) is a metabolite of the hormone progesterone excreted in the feces and has been validated as a reliable indicator of circulating progesterone concentrations (Bales, 2000; French et al., 2003). Cortisol is excreted directly into the feces. PdG and cortisol were extracted simultaneously from fecal samples. Fecal samples were thawed at room temperature, processed by removing large plant and insect fragments, and dried prior to weighing in a drying oven at 37 ° C. Extraction of both PdG and cortisol was performed by briefly vortexing and then shaking 0.125 g of dried fecal matter in 2.5 ml of solubilizing extraction buffer (40% methanol (MeOH):60% phosphate buffered saline (PBS)) for 12-16 hours on a shaker rack. Samples were then briefly vortexed to remove residue along the tube walls and centrifuged for 15 min at 2000 rpm at 6 ° C. The supernatant was decanted into a clean test tube and refrozen for storage until further diluted for assay.

Enzyme immunoassay (EIA) for PdG

PdG was measured using an assay previously described (Chapter 1, this dissertation), validated against circulating hormone levels and tested for accuracy (Bales, 2000; French et al., 2003). Extracted fecal samples were diluted 1:5 in PBS prior to assay. PdG standards ranged from 10,000 to 78 pg/well and were prepared using halving dilutions in 1:5 extraction buffer:PBS. Controls were 1:5 extraction buffer:PBS. Internal quality control pools consisted of female Geoffroy's marmoset (*Callithrix geoffroyi*) urine. They were run at high concentrations (1:80 in 1:5 extraction buffer:PBS) and low concentrations (1:640 in 1:5 extraction buffer:PBS). PdG concentrations were determined through standardized enzyme immunoassay techniques (EIA) and

calculations resulting from a four-parameter sigmoidal curve-fitting function. The intra- and inter-assay coefficients of variation for high and low concentrations of a urine quality control pool for the PdG assay were 9.1% and 19.9% (high), and 7.4% and 26.7% (low), respectively.

Enzyme immunoassay (EIA) for cortisol

Fecal cortisol was measured using an assay previously described (Chapter 1, this dissertation), validated against circulating hormone levels and tested for accuracy (Bales, 2000; Bales et al., 2005). Extracted fecal samples were diluted 1:10 in PBS prior to assay. Cortisol standards ranged from 1,000 to 7.8 pg/well and were prepared using halving dilutions in 1:10 extraction buffer:PBS. Controls were 1:10 extraction buffer:PBS. Internal quality control pools consisted of female Geoffroy's marmoset urine. They were run at high concentrations (1:2560 in 1:10 extraction buffer:PBS) and low concentrations (1:20,480 in 1:10 extraction buffer:PBS). Cortisol concentrations were determined through standardized EIA techniques and calculations resulting from a four-parameter sigmoidal curve-fitting function. The intra- and inter-assay coefficients of variation for high and low concentrations of a urine quality control pool for the cortisol assay were 3.9% and 11.4% (high), and 3.9% and 20.7% (low), respectively.

Detection of ovulation, pregnancy, parturition, and abortion

I plotted PdG and cortisol concentrations over time to help visualize reproductive patterns for individual GLT females. Variation in progesterone levels corresponds to ovulation, the formation of the *corpus luteum*, and placental development (Ojeda, 1996; Nelson, 2005) and has been used to trace ovarian cycles and pregnancy in GLTs (French & Stribley, 1985; French & Stribley, 1987; Bales, 2000; French et al., 2002; French et al.,

2003). I examined progesterone profiles of subordinate adult GLT females from 18 months of age until conception of their first pregnancy. Subordinate adult females were considered ovulatory if non-pregnant progesterone profiles showed cyclical elevation in PdG concentrations averaging 20 days in periodicity (French et al., 2002).

Pregnancy was diagnosed primarily by the prolonged elevation of PdG concentrations (Bales, 2000; French et al., 2002; French et al., 2003). Cortisol, a glucocorticoid responsible for mobilizing fat and protein reserves for use by the body in times of food deprivation or stress (Nelson, 2005), also shows a significant increase in concentration during the 3rd trimester of GLT pregnancy indicative of fetal and placental development (Bales, 2000; Bales et al., 2005), so can be used as a late pregnancy diagnostic. In addition, pregnant GLT females demonstrate steady and considerable weight gain beginning in their 2nd trimester of pregnancy and continuing throughout gestation (Bales et al., 2001; Hankerson, 2008). Parturition was diagnosed by a sudden drop in PdG concentrations to baseline levels (Bales, 2000; French et al., 2002; French et al., 2003) accompanied by a rapid and large amount of weight loss (mean=112.7 g; range 73 to 142 g; n=12 full term pregnancies for which immediate pre- and post-partum weights were available (Siani, 2009)). I defined successful pregnancies as those that were carried to full term and that resulted in observations of new infants carried and nursed during the first week after birth by the female I identified as the mother. Birth dates were recorded within one or two days of parturition for most infants and within one week for all observed infants born during this study. To establish a calendar for each successful pregnancy I divided the 125-day gestation period (French et al., 2002) into trimesters. Trimesters were assigned by counting back from known parturition dates: 84-

125 days (3rd trimester), 42-83 days (2nd), and 0-41 days (1st) (French & Stribley, 1985; French et al., 2002). Because hormone profiles are highly individualized, for each reproductive female I calculated average PdG concentrations during each trimester of pregnancy and during non-pregnant periods to provide “typical” values for successful pregnancies. These trimester averages were used as a guide in diagnosing suspected pregnancies for which infants were not observed and to determine the probable trimester in which pregnancies were aborted.

Pregnancy diagnoses and assignment of trimesters when no infants were observed were made by consulting multiple sources of information on a case by case basis as described previously (Chapter 1, this dissertation). First, I consulted average trimester PdG values for successful pregnancies. Mean PdG concentrations of 1500 ng PdG/g feces, 3500 ng/g, 5000 ng/g, and 10,000 ng/g were indicative of an adult female that was either non-pregnant or in her 1st, 2nd, or 3rd trimester of pregnancy, respectively. Consistently high levels of PdG that suddenly dropped to titer levels indicated pregnancy loss or parturition depending on when concentrations returned to baseline values (Bales, 2000; French et al., 2002; French et al., 2003). Second, a large and consistent rise in cortisol reaching a mean of 15,000 ng cortisol/g feces was used to diagnose pregnancies that had proceeded into the middle to late 3rd trimester. Third, I used patterns of weight gain in females in the current study to establish general guidelines for diagnosing pregnancy from the 2nd trimester onward. Females gaining 5-10% or in excess of 10% of their non-pregnant average weight in a consistently rising pattern were diagnosed as being in their 2nd or 3rd trimester, respectively. Females that gained approximately 20% of their body mass were considered to have reached full term, since neonatal weight for

Leontopithecus is on average 20% of the mother's body weight (Tardif et al., 1993). Average weight loss for 12 births during the current study for which immediate pre- and post-partum weights were available was 18.6% of the females' post-partum weight (Siani, 2009). Rapid weight loss was considered indicative of parturition or the loss of a 2nd or 3rd trimester pregnancy. Fourth, bi-annual capture records including each female's weight, nipple length, whether a female was lactating or not, and the results of uterus palpation for pregnancy and trimester diagnosis at the time of capture (Dietz & Baker, 1993; Dietz et al., 1994) provided data points during early pregnancy in late May or June when field weights were not available and pregnancy diagnoses were not often possible given hormonal concentrations that remain low during this early stage. *Ad libitum* field observations regarding female appearance and behavioral changes were consulted for additional confirmation, though were not considered diagnostic.

STATISTICAL ANALYSES

Threat of eviction and inbreeding avoidance

I used logistic regression analyses to test for a statistical relationship between the presence within the group of a male assumed to be unrelated to the pregnant female and the likelihood that the pregnancy would result in the birth of live infants (SAS 9.2, SAS Institute, Cary, North Carolina). The full dataset of 37 pregnancies conceived by 14 dominant and subordinate adult females (26 successful to 10 females and 11 non-successful to 7 females) was used in this analysis. Individual female identity (FEMID) was included as a covariate in the model to account for multiple pregnancies by some females. All assumptions were met for this model.

To identify variables useful in predicting a successful pregnancy to a subordinate female pregnant at the same time as the dominant female in her group I used the logistic regression procedure with removal of non-significant effects (those with the largest p -value > 0.05) one at a time through backward selection. Explanatory variables included the age of the dominant female, the presence within the group of a male assumed to be unrelated to the subordinate female at the time of conception, and whether the dominant or subordinate female became pregnant first. The dataset consisted of 11 cases of simultaneous pregnancies in 2 females within the same group (4 cases where both the dominant and subordinate females were successful and 7 cases in which only the dominant female was successful). FEMID was again included in the model, but removed from the model when the effect was non-significant such that each reproductive attempt by the same female was treated as an independent observation (Bales et al., 2001; Bales et al., 2002). All assumptions were met for this model.

RESULTS

Subordinate ovulation without conception

Subordinate females between 18 months of age and the conception of their first pregnancy showed cyclical elevation in PdG concentrations from less than 500 ng PdG/g feces to an average of 1000 ng PdG/g feces with 15-30 day periodicity consistent with ovulatory patterns observed in adult GLTs (Figure 2.1). Age of first conception ranged from 2.5 to 3.9 (mean = 3.1 ± 0.2 standard error) years for 8 GLT females conceiving for the first time during this study (Table 2.1). Five adult females did not conceive. Four of the five were younger than three years of age but did show cyclical elevations in PdG concentrations. The fifth female was of unknown age and remained within a habituated

study group for just three months during which time she did not become pregnant. Sample frequency was insufficient to determine the ovulatory status of this female.

Threat of eviction and inbreeding avoidance

The presence within the group of a male unrelated to the pregnant female at the time of conception was not a significant predictor (Wald Chi-Square=0.0017, df=1, $p=0.9673$) of the birth of live infants to either a pregnant dominant or subordinate female. Thirty pregnancies were conceived while a male unrelated to the pregnant female was present; twenty-two of these resulted in live births. Seven pregnancies were conceived when there was no unrelated male present, with four of these resulting in live births. Eight of eleven non-successful pregnancies were conceived while there was an unrelated male present in the group.

A logistic regression model including both the age of the dominant female (Wald Chi-Square=1.32, df=1, $p=0.2499$) and whether the dominant or subordinate female was pregnant first (Wald Chi-Square=2.23, df=1, $p=0.1353$) as predictors of a successful pregnancy to a subordinate female whose pregnancy overlapped with that of a dominant female was marginally significant (Likelihood Ratio Chi-Square=4.98, df=2, $p=0.0829$). Though neither of these pieces of information was a significant predictor of subordinate success, knowing both of these pieces of information provided an 85.7% likelihood of correctly predicting a successful pregnancy to a subordinate female. As the age of the dominant female increased, the likelihood of success by a subordinate female increased. Under this model, for every year of age of the dominant female, a pregnancy by the subordinate female was 2.0 times as likely to be successful (95% confidence interval was 0.6-6.6). The mean age of the dominant female during a non-successful pregnancy by a

subordinate was 6.4 years compared to 10.9 years during a successful pregnancy by a subordinate. All four successful pregnancies by subordinate females occurred when the dominant female in each of the two groups was 10 years old or older. The presence or absence of a male unrelated to the subordinate female in the group at the time of conception was removed from the model as non-significant predictor variable (Wald Chi-Square=0.04, df=1, p=0.8399). Continuing past this point with backward selection of non-significant terms resulted in a non-significant model (Likelihood Ratio Chi-Square=2.28, df=1, p=0.1307) without any statistically significant predictor variables.

DISCUSSION

Subordinate ovulation without conception

The findings herein are consistent with those of French et al. (2003) and suggest that subordinate adult GLT females younger than 3.1 years of age exercise reproductive self-restraint by delaying conception when they reside in groups containing a young dominant female and no unrelated males. I suggest that limits on reproduction by young subordinate females are self-imposed in response to conditions that reduce the probability of a successful reproductive investment (Reyer et al., 1986; Hamilton, 2004; Young et al., 2008; Saltzman et al., 2009) rather than being actively enforced by dominant females through physical aggression. However, the physical condition of the dominant female may serve as a cue by which subordinates gauge the ability of dominants to interfere in subordinate reproduction, thus playing a determining role in whether or not subordinate GLTs exercise restraint (Young et al., 2008; Saltzman et al., 2009).

Physiological suppression of ovarian activity in subordinate adult females does not appear to be limiting reproduction in subordinate female GLTs. Subordinate females

older than 18 months of age ovulated while residing within their natal group, but conceptions were delayed one to two years following the onset of ovulation (Figure 2.1) as predicted if young subordinate females were exercising reproductive self-restraint. These findings corroborate studies in captivity that point to the lack of ovarian suppression in subordinate females older than 18 months of age in the genus *Leontopithecus* (French, 1987; French & Stribley, 1987; French et al., 1989; Inglett, 1993; Monfort et al., 1996; French et al., 2002), but see French et al. (2003) for evidence of anovulation in subordinate GLT daughters. Young adult subordinate females undergoing regular ovulatory cycles should be hormonally competent to reproduce, but the mean age at first conception for females in the current study was 3.1 years (similar to the 3.6 years reported by Bales et al. (2001)). Perhaps younger subordinate females delay conceptions by not engaging in sexual behavior while residing in groups containing a young dominant female and no unrelated males (Abbott, 1984; French et al., 2003). A delay in first conception was also found for young subordinate common marmoset females (Arruda et al., 2005; Sousa et al., 2005). A review of the literature for common marmosets from both field and captive settings concluded that the delay in onset of reproduction was due to reproductive self-restraint on the part of most subordinates in response to the threat of dominant infanticide (Saltzman et al., 2009). But since infanticide has not been documented in wild populations of GLTs to date (Dietz, personal communication), it appears unlikely that infanticide serves as the selective pressure promoting reproductive self-restraint in GLTs.

Threat of eviction and inbreeding avoidance

Reproductive restraint on the part of young adult female GLTs occupying a subordinate position within their natal group is the product of both the threat of eviction from the natal group and incest avoidance (Baker et al., 2002; French et al., 2002; French et al., 2003). In the only other study to diagnose pregnancy in wild GLTs based upon hormonal profiles, both the presence of an elderly dominant female and the presence of a male unrelated to the subordinate female were key factors in determining whether a subordinate female ovulated and became pregnant within her natal group (French et al., 2003). Subordinate GLT females faced with the high risks associated with both emigration and immigration (Baker & Dietz, 1996; Goldizen et al., 1996; Baker et al., 2002) forego their own reproduction in an attempt to avoid conflict with a strong dominant female that may lead to their eviction from the group. When the dominant female in GLT groups was young (potentially weighed more (Dietz et al., 1994) and had longer canine teeth (Dietz, unpublished data)) and was physically able to mount and win attacks on subordinates (Hodge et al., 2008) successful reproduction by subordinate GLTs was rare. All successful pregnancies by subordinate females occurred when the dominant female was at least 10 years of age. In addition, the likelihood of a pregnancy by a subordinate female resulting in the birth of live infants doubled with each year of age of the dominant female according to a marginally significant logistic regression model based upon only 11 cases of simultaneous pregnancy by two females within the same group. These results, combined with those of French et al. (2003) suggest that elderly dominant female GLTs may not be in good enough physical condition to either prevent a pregnancy by their subordinate daughters or interfere with subordinate

pregnancies through the persistent harassment and aggressive attacks associated with eviction from the natal group (Baker et al., 2002). The presence of an elderly dominant female may not pose a high enough threat to subordinate females for them to exercise reproductive self-restraint. In contrast, the presence of a young dominant female significantly reduced the likelihood that a costly reproductive investment would result in the birth of live infants; providing the selective pressure necessary to promote self-restraint of reproduction in young subordinates (Wasser & Barash, 1983; Reyer et al., 1986; Jaquish et al., 1991; Digby, 1995a; Abbott et al., 1997; Saltzman, 2003; Hamilton, 2004; Gilchrist, 2006a; Young et al., 2008; Saltzman et al., 2009).

Though young subordinate females in this study ovulated, conceptions were rare under incestuous mating conditions. Only 7 of 37 pregnancies were conceived while there was no unrelated male present within the group, demonstrating the tendency in GLTs to avoid incestuous matings. Inbreeding depression has been suggested as a potential cause for infant mortality and a selective pressure leading to incest avoidance in this population of wild GLTs (Dietz & Baker, 1993; Dietz et al., 2000); however, my data provide no evidence that the risk of pregnancy loss is higher for GLT females that become pregnant under potentially incestuous mating conditions (see Bales et al. (2001) for corroborating results). Specifically, whether a pregnancy was conceived under incestuous or non-incestuous mating conditions had no effect on whether that pregnancy resulted in the birth of live young. These results corroborate those of Baker et al. (2002) whose authors reported that success rates for pregnancies by natal females older than three to four years of age were unaffected by the relationship between resident males and the natal female. The long delay from puberty to conception, the low number of

conceptions under incestuous mating conditions, and the lack of evidence for inbreeding depression all suggest that young subordinate females may not conceive under incestuous conditions in favor of delaying their investment until a non-natal male joins the group or they are able to secure non-incestuous matings outside their natal group, perhaps during intergroup encounters (Digby, 1999; French et al., 2003).

However, my analysis was based upon the assumption of non-relatedness among non-natal group members. At PDA, neighboring groups contain close relatives due to habitat saturation (Dietz et al., 2000). As a result, extra-group copulations as well as copulations with non-natal males that immigrate into the natal groups of subordinate females may result in inbred offspring (Dietz et al., 2000). Cross-checking with a long term genealogical database that also monitors immigration and emigration helped to reduce errors in my assignment of “unrelated” to non-natal males, but without molecular-genetic data confirming paternity in GLTs, there is no way of knowing whether conceptions by subordinate females were indeed incestuous. It has also been hypothesized that callitrichids may be less adversely affected by inbreeding depression since blood chimerism between twins results in low allozyme diversity in callitrichids and may serve as an adaptation to the homozygosity that results from inbreeding (Pope, 1996). Given these limitations, the lack of support for inbreeding depression provided in this study is not surprising. It is possible, however, that in measuring infant survival past the period of infant dependency as was done by Dietz & Baker (1993) and Dietz et al. (2000), differential survival based upon incestuous mating conditions may become apparent.

Further supporting the idea of subordinate self-restraint rather than dominants imposing constraints upon subordinate reproduction is the finding that subordinate female GLTs do not appear to suffer from chronic social stress (Chapter 3, this dissertation). Cortisol concentrations in subordinate female GLTs do not differ from those of dominant females (Bales et al., 2005) (Chapter 3, this dissertation), in contrast with what would be expected if they were being aggressively harassed by dominant females as a deterrent to reproduction (Abbott et al., 2003). In addition, pregnancy loss in subordinate GLT females could not be attributed to high levels of social stress as the result of dominant aggression since failed pregnancies did not differ significantly from successful pregnancies in their starting non-pregnant cortisol levels, nor in cortisol concentrations during the 1st trimester (Chapter 3, this dissertation). Aggression was low and social support high among females occupying the same group except for those brief periods of one to two days marking the eviction of a female from a group (Baker, 1991; Dietz & Baker, 1993; Bales et al., 2005). And though dominant female callitrichids have been observed to interfere actively with mating attempts by the subordinate (Abbott, 1984), these occurrences are rare and this behavior was not observed during my study. It is unlikely that dominant females are able to monitor and successfully intercede in subordinate reproductive attempts over such a prolonged period (Saltzman et al., 2009). A more parsimonious explanation is that a younger subordinate adult female exercises reproductive restraint for the first one to two years of adulthood within her natal group (while the dominant female is young and the threat of eviction high, while non-incestuous mating opportunities do not exist, and while the subordinate still has a long reproductive life span ahead of her (French et al., 2003)) as she waits for her chances of successfully

investing in reproduction to improve. Meanwhile, the threat of being evicted from the group and incest avoidance are enough to restrain attempts at reproduction by young subordinates without the need for constant aggression (Young et al., 2008; Saltzman et al., 2009).

ACKNOWLEDGEMENTS

Funding for this project was provided by the American Society of Mammalogists, the Copenhagen Zoo Lion Tamarins of Brazil Fund, the University of Maryland Center for Biodiversity, a Darwin Fellowship from the University of Maryland BEES Program, and a Wylie Dissertation Fellowship from the University of Maryland Graduate School to M. Henry and by the National Science Foundation (SBR-9727687; BCS-0216096) to J. Dietz. I thank the Brazilian Science Council (CNPq), Brazilian Institute for the Environment and Renewable Natural Resources (IBAMA), and Golden Lion Tamarin Association (AMLD) for logistic support and permission to conduct this study. This research complies with the guidelines of the University of Maryland Animal Care and Use Committee and all applicable Brazilian laws. Importation of fecal samples into the U.S. was conducted under the auspices of CITES, USDA, and CDC. Special thanks to Jim Dietz and Jeff French for their guidance and support throughout this project. I thank Ecología research assistants Otávio Narciso, Synval de Melo, Jadir Ramos, Ademilson de Oliveira, and Andréia Martins for help with data collection in the field. I thank Jeff Fite, Kate Townley, and Tom Shirazi for assistance with endocrine analyses. Thanks to Jennifer Siani for providing tamarin weight data. I sincerely appreciate the statistical analyses performed by Sarah Hankerson. I thank Karen Bales for setting the precedent for endocrine work in this population of tamarins.

TABLES

Table 2.1. Ovulatory status (O=ovulatory, N=non-ovulatory) and age at first conception for 21 GLT females from 7 free-ranging golden lion tamarin groups for which fecal samples were collected from March 2004 through February 2007.

Female ID	Group	Dominance status	Age (years) during sample collection	Age category	Number of PdG samples	Ovulatory status	Age (years) at first conception if occurred during study
539	AL	Dominant then subordinate	10.6-13.3	Adult	97	O	
720	BO2	Dominant	9.4-12.3	Adult	125	O	
750	PP3	Dominant	8.7-10.5	Adult	77	O	
766	GF	Dominant	5.6-6.9	Adult	35	O	
782	3M5	Dominant	4.5-6.7	Adult	32	O	
846	AL	Subordinate then dominant	2.8-5.3	Adult	78	O	2.9
848	BO2	Subordinate	2.4-5.3	Adult	136	O	2.5
869	PA	Dominant	4.7-7.3	Adult	98	O	
880	BO2 to POR	Subordinate in BO2, dominant in POR	1.4-4.1	Subadult to adult	88	O	2.8
884	PA	Subordinate	1.7-3.3	Adult	60	O	2.7
889	GF	Subordinate	1.6-3.0	Adult	18	O	2.5
899	BO2 to POR	Subordinate	1.1-2.4	Subadult to adult	39	O	Did not conceive
1227	BO2 to POR	Subordinate	0.7-2.9	Subadult to adult	68	O	Did not conceive
1238	PP3	Subordinate	0.3-1.9	Juvenile to adult	56	O	Did not conceive
1241	BO2 to POR	Subordinate	0.8-2.0	Subadult to adult	52	O	Did not conceive
1264	PP3	Dominant	4.0-4.3	Adult	12	O	3.9
1265	PP3	Subordinate	3.3-4.2	Adult	10	O	3.9
1266	GF	Dominant	2.9-4.0	Adult	32	O	3.5
1267	AL	Subordinate	0.2-1.3	Infant to subadult	21	N	Did not conceive
1271	PA	Subordinate	0.4-1.4	Juvenile to subadult	32	N	Did not conceive
TOPP3	PP3	Dominant	Unknown	Adult	10	Unknown	Did not conceive
$\Sigma=1176$							$\bar{x}=3.1 \pm 0.2$

FIGURE LEGENDS

Figure 2.1. Ovulatory cycles as demonstrated by cyclical elevation in PdG concentrations in two subordinate adult females a) GLT 880 from 1.6-2.5 years of age and b) GLT 1227 from 1.5-2.9 years of age prior to first conception.

FIGURES

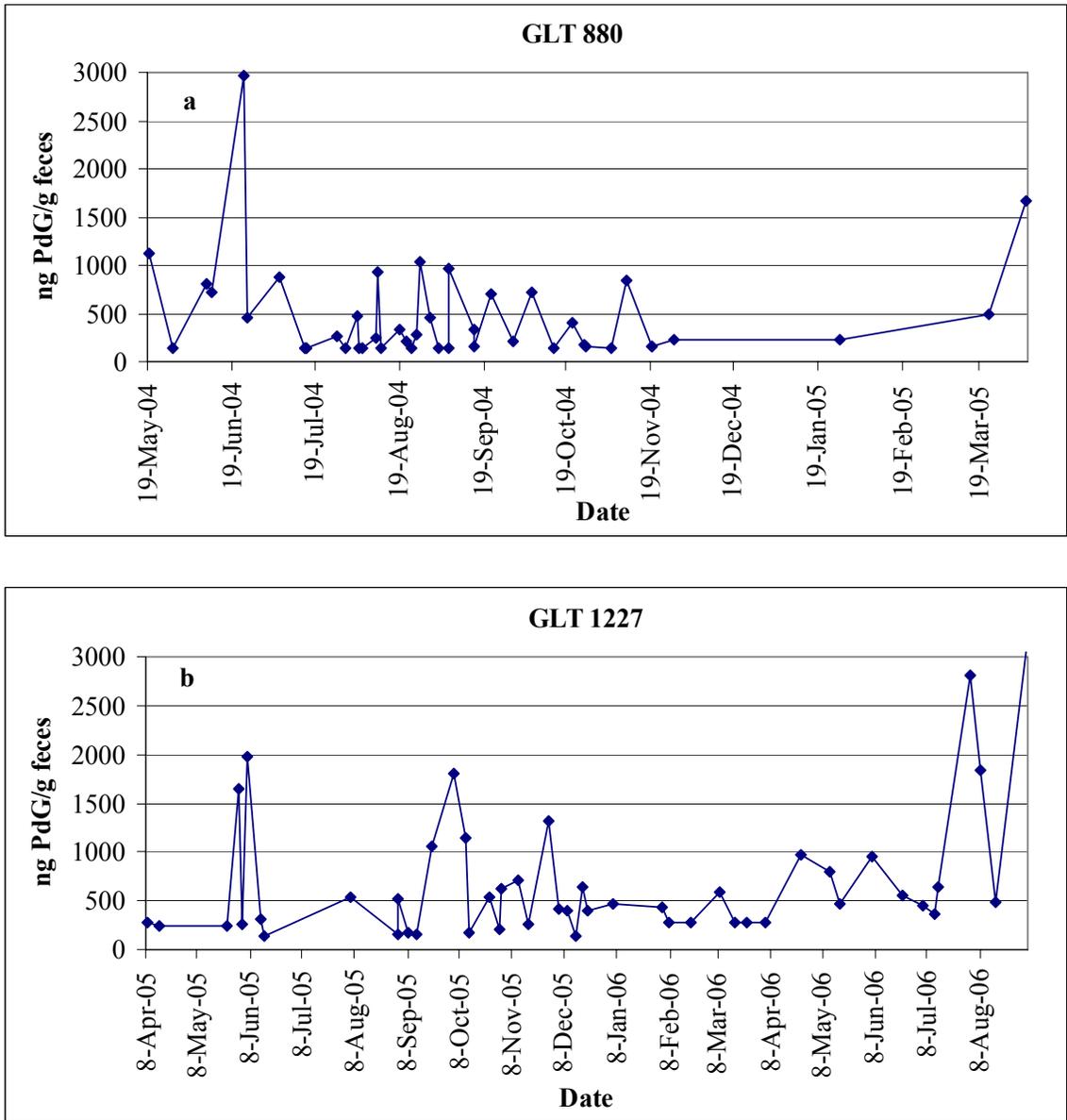


Figure 2.1.

Chapter 3: Incomplete control limits reproduction in older subordinate female golden lion tamarins (*Leontopithecus rosalia*)

ABSTRACT

Many cooperatively breeding species exhibit high reproductive skew. One hypothesized evolutionary pathway linking the two relies upon the premise that reproduction by subordinates reduces the fitness of the dominant; therefore, selection should favor dominants able to control subordinate reproduction. The current study examines both the proximate mechanisms and ultimate causes of female reproductive skew in cooperatively breeding golden lion tamarins (*Leontopithecus rosalia*). I tested whether reproduction by subordinate adult female tamarins is limited by dominant females who had incomplete control (incomplete control model, ICM) or complete control (optimal skew model, OSM) over subordinate reproduction. I tested the ICM prediction that subordinate females would ovulate and conceive, but only those subordinates capable of winning fights with the dominant female would give birth to live young. I tested the OSM prediction that ovulation, conception and successful reproduction would be allowed only by subordinate females providing inclusive fitness benefits to the dominant female. I used three years of data from seven free-ranging groups of tamarins in Poço das Antas Biological Reserve, Rio de Janeiro, Brazil, and used hormonal (progesterone and cortisol) profiles obtained through non-invasive immunoassay of feces to detect ovulation in subordinates. I also used changes in body mass, bi-annual physical examinations, and behavioral observations to diagnose pregnancies of both dominant and subordinate females. I defined reproductive success as pregnancies that resulted in the birth of live infants, and used circulating cortisol

concentrations as a measure of stress. I performed phenological surveys to quantify average monthly caloric availability, and recorded group compositions daily. I compared hormonal profiles of successful vs. non-successful pregnancies using linear mixed model analysis of variance, and identified hormonal, social, and ecological variables useful in predicting a successful pregnancy to a subordinate female by using logistic regression analyses. Whereas subordinate females younger than 2.5 years of age ovulated but did not conceive, all females older than 3.9 years of age became pregnant. In support of the hypothesis of incomplete control, reproduction in subordinate adult females was not limited by hormonal suppression of ovulation or conception, but by the failure of pregnancies to produce live offspring. Seven of eleven subordinate pregnancies were not successful. Subordinate pregnancy loss could not be attributed to stress; subordinate females did not experience higher levels of stress than dominants. Caloric availability in all home ranges was more than adequate to support tamarin reproduction. Group size limited the number of females that successfully reproduced; the likelihood of reproductive success increased 1.7 times with each additional group member. My results suggest that when caloric availability is sufficient to support reproduction by two breeding females and the group members necessary to provide allocare for two litters, subordinate females do not abide by a social contract that would limit their reproduction (OSM). Instead, older subordinates compete with dominant females for reproduction and succeed in producing live young if the dominant female is at least 10 years old, if subordinates conceive while the dominant is heavily pregnant, and if they reside within larger groups (ICM).

INTRODUCTION

Cooperative breeding in which the young born to one or more breeding females are reared by non-reproductive helpers is rare among social mammals and is most highly developed in four taxa (Clutton-Brock, 2009): the marmosets and tamarins (*Callitrichidae*) (Goldizen, 1987a; Goldizen, 1987b; Tardif et al., 2002; Digby et al., 2007); the dogs (*Canidae*) (Moehlman, 1986; Creel & Creel, 2001); the diurnal mongooses (*Herpestidae*) (Rood, 1986; Creel & Waser, 1997; Clutton-Brock, 2006); and African mole-rats (*Bathyergidae*) (Bennett & Faulkes, 2000; Faulkes & Bennett, 2007). Across taxa, cooperative breeding is associated with high reproductive skew (Clutton-Brock, 2009). Clutton-Brock (2009) suggested a potential evolutionary pathway linking reproductive skew to cooperative breeding in mammals. When simultaneous breeding by multiple females dilutes the investment of helpers and/or reduces the survival or growth of offspring born to the dominant (Clutton-Brock et al., 2001b; Hodge, 2009), selection should favor dominant females able to control subordinate reproduction. Monopolization of reproduction by dominant group members by means of suppression of subordinate reproduction has been documented in several taxa of cooperative breeders including mammals (Solomon & French, 1997a), birds (Reyer et al., 1986; Mays et al., 1991; Schoech et al., 1991), fishes (Fitzpatrick et al., 2008), and invertebrates (Hamilton, 2004). Limited opportunities for subordinate reproduction within the group combined with few options for successful dispersal and reproduction outside the group (Baker & Dietz, 1996; Goldizen et al., 1996; Clutton-Brock et al., 1998a; Clutton-Brock et al., 2001a; Baker et al., 2002; Clutton-Brock et al., 2006) may lead to the evolution of non-breeding helpers. Helpers improve growth and survival of the dominant's offspring (in birds: (Brown,

1987); coyotes (*Canis latrans*): (Bekoff & Wells, 1982); African wild dogs (*Lycaon pictus*): (Malcolm & Marten, 1982; Creel & Creel, 2001); blackbacked jackals (*Canis mesomelas*): (Moehlman, 1979); meerkats (*Suricata suricatta*): (Clutton-Brock et al., 2001b; Russell et al., 2003); dwarf mongooses (*Helogale parvula*): (Rood, 1990); badgers (*Meles meles*): (Kruuk, 1989); and marmosets and tamarins: (Dietz, 2004)). By helping to rear the young of related dominants (typically a mother or a sister), subordinates with few options for their own reproduction benefit by increasing their own inclusive fitness (West-Eberhard, 1975; Sherman et al., 1995; Bourke, 1999; Ratnieks & Helanterä, 2009). Cooperative care reduces fitness costs associated with reproduction for the dominant female and increases her rate of reproduction (Clutton-Brock et al., 1998b; Russell et al., 2003; Fite et al., 2005). Dominant females in cooperatively breeding species also have relatively long life spans (Arnold & Owens, 1998; Carey, 2001; Sherman & Jarvis, 2002), further augmenting the degree of reproductive skew (Hauber & Lacey, 2005; Clutton-Brock et al., 2006).

Golden lion tamarins (*Leontopithecus rosalia*) are cooperatively breeding callitrichid primates that display a high degree of reproductive skew. Golden lion tamarins (GLTs) reside in family groups of 2–11 individuals (Dietz & Baker, 1993; Dietz et al., 1994). Lion tamarin offspring typically delay dispersal and reproduction, and remain in their natal group to help with the care of infant siblings (Dietz & Baker, 1993). Cooperative care has been suggested to be instrumental in the ability of callitrichids to meet the energetic needs associated with successfully rearing the litters of twins they are capable of producing either once or twice a year (Kleiman, 1977a; Sussman & Garber, 1987; Baker et al., 1993; Dietz & Baker, 1993). Dietz and Baker (1993) reported that

reproduction was limited to a single dominant female (monogyny) in most GLT groups. Reproduction by two females in the same group (polygyny) occurred in only 10% of GLT groups. As long-term study continued the incidence of rearing polygyny (more than one female rearing offspring to weaning) remained low (26.2% reported by Baker et al. (2002)), but pregnancy polygyny (more than one female confirmed as being pregnant within the same breeding season) was common (44.3% reported by Baker et al. (2002); 83% reported in chapter one of this dissertation).

As long-term field research on callitrichids continues, the presence of multiple breeding females within callitrichid groups has been observed in an increasing number of species (common marmosets (*Callithrix jacchus*): (Hubrecht, 1984; Digby & Ferrari, 1994; Digby, 1995b; Arruda et al., 2005); pygmy marmosets (*Cebuella pygmaea*): (Soini, 1982); cotton-top tamarins (*Saguinus oedipus*): (Savage et al., 1996a); saddle-back tamarins (*Saguinus fuscicollis*): (Goldizen et al., 1996); and moustached tamarins (*Saguinus mystax*): (Garber et al., 1984; Ramirez, 1984; Garber et al., 1993; Smith et al., 2001)). However, subordinate reproductive success remains lower than that of dominant females in both marmosets (Digby, 1995a; Arruda et al., 2005; Sousa et al., 2005; Saltzman et al., 2008; Saltzman et al., 2009) and tamarins (Goldizen et al., 1996; Garber, 1997). In both captive and wild groups of cotton-top tamarins only one female per group gives birth regardless of the number of other pregnant females in the group (Price & McGrew, 1991; Savage et al., 1996a). The contradiction between high rates of pregnancy polygyny and low reproductive success by subordinate females encourages a re-examination of explanations for singular breeding in callitrichids.

Reproductive skew models

Models of reproductive skew attempt to explain limits on subordinate reproduction in terms of fitness costs and benefits to dominant and subordinate individuals under existing ecological and social circumstances (Clutton-Brock, 2009). Incomplete control models (ICM) of reproductive skew, also called tug of war models, presume that there is an ongoing contest or power struggle for successful reproduction between dominant and subordinate females (Johnstone, 2000; Beekman et al., 2003; Hager, 2003) in which both the dominant and the subordinate females will try to disrupt each other's reproductive attempts (Young & Clutton-Brock, 2006; Saltzman et al., 2009). Under ICM subordinate reproductive success is determined by the physical condition, size, or strength of each contender (Reeve & Sherman, 1991; Clarke & Faulkes, 1997; Bernasconi & Strassmann, 1999; Hodge et al., 2008). Dominant females are assumed to win most, but not all of these contests (Clutton-Brock, 1998; Reeve & Shen, 2006). Subordinate females are occasionally able to breed when dominants cannot prevent them from doing so (Clutton-Brock et al., 2001a; French et al., 2003; Clutton-Brock et al., 2008). The frequency of successful breeding by subordinates depends upon the costs and benefits accrued by dominants as a result of suppressing subordinate reproduction as well as the costs and benefits accrued by subordinates in attempting to breed (Emlen, 1995; Emlen et al., 1998; Reeve et al., 1998; Dietz, 2004; Clutton-Brock et al., 2008).

In optimal skew models (OSM), also called concessions models, it is assumed that dominant females have complete control over reproduction by subordinate females (Johnstone, 2000; Hager, 2003; Dietz, 2004; Buston et al., 2007). When it is of benefit to

the dominant female, as when subordinate daughters in this cooperatively breeding species remain in their natal group and provide care for the offspring of the dominant mother (Bales et al., 2001; Dietz, 2004), she is predicted to share reproduction with her daughter as a concession to entice subordinates to remain in the group (Emlen, 1982; Clutton-Brock, 1998; Reeve et al., 1998; Reeve & Shen, 2006). Under OSM dominant females weigh the costs and benefits to themselves of each potential mating by a subordinate female under the current set of demographic and ecological conditions, and either allow or deny reproductive opportunities to subordinate females within their group according to what would be most likely to increase their own inclusive fitness (Emlen et al., 1998; Johnstone, 2000; Hager, 2003; Dietz, 2004). In contrast to ICM, OSM assumes that subordinate females only succeed in reproducing when allowed to do so by the dominant female (Clutton-Brock, 1998; Reeve et al., 1998; Johnstone, 2000; Hager, 2003; Buston et al., 2007).

Under both ICM and OSM models of reproductive skew, reproductive success is expected to be higher in dominants than in subordinates (Emlen et al., 1998; Johnstone, 2000; Hager, 2003; Dietz, 2004) as seen in many cooperatively breeding taxa (mammals: (Solomon & French, 1997a; Gilchrist, 2006a; Gilchrist, 2006b; Young et al., 2006; Clutton-Brock et al., 2008; Hodge et al., 2008) including marmosets: (Digby, 1995a; Arruda et al., 2005; Sousa et al., 2005; Saltzman et al., 2008; Saltzman et al., 2009) and tamarins: (Dietz & Baker, 1993; Goldizen et al., 1996; Garber, 1997); birds: (Reyer et al., 1986; Mays et al., 1991; Schoech et al., 1991; Koenig & Dickinson, 2004); fish: (Fitzpatrick et al., 2008); and invertebrates: (Hamilton, 2004)).

Hormonal control of subordinate reproduction

Under the model of incomplete control, selection should favor subordinates that are capable of taking advantage of any reproductive opportunity. Thus, one assumption is that adult subordinate females are physiologically capable of reproducing and attempt to do so when presented with the opportunity. For example, in cooperatively breeding pied kingfishers (*Ceryle rudis*) secondary male helpers that are not behaviorally dominated by breeding males and may be able to gain the occasional reproductive opportunity as a result of competing with breeding dominant individuals do not exhibit reduced fertility in terms of lowered testosterone levels or a reduction in gonad size and sperm production (Reyer et al., 1986). In contrast, primary male helpers that are behaviorally dominated by breeding males and are less likely to be able to win reproductive rights from the dominant male have lower testosterone levels, smaller gonads, and do not produce sperm. Similarly, male Harris' hawk (*Parabuteu unicinctus*) helpers were hormonally ready to take advantage of breeding opportunities during the nesting season; but female helpers, weighing on average 10% less than the dominant breeding female, showed no elevation in reproductive hormone concentrations (estradiol and luteinizing hormone) associated with breeding readiness (Mays et al., 1991).

Under the model of optimal skew, only those subordinate females whose continued presence within the group provide benefits in terms of inclusive fitness to the dominant female will be allowed to ovulate and conceive within their natal group. As group size increases, the relative benefits to the dominant female of allowing each additional subordinate female to remain within the group and breed become smaller (Reeve & Emlen, 2000; Clutton-Brock et al., 2008). Therefore, not all subordinate adult

females are expected to be allowed to reproduce within the group. Dominant females may exert their control over subordinate reproduction through the reduction of reproductive hormone concentrations (Florida scrub jays (*Aphelocoma coerulescens*): (Schoech et al., 1991); Harris' hawks: (Mays et al., 1991); dwarf mongooses: (Creel et al., 1992); and African mole-rats (*Cryptomys* spp. and *Heterocephalus* spp.): (Faulkes & Bennett, 2001)) and the suppression of subordinate ovulation (African mole-rats: (Faulkes & Abbott, 1997; Molteno & Bennett, 2000; Faulkes & Bennett, 2001); and pine voles (*Microtus pinetorum*): (Solomon et al., 2001)). Singular breeding in callitrichid groups is maintained by inhibition of subordinate sexual behavior and hormonal suppression of subordinate female ovulation (marmosets: (Rothe, 1975; Abbott & Hearn, 1978; Abbott et al., 1981; Abbott, 1984; Evans & Hodges, 1984; Hubrecht, 1989; Abbott, 1993; French, 1997; Saltzman et al., 1997a; Digby, 1999; Albuquerque et al., 2001; Sousa et al., 2005); and tamarins: (Epple & Katz, 1984; French et al., 1984; Abbott, 1993; French, 1997)).

The genus *Leontopithecus* differs from other callitrichids in that dominant females do not appear to control subordinate reproduction through the suppression of ovulation in captive populations (French, 1987; French & Stribley, 1987; French et al., 1989; Inglett, 1993; Monfort et al., 1996; French et al., 2002), suggesting that subordinate daughters may be hormonally primed to take advantage of reproductive opportunities. Results from endocrine sampling of GLTs in the wild suggest that the majority of subordinate females are anovulatory while remaining within their natal group; however, the presence of an elderly dominant female or immigration of a non-related male into the natal group may be followed by ovulation and conception by some subordinate daughters (French et al.

2003). These studies demonstrate not only the incomplete ability of dominant females to suppress the reproductive hormones controlling ovulation and sexual behavior in subordinate female GLTs, but also the opportunistic flexibility of the female GLT reproductive system.

The neuroendocrine pathway responsible for suppression of ovulation in subordinate marmosets and tamarins is remarkably flexible in responding to a changing social environment, especially the presence or absence of a dominant female (Saltzman et al., 2009). Subordinate females begin to ovulate, mate, and may conceive shortly after removal of the subordinate female from her natal group or the removal of the dominant female from the group (Evans & Hodges, 1984; Abbott et al., 1988; Abbott & George, 1991). Upon introduction of a non-natal male into the group, subordinate females began to engage in sexual behavior (Anzenberger, 1985; Hubrecht, 1989; Kirkpatrick-Tanner et al., 1996; Saltzman et al., 1997b; Saltzman et al., 1997c; Saltzman et al., 2004). In the common marmoset, inhibition of ovulation is the result of suppression of chorionic gonadotropin (CG) released from the anterior pituitary (Abbott et al., 1990; Abbott et al., 1998). Though the precise neuroendocrine mechanism responsible for the suppression of chorionic gonadotropin release remains unknown, the pathway does not appear to be mediated by stress (Abbott et al., 1997). Instead, the receipt of olfactory (pheromonal) and visual signals sent by the dominant female appears to be sufficient to initiate and maintain ovulatory suppression in subordinates (Barrett et al., 1990; Abbott et al., 1993; Barrett et al., 1993; Smith & Abbott, 1995; Abbott et al., 1998). Because this pathway is reliable, rapid, and reversible, some authors have suggested that it may have evolved in cooperative breeders (Faulkes & Abbott, 1997; French, 1997; Molteno & Bennett, 2000;

Solomon et al., 2001; Saltzman et al., 2009) as a means to quickly turn the female reproductive system on or off in response to a socially dynamic and unpredictable environment (Puffer et al., 2004; Saltzman et al., 2009). This neuroendocrine pathway may allow subordinate females to take advantage of temporary reproductive openings (ICM). Alternatively, this pathway may provide the mechanism by which dominant females are able to prevent ovulation in some subordinate females and allow ovulation in others under circumstances when subordinate reproduction would provide greater benefits to the dominant (OSM).

Behavioral control of subordinate reproduction

Dominant females may limit subordinate access to mates when conceptions are more likely. The timing of female emigration in GLTs suggests that subordinate daughters may be evicted from the group shortly after reaching puberty (Baker, 1991). Dominant females may also prevent conceptions by ovulatory subordinate females that remain within the group by interfering with subordinate mating attempts (Epple, 1967; Rothe, 1975; Abbott, 1984). In green sea turtles (*Chelonia mydas*), males escort mounted pairs perhaps in an effort to disrupt copulation attempts by rivals and increase their own reproductive success (Comuzzie Crowell & Owens, 1990). Male chimpanzees (*Pan troglodytes schweinfurthii*) respond aggressively to copulatory attempts of other males with a female they are courting (Tutin, 1979). Mate guarding by dominant individuals may also limit subordinate access to mating partners and reinforce reproductive skew (acorn woodpeckers (*Melanerpes formicivorus*): (Mumme et al., 1983); mandrills (*Mandrillus sphinx*): (Setchell et al., 2005); long-tailed macaques (*Macaca fascicularis*): (Engelhardt et al., 2006); black howler monkeys (*Alouatta pigra*): (Van Belle et al.,

2009)). Long-term patterns of reproductive skew in male savannah baboons (*Papio cynocephalus*) were maintained according to a dominance hierarchy in which dominant individuals were able to monopolize access to fertile females by means of sexual consortships (Alberts et al., 2003).

As an alternative to suppressing conceptions, aggression, eviction, stress-induced abortion, and infanticide may be used to skew post-conceptive reproductive success in favor of dominant females (Arabian babblers (*Turdoides squamiceps*): (Zahavi, 1990); meerkats: (Clutton-Brock et al., 1998a; Clutton-Brock et al., 2001a; Kutsukake & Clutton-Brock, 2006; Young et al., 2006; Clutton-Brock et al., 2008); dingos (*Canis familiaris dingo*): (Corbett, 1988); African wild dogs: (Creel et al., 1997); dwarf mongooses: (Creel & Waser, 1991; Rasa, 1994; Creel & Waser, 1997); banded mongooses (*Mungos mungo*): (Gilchrist, 2006a; Cant et al., 2010); naked mole-rats (*Heterocephalus glaber*): (Faulkes & Abbott, 1997); prairie dogs (*Cynomys ludovicianus*): (Hoogland, 1985); and in Mongolian gerbils (*Meriones unguiculatus*): (Saltzman et al., 2006a)). Subordinate eviction upon conception within the natal group could lead to pregnancy loss (Gilchrist, 2006a; Young et al., 2006), but observations to support this mechanism are lacking for wild callitrichids (where early pregnancy loss often goes undetected). In common marmoset groups where the potential hormonal and behavioral mechanisms responsible for reproductive skew have been examined in detail through a series of investigations carried out in captive as well as wild groups, infanticide appears to be responsible for limiting reproductive success in subordinate females (Saltzman, 2003; Saltzman et al., 2009). However, infanticide has never been observed in the long term study of GLTs in Poço das Antas Biological Reserve (PDA) (Dietz,

personal communication). Overt aggression by dominant females toward subordinate females has been suggested as a potential mechanism limiting reproduction by subordinate GLT females (Kleiman, 1979; Inglett et al., 1989; De Vleeschouwer et al., 2001; French et al., 2002). But in both captive and wild groups of common marmosets once a subordinate female has conceived within her natal group, aggression by the dominant female does not appear to interfere with gestation, parturition, or lactation (Saltzman, 2003; Saltzman et al., 2009).

Stress in subordinate females

Circulating concentrations of the glucocorticoid stress hormone, cortisol, should be relatively high among reproductive subordinates (Abbott et al., 2003) that must struggle against dominant females to win the right to reproduce. As a result of this struggle, both dominant and subordinate females in cooperatively breeding birds, carnivores, and primates may experience stress (see summary Table 1 in Creel (2005)). An animal's primary response to stress is an increase in the activity of the hypothalamic-pituitary-adrenocortical axis which increases the concentration of circulating adrenal glucocorticoids (Sapolsky, 1992; Sapolsky, 2000; Sapolsky, 2002). Corticosterone concentrations were higher during nesting periods than during non-nesting periods in both male and female Harris' hawks (Mays et al., 1991). Higher rates of agonistic and aggressive behaviors on the part of dominant female dwarf mongooses were associated with higher basal levels of glucocorticoids (Creel et al., 1996; Creel, 2005). High cortisol concentrations among dominant members of cooperatively breeding ring-tailed lemur (*Lemur catta*) groups were associated with the initiation of aggression, whereas high cortisol in subordinates was associated with the receipt of aggression (Cavigelli et al.,

2003). Circulating concentrations of cortisol have been shown to be higher in both Old and New World primates when subject to higher rates of stress and less social support (see meta-analysis by Abbott et al. (2003)). Rises in cortisol concentrations in both common marmosets and Wied's black tufted-ear marmosets (*Callithrix kuhlii*) were documented following exposure to social stressors such as isolation or changes in the social group (Johnson et al., 1996; Smith & French, 1997a; Smith & French, 1997b; Smith et al., 1997; Albuquerque et al., 2001; Ziegler & Sousa, 2002).

Cortisol concentrations also rise significantly during late pregnancy in callitrichids (Ziegler et al., 1995; Smith & French, 1997b; Albuquerque et al., 2001; Ziegler & Sousa, 2002; Ziegler et al., 2004; Bales et al., 2005; Tardif et al., 2005), but this precipitous rise is driven primarily by a positive feedback loop between the placenta, fetal pituitary gland, and fetal adrenal gland that stimulates placental corticotropin-releasing hormone production culminating in higher levels of circulating maternal cortisol (Goland et al., 1994; Coulter & Jaffe, 1998; Smith et al., 1998; Smith et al., 1999; Challis et al., 2000; Umezaki et al., 2001; Mastorakos & Ilias, 2003). Rather than being indicative of aggression received or initiated by subordinate females attempting to reproduce, cortisol concentrations during late pregnancy are indicative of increased placental activity and fetal development (Bales et al., 2005; Tardif et al., 2005; Power et al., 2006). To avoid this confound, assessments of stress in subordinate females that are based upon cortisol concentrations are best conducted outside of late pregnancy.

Following the OSM logic, pregnant subordinate females that were allowed to breed should not be the targets of aggression by the dominant female as aggression may reduce the likelihood of carrying a pregnancy to term. Constant agonistic and aggressive

interactions between dominant and subordinate females are energetically expensive, come with a risk of injury for both the dominant and subordinate female, and may lead to the long term elevation of glucocorticoid concentrations (Creel, 2005; Sapolsky, 2000). Glucocorticoids divert energy from costly physiological processes that are not immediately necessary for survival including digestion, energy storage, growth, immunity, and reproduction (Munck et al., 1984; Sapolsky, 1992; Wingfield, 1994; Sapolsky, 2000; Sapolsky, 2002; Nelson, 2005). The chronic elevation of cortisol has been implicated in the reduction of female fertility in primates (Wasser & Barash, 1983; Chrousos & Gold, 1992; Sapolsky, 1992; von Holst, 1998; Pottinger, 1999) and may result in the loss of pregnancies by subordinate females (Wasser & Barash, 1983; Dunbar, 1988; Chrousos & Gold, 1992; Sapolsky, 1992; Ebensperger, 1998; von Holst, 1998; Pottinger, 1999; Young et al., 2006). Subordinate females reproducing in cooperatively breeding groups are not necessarily subject to high levels of aggression or social stress as reflected in elevated basal glucocorticoid concentrations (Creel, 2005). In low skew cooperatively breeding Florida scrub jays (Schoech et al., 1991) and ring-tailed lemurs (Cavigelli, 1999; Cavigelli et al., 2003), subordinate females breed alongside dominant females and glucocorticoid levels were lower among subordinates than they were among dominant females. In cooperatively breeding carnivores exhibiting high reproductive skew such as dwarf mongooses (Creel et al., 1992; Creel et al., 1996), African wild dogs (Creel et al., 1996; Creel et al., 1997), and gray wolves (*Canis lupus*) (Sands & Creel, 2004), dominants usually have higher reproductive success but cortisol levels were lower in subordinates than in dominants. Established wild and captive marmoset (Rothe, 1975; Abbott, 1984; Digby, 1995b; Saltzman et al., 1997c; Saltzman et

al., 2004; Sousa et al., 2005) and tamarin groups (Baker, 1991; Dietz & Baker, 1993; Savage et al., 1996a; Garber, 1997; Baker et al., 2002; Bales et al., 2005) demonstrate high degrees of affiliative behavior rather than aggression. Aggression is also not directed at higher rates toward pregnant subordinates (Saltzman et al., 1997c; Saltzman et al., 2004; Alencar et al., 2006; Saltzman et al., 2008) as might be expected under ICM; and cortisol levels are no higher in subordinates than in dominant females regardless of whether those subordinates are reproductively active within the group or not (Abbott et al., 1981; Saltzman et al., 1994; Johnson et al., 1996; Smith & French, 1997b; Saltzman et al., 1998; Ziegler & Sousa, 2002; Bales et al., 2005; Sousa et al., 2005; Saltzman et al., 2006b; Saltzman et al., 2006c).

Age effects on subordinate reproduction

As subordinate daughters age within their natal group and their reproductive life spans become shorter, the cost of remaining non-reproductive in terms of lifetime fitness increases. Therefore, aging subordinate daughters may be more likely to challenge the dominant female for an opportunity to reproduce within their natal group rather than forego reproduction altogether (Dietz & Baker, 1993; Baker et al., 2002; French et al., 2003). The dominant female in a GLT group is most commonly the eldest female in the group as well as the predominant aggressor and winner of fights (Dietz & Baker, 1993). But as dominance asymmetry decreases, as it should when subordinates are older and closer in both age and weight to the dominant (Dietz et al., 1994), the subordinate becomes more likely to challenge the dominant and win, and the dominant runs a greater risk of injury and losing her breeding position to an older subordinate (Emlen, 1995). Age and weight significantly affected breeding frequency of subordinate female meerkats

reflecting the capability of older subordinates to breed and their ability to resist dominant attempts to suppress them (Clutton-Brock et al., 2008). This principle can also be seen in polygynous callitrichid groups, as it is most often the eldest daughter that reproduces alongside her mother (Abbott, 1984; Dietz & Baker, 1993; Goldizen et al., 1996). The likelihood of a subordinate female undergoing physiological suppression of reproduction decreases with age in captive common marmosets (Saltzman et al., 1996; Saltzman et al., 1997a), reflecting the idea that subordinates are less willing to either restrain their own reproduction or be restrained by dominants as they age. Whereas only a small percentage of two year old GLT daughters were known to conceive while co-resident with their mothers, over 50% of subordinate daughters remaining within the natal group until the age of three to four years became pregnant regardless of whether an immigrant male was present in the group (Baker et al., 2002).

If subordinate reproduction is the result of subordinate females winning battles against dominant females, then one would also expect subordinate reproductive success to be higher in groups in which the dominant female is elderly and in poor physical condition. Under the model of incomplete control, subordinate reproduction is more likely to be successful when dominants are physically unable to prevent it (Clutton-Brock et al., 2001a; Clutton-Brock et al., 2008). As female callitrichids reach advanced ages, average body mass decreases (Dietz et al., 1994) and canine teeth get shorter (Dietz, unpublished data). As body mass decreases, elderly females may lose the ability to win physical battles with younger and potentially stronger subordinate daughters (Clutton-Brock et al., 2008; Hodge et al., 2008). Subordinate females that are in better physical condition (weigh more) and do get pregnant may be able to rebuff aggressive attacks or

attempts at eviction by the dominant female (Clutton-Brock et al., 1998a; Gilchrist, 2006a; Cant et al., 2010) and are more likely to carry their pregnancies to term (Bales et al., 2001; Tardif et al., 2004; Tardif et al., 2005). Subordinates able to overpower an older dominant may be better able to secure resources for and defend their offspring from potential infanticide perhaps increasing their chances of survival (Young & Clutton-Brock, 2006). Supporting this idea of incomplete control by elderly dominant GLT females, the likelihood of ovulation and pregnancy by subordinate GLT daughters increased with the age of the dominant mother (French et al., 2003). In an examination of 16 years of demographic data for this population of GLTs, Dietz and Baker (unpublished data) also found a significant positive relationship between the age category of the dominant female and the occurrence of polygyny in GLT groups. Suggesting that elderly dominant females in those groups in which subordinate daughters successfully reproduced were in poor physical condition, elderly dominant females either died or disappeared from the group less than a year following the onset of polygyny. The authors concluded that some older dominant female GLTs could no longer physically evict or control reproduction by their daughters.

The ability of dominant females to hormonally suppress subordinate reproduction may also wane with the age of the dominant female. Captive callitrichids have been shown to experience age-related effects on ovarian function including reduced follicle number, irregular hormonal cycles, and even the cessation of ovulation in very old females (Tardif, 1985; Tardif & Ziegler, 1992; Caro et al., 1995). Rather than occurring gradually, as has been shown for Old World primates (Wasser et al., 1998; Atsalis & Margulis, 2008; Borries & Koenig, 2008; Videan et al., 2008), loss of reproductive

function in callitrichids occurs abruptly near the end of the life span (Tardif et al., 2008). In Old World primates, the cyclical production of steroid hormones becomes irregular and eventually halts as follicles fail to mature (Ojeda, 1996; Atsalis & Margulis, 2008; Borries & Koenig, 2008; Videan et al., 2008). In reproductively senescent callitrichid females, it appears that luteal cells within the interstitial gland of the ovary continue to produce steroid hormones in the absence of normal follicular development (Tardif & Ziegler, 1992; Tardif et al., 2008). The lack of obvious peaks in luteinizing hormone in old anovulatory females may be due to the negative feedback that results from this continued production of steroids (Tardif & Ziegler, 1992). In the absence of surges in luteinizing hormone and the behavioral or olfactory cues presented by dominant females as they undergo regular ovulatory cycles, subordinate females may begin to ovulate and attempt to reproduce (Barrett et al., 1990; Abbott et al., 1993; Barrett et al., 1993; Smith & Abbott, 1995; Abbott et al., 1997; Abbott et al., 1998).

Reproductive senescence in primates has been suggested to be an adaptation that increases the inclusive fitness of the elderly female by forcing her to stop investing in her own reproduction when her imminent death would compromise the survival of an additional litter (Rhine et al., 1980; Paul et al., 1993). Under this hypothesis, older females that are unable to reproduce should continue to invest in their offspring or grand-offspring, exploiting their only remaining avenue for increasing their own inclusive fitness (Hawkes et al., 1997). Reproductive senescence (Tardif, 1985; Tardif & Ziegler, 1992; Caro et al., 1995) and/or reduced body mass (Dietz et al., 1994) associated with advanced age in callitrichid females may reduce the likelihood of a successful pregnancy by an elderly dominant female (Dietz & Baker, 1993; Tardif & Jaquish, 1994; Tardif &

Jaquish, 1997; Bales et al., 2001; Tardif et al., 2001; Bales et al., 2002; De Vleeschouwer et al., 2003; Tardif & Bales, 2004; Tardif et al., 2004; Tardif et al., 2005; Tardif et al., 2008). Unable to become pregnant or carry her own pregnancy to term, an elderly dominant mother may allow her subordinate daughter to breed within the natal group, perhaps as a means of securing a rare opening as a reproductive dominant (Baker & Dietz, 1996; Goldizen et al., 1996; Baker et al., 2002) for her daughter upon her death. In support of this idea, French et al. (2003) found that elderly GLT mothers died or disappeared less than a year following the onset of reproduction by their subordinate daughters within the natal group. In addition, evidence has been found in support of matrilineal inheritance of breeding positions in marmosets (Abbott, 1984; Ferrari & Diego, 1992; Digby & Ferrari, 1994) and tamarins (Dietz & Baker, 1993; Baker & Dietz, 1996; Goldizen et al., 1996; Baker et al., 2002; French et al., 2003). If providing care for not only their own offspring, but also for their grandoffspring increases the survival and fecundity of these offspring, then the genes of elderly females that provide extended care should be favored by selection (Williams, 1957; Hamilton, 1966; Hawkes et al., 1997; Packer et al., 1998). Maternal grandmothers in the Hadza society significantly increase their foraging efforts right after the birth of a grandchild, making up for a reduction in foraging by mothers of newborns, and positively affecting the welfare of their grandchildren (Hawkes et al., 1997). Grandmother vervet monkeys (*Cercopithecus aethiops sabaesus*) actively contribute to the reproductive success of their adult daughters and to the survival of their grandinfants (Fairbanks & McGuire, 1986) by engaging in affiliative behaviors with grandinfants at an intensity proportional to the vulnerability of the grandinfant to mortality and their own ability to provide effective social support

(Fairbanks, 1988). Grandmother baboons (*Papio* spp.) provide care for their grandoffspring by determining their daughter's dominance rank, intervening on the behalf of their kin, and grooming their grandoffspring (Gouzoules & Gouzoules, 1987). Grandmother lions (*Panthera leo*) defend communal territories and allonurse their daughter's infants as often as their own (Packer et al., 1990; McComb et al., 1994; Heinsohn & Packer, 1995). However, Packer et al. (1998) found no evidence to support the idea that this behavior enhanced the fitness of either older offspring or grandoffspring.

Timing of subordinate reproduction

If reproduction by subordinate females is the result of a struggle between dominant and subordinate females, successful reproduction by subordinate females may increase when dominant females are physically unable to interfere with subordinate matings and/or when hormonal suppression of subordinate reproduction is minimal. These two conditions are met when dominant females are heavily pregnant. Subordinate females mating at this time may be more likely to conceive and produce live offspring. High clutch mass during reptilian pregnancies significantly reduces locomotor capabilities (Shine, 1980; Bauwens & Thoen, 1981; Garland Jr., 1985; Seigel et al., 1987) and may have a detrimental effect on survival, especially in species that rely mainly on speed for predator avoidance (Vitt & Congdon, 1978; Vitt, 1981; Vitt & Price, 1982; Magnusson et al., 1985). Perhaps in response to this selective pressure, female garter snakes (*Thamnophis ordinoides*) reduce locomotion and tend more toward crypsis as a means of predator avoidance while gravid (Brodie III, 1989). Similarly, heavy maternal-fetal weight ratios (Leutenegger, 1973) and increased maternal body weight in late

pregnancy (Lunn, 1983) may limit the mobility of female callitrichids (Evans & Poole, 1984; Price, 1992b; Miller et al., 2006) and increase the risk of falling or serious injury during chases or fights. Subordinate female cotton-top tamarins were infrequent targets of aggression by heavily pregnant dominant females, but aggression by dominants toward subordinates increased following the birth of infants by the dominant female (Snowdon et al., 1993). In addition, GLT females in late pregnancy tend to avoid energetically expensive and potentially dangerous fights during inter-group encounters. Rather than taking positions at the forefront of encounters with neighboring groups, as is typical (French et al., 2003), heavily pregnant dominant females tend to remain at the rear of the group and do not engage in the aggressive posturing, chases, or fights that characterize inter-group encounters (unpublished observations).

In addition, subordinate females may be released temporarily from hormonal suppression when the dominant female is in late pregnancy. Chemical communication of fertility replaces aggression in queenless ant colonies (*Streblognathus peetersi*) (Monnin & Peeters, 1999; Cuvillier-Hot et al., 2002; Cuvillier-Hot et al., 2004). Olfactory investigation through flehmen behavior among female sable antelopes (*Hippotragus niger*) may serve to alter the timing of conceptions and parturitions as well as play a potential role in reproductive maturation (Thompson, 1995a; Thompson, 1995b). In contrast, behavioral contact with an aggressive queen naked mole-rat was sufficient to suppress ovulation in subordinate group members (Faulkes et al., 1990; Faulkes & Abbott, 1993; Faulkes & Abbott, 1997). A series of experiments with captive common marmosets showed that ovulation in subordinate females is sensitive to the olfactory and

behavioral signals sent by the dominant female of the group (Barrett et al., 1990; Abbott et al., 1993; Barrett et al., 1993; Smith & Abbott, 1995; Abbott et al., 1998).

Both types of signals are capable of conveying information about the reproductive status of the dominant female (Smith & Abbott, 1998), and may either inhibit or stimulate ovulation and conception in subordinates (lab rats (*Rattus norvegicus*): (McClintock, 1978); golden hamsters (*Mesocricetus auratus*): (Handelmann et al., 1980); opossums (*Mondelphis domestica*): (Fadem, 1987); domestic cattle (*Bos taurus*): (Vandenbergh & Izard, 1983); squirrel monkeys (*Saimiri oerstedii*): (Boinski, 1987); and humans (*Homo sapiens*): (Russell et al., 1980)). For example, eldest daughters in captive cotton-top tamarin groups exhibit a reduction in both estrogen and luteinizing hormone concentrations during their mother's post-partum estrus period, corresponding with the resumption of ovulation by the dominant, and an increase in aggressive behavior by the dominant toward older subordinate daughters (Snowdon et al., 1993). This mechanism has been proposed as a means of controlling subordinate reproduction during the post-partum ovulation period of the dominant female (Snowdon et al., 1993; Lazaro-Perea et al., 2000). This reduction in reproductive hormone levels accompanied by an increase in aggression toward subordinate females at this time may limit the timing of matings and conceptions by subordinate females to the period prior to the arrival of the dominant female's first litter of the season. In contrast, work by Puffer et al. (2004) demonstrated the lack of hormonal suppression in post-pubertal Wied's black tufted-ear marmoset daughters just prior to and directly following the birth of infant siblings to the dominant mother. Hormonal concentrations in subordinate daughters late in their mother's pregnancy and immediately post-partum were typical of a non-pregnant, breeding adult

female in this population. Instead of hormonal suppression, the authors reported a non-significant increase in reproductive hormones in post-pubertal subordinate Wied's black tufted-ear marmoset daughters during weeks one through three following parturition by their mother. The authors suggested that the absence of hormonal suppression and the trend toward increasing steroid concentrations in subordinate daughters following parturition by the mother may represent a type of hormonal priming that allows subordinates to take advantage of potential mating opportunities that may arise as a consequence of changes in group composition or emigrations that typically follow infant births in wild marmoset populations (Lazaro-Perea et al., 2001). Similarly, ovulation by subordinate common marmosets was more common in groups in which the dominant female was either anovulatory or ovulated and conceived, but was unable to carry pregnancy to term (Saltzman et al., 1997c). French et al. (2003) suggested that the onset of subordinate ovulation and reproduction in wild GLT daughters may be based upon their assessment of the reproductive status of their dominant mothers.

Selection should favor subordinate females that conceive while the dominant female is heavily pregnant with her first litter of the year; and, in doing so reduce competition for resources and allocare among infants from multiple litters. GLT females giving birth twice a year typically give birth to their first litter in late September or early October and to their second litter in mid-February. Females giving birth to only a single litter annually typically give birth in November. The two annual peaks in infant births, one from October through November and another in February (Dietz et al., 1994) may reflect the staggering of births among GLT females. Given an approximate 125-day gestation period in GLTs (French et al., 2002), a subordinate female that conceives while

the dominant female is heavily pregnant with her first litter of the year will give birth approximately four months after the first litter of the dominant female and at a minimum of two weeks prior to the second litter of the dominant female (given dominant conception upon first ovulation 10-20 days post-partum (French et al., 2002)). Infants of the subordinate female born at this time avoid competition for allocare for at least the first two to five weeks of life. The previous litter by the dominant mother has already been weaned and as juveniles they are largely independent in terms of nutrition and locomotion (Baker, 1991; Ruiz-Miranda et al., 1999; Tardif et al., 2002; Siani, 2009). The subsequent litter by the dominant mother will not arrive for at least another two weeks and will be cared for almost entirely by their mother for the first three weeks of their life (Hoage, 1978; Baker, 1991; Santos et al., 1997; Tardif et al., 2002). Infants of the subordinate female born prior to the dominant's second annual litter will have exclusive access to maternal milk and allocaregivers until the arrival of the second litter (Digby, 1995a). In the face of competition among litters, offspring of subordinate female banded mongooses that arrive following other litters have reduced survival rates (Hodge et al., 2010).

If dominant females allow subordinate reproduction, selection should favor dominants that control the timing of subordinate pregnancies such that competition for food and allocare is reduced. During the post-partum ovulatory period of the dominant female, subordinate reproduction may be suppressed by the reduction in concentrations of hormones associated with ovulation and by increased aggressive behavior by the dominant toward the subordinate (Snowdon et al., 1993). In this way, the dominant female may reduce the likelihood of subordinate conceptions during her own fertile

period, effectively staggering infant births. Subordinate reproduction should succeed more often when interfemale interbirth intervals are longer, extending the period of reduced competition between litters for resources such as food and helpers (Digby, 1995a; Goldizen et al., 1996; Clutton-Brock et al., 2008) (but see Gilchrist (2006a) and Hodge et al. (2010) for birth synchrony as a means of minimizing competitive asymmetry between pups born to different females). In an effort to reduce reproductive competition in the communal nest, female greater ani cuckoo birds (*Crotophaga major*) eject each other's eggs from the nest, with total egg loss being higher in large groups (Riehl, 2010). Pregnant subordinate banded mongoose females may be evicted from the group by the dominant, causing stress-induced abortions (Gilchrist, 2006a). After aborting her litter, the evicted female may be allowed to reenter the group, suggesting that resources may be limited, and a reduction in communal litter size may be the selective pressure leading to the eviction (Gilchrist, 2006a). In meerkats, simultaneous litters by dominant and subordinate females dilute helping investment and reduce food intake and growth of pups, variables closely associated with survival (Clutton-Brock et al., 2001b; Hodge, 2009). Infanticide in meerkats has been interpreted as a means to reduce competition for resources among litters (Young & Clutton-Brock, 2006). Meerkat litters were more likely to survive their first four days of life if they were born when no other female in the group was pregnant; dominant females were more likely than subordinates to give birth when no other female was pregnant, thus reducing the likelihood of infanticide and increasing their reproductive success (Young & Clutton-Brock, 2006). Subordinate common marmosets were successful in rearing young in polygynous groups only when the timing of births was such that they did not overlap with the dependency period of

infants born to the dominant female (Digby, 1995a). Successful breeding by subordinate daughters in wild saddle-back tamarin groups occurred only if the subordinate female gave birth either three months prior to or three months following the litter of the dominant female so that infant carrying periods were staggered (Goldizen et al., 1996).

Ecological constraints on subordinate reproduction

Under ICM subordinate reproduction is assumed to be unaffected by ecological constraints such as caloric availability or group size (Emlen, 1995; Clutton-Brock, 1998; Emlen et al., 1998; Reeve et al., 1998; Johnstone, 2000; Dietz, 2004). Under OSM, reproductive sharing is expected to increase as ecological constraints to emigration decrease and the option of subordinate dispersal and successful reproduction outside the natal group becomes more profitable and likely to succeed (Emlen, 1995; Clutton-Brock, 1998; Emlen et al., 1998; Reeve et al., 1998; Johnstone, 2000). As ecological constraints diminish (e.g., high caloric availability outside the natal home range), dominant females occupying home ranges with relatively low food availability are expected to offer reproductive incentives to subordinate females as a means of enticing subordinates to remain within their natal group as helpers rather than look for opportunities on richer territories (Reeve & Nonacs, 1992; Reeve & Ratnieks, 1993). In white-fronted bee-eaters (*Merops bullockoides*) and Galápagos mockingbirds (*Nesomimus parvulus*) the frequency of shared breeding was greatest during seasons when ecological constraints were relaxed (Emlen, 1982; Curry, 1988).

According to the model of optimal skew, dominant females in small groups with few potential allocaregivers should be more likely to allow subordinate females to breed (Dietz & Baker, 1993; Reeve & Emlen, 2000; Dietz, 2004; Clutton-Brock et al., 2008) as

a means of enticing them to remain within the group and provide care for the offspring of the dominant female. Inherent in this prediction is the assumption that helpers augment the fitness of the dominant breeding female either by decreasing the workload of the dominant such that survivorship of the dominant increases, or by increasing the number of surviving offspring produced by the dominant (Dietz, 2004). Several studies in species of cooperative breeders have presented evidence that cooperative care in the form of feeding, nursing, grooming, guarding, and/or transporting improves infant welfare and increases infant survival such that for most species providing cooperative care there is a positive correlation between the number of helpers and the number of offspring raised (in birds: (Brown, 1987); greater ani cuckoo: (Riehl, 2010); coyotes: (Bekoff & Wells, 1982); lions: (Bygott et al., 1979); African wild dogs: (Malcolm & Marten, 1982); blackbacked jackals: (Moehlman, 1979); dwarf mongooses: (Rood, 1990); and badgers: (Kruuk, 1989)). In Hadza foragers, an increase in foraging time by grandmothers (which allowed grandmothers to provide additional food for grandchildren) was correlated with a significant weight gain in provisioned grandchildren (Hawkes et al., 1997). In callitrichids (as in other communally breeding species (Creel & Creel, 1991)), cooperative breeding has been hypothesized to have evolved as a means of meeting the high energetic demands of reproduction that would otherwise fall only on the breeding female (Leutenegger, 1980; Garber et al., 1984; Terborgh & Goldizen, 1985). The majority of infant carrying and provisioning is done by alloparents in callitrichid groups (Tardif et al., 1993; Snowdon, 1996; Tardif et al., 2002). In a review of the literature for both captive and wild callitrichids (including common marmosets: (Koenig, 1995); moustached tamarins: (Garber et al., 1984; Sussman & Garber, 1987); cotton-top

tamarins: (Price, 1992a; Savage et al., 1996b); and saddle-back tamarins: (Terborgh & Goldizen, 1985)), Dietz (2004) concluded that the presence of subordinate helpers increases the fitness of dominants in the group by increasing the amount of food and transport received by infants in captivity and increasing infant survival in the wild. In 8 years of observations of 19 GLT groups at PDA, a breeding female was never observed to rear offspring successfully without the help of at least one male (Dietz & Baker, 1993); two five-week old infants were able to survive the death of their mother by being provisioned and carried by other members of the group (Bales et al., 2001). Infant GLTs in larger groups at PDA have also been shown to receive more food transfers than infants who are members of smaller groups (Siani, 2009). In addition, the presence of allocaregivers may reduce the energetic burden of infant carrying on mothers such that more energy may be directed toward reproduction in the following season (Price, 1992a; Sánchez et al., 1999; Fite et al., 2005). Supporting this idea for wild GLTs, Bales et al. (2001) found that the number of live births in second litters of the annual breeding season was positively correlated with the number of available helpers.

As group size increases, the marginal benefits accrued by the dominant female in allowing additional subordinate females to remain within the group and breed become smaller (Reeve & Emlen, 2000; Clutton-Brock et al., 2008). Therefore, optimal skew models predict that subordinate breeding in cooperatively breeding species should be allowed more frequently in small groups than in larger groups. This prediction was supported in meerkats; dominant females were less likely to evict pregnant subordinate females from small groups than they were from large groups (Clutton-Brock et al., 2008). As a result of lower rates of subordinate eviction and, in turn, reduced abortion rates

(Clutton-Brock et al., 2006; Young et al., 2006), successful breeding by subordinate female meerkats was more frequent in small groups when compared to large groups (Clutton-Brock et al., 2008). Similarly, dominant Wied's black tufted-ear marmosets are more likely to allow immigration of females into small groups and direct less aggression toward subordinates when occupying smaller groups (Schaffner & French, 1997).

Hypotheses and predictions

Incomplete control I tested the following predictions derived from the hypothesis that reproduction in subordinate adult female GLTs is limited by the ability of dominant females to interfere with subordinate reproduction, with dominants winning the majority, but not necessarily all battles with subordinate females over reproductive sovereignty:

Prediction 1: Subordinate adult females will ovulate and conceive, indicative of the inability of dominant females to suppress hormonally and/or behaviorally reproduction in subordinates.

Prediction 2: Pregnancies by dominant females will be more likely to succeed than pregnancies by subordinate females, indicative of dominant interference with subordinate pregnancies.

Prediction 3: Relative to subordinate females whose pregnancies do not result in live births, subordinate females whose pregnancies result in live births will have higher cortisol concentrations just prior to conception and during the 1st trimester of pregnancy, indicating higher stress levels in subordinate females that struggle with the dominant female to reproduce successfully.

Prediction 4: Pregnancies by subordinate females will be more likely to succeed when the subordinate female is older, reducing the asymmetry in age and weight between dominant and subordinate females.

Prediction 5: Pregnancies by subordinate females will be more likely to succeed when the dominant female is very old, reducing the physical ability of the dominant female to control subordinate reproduction.

Prediction 6: Pregnancies by subordinate females will be more likely to succeed when the dominant female is heavily pregnant and is least likely to be able to suppress subordinate reproduction either hormonally or behaviorally. Specifically, conceptions by subordinate females that occur just prior to the arrival of the dominant female's first litter of the year are more likely to result in the birth of live offspring.

Optimal skew I tested the following predictions derived from the hypothesis that reproduction in subordinate adult female GLTs is limited by dominant females exercising complete control over subordinate reproduction and allowing reproduction in subordinates only when the dominant obtains a benefit by doing so.

Prediction 1: Ovulation and conception in subordinate adult females will be limited to subordinate females providing benefits to the dominant, indicative of hormonal and/or behavioral suppression of subordinate reproduction by the dominant female.

Prediction 2: Pregnancies by dominant females will be more likely to succeed than pregnancies by subordinate females, indicative of dominant interference with subordinate pregnancies.

Prediction 3: Relative to subordinate females whose pregnancies do not result in live births, subordinate females whose pregnancies result in live births will have lower

cortisol concentrations just prior to conception and during the 1st trimester of pregnancy, indicating lower stress levels in subordinate females that the dominant female allowed to reproduce.

Prediction 4: Pregnancies by subordinate females will be more likely to succeed when the dominant female is very old. By allowing her subordinate daughter to breed prior to her own death, an elderly dominant may increase her own inclusive fitness by securing the breeding position for one of her own offspring and providing allocare for her grandchildren.

Prediction 5: Pregnancies by subordinate females will be more likely to succeed when the interfemale interbirth interval is longer, staggering pregnancies and the arrival of litters from multiple breeding females and reducing the length of time when the pregnant dominant and subordinate females and their infants must compete for resources and allocare.

Prediction 6: Pregnancies by subordinate females will be more likely to succeed as caloric availability within the home range decreases and dominants offer reproduction as an incentive for subordinates to stay instead of looking for reproductive opportunities on richer territories.

Prediction 7: Pregnancies by subordinate females will be more likely to succeed as group sizes decrease and dominants offer reproduction as an incentive for subordinates to stay and help.

METHODS

Study site

Data were collected within the 6300 ha Poço das Antas Biological Reserve (PDA), Rio de Janeiro State, Brazil (22° 30' - 33' S, 42° 15' - 19' W) (Miller & Dietz, 2006). The reserve is predominantly secondary forest consisting of a patchwork of habitat types resulting from the various stages of secondary succession following human occupation (Dietz et al., 1997). The areas of secondary forest used by GLTs include hillside, lowland transitional, and swamp.

PDA has a wet (October through April (Dietz et al., 1994; Hankerson, 2008)) and a dry season (June through August (Dietz & Baker, 1993; Hankerson, 2008)) each year. During the three years of this study, PDA received an average of 2135.6 ± 184.1 (mean \pm standard error) mm of precipitation each year (unpublished data). An average of 260.2 ± 18.9 mm of rain fell during each wet month as compared to an average of 62.9 ± 7.4 mm of rain during each dry month (unpublished data). Average maximum temperatures were 27.6 ± 0.2 ° C during the wet season and 25.0 ± 0.2 ° C during the dry season (unpublished data).

Study species

Golden lion tamarins once occupied much of the Atlantic Coastal Forest of Rio de Janeiro State, Brazil. Today, primarily as a result of habitat loss, fragmentation, and forest degradation and with the exception of a few small coastal populations, GLTs are found only in small patches of remnant forest centered around the São João river basin (Rylands et al., 2002; Ruiz-Miranda et al., 2008). GLTs were ranked as “critically endangered” from 1963 to 2002 due to low numbers, narrow distribution, and threat of

continued habitat loss (Hilton-Taylor, 2000; Rylands et al., 2002). Due to successful local, national, and international conservation efforts, GLTs were reclassified as “endangered” in 2003 (IUCN, 2010). Still, only an estimated 1500 GLTs remain in the wild (Ruiz-Miranda et al., 2008); PDA holds the largest remaining population (Rylands et al., 2002; Ruiz-Miranda et al., 2008). Currently, an estimated 350 GLTs exist within the secondary forests protected by the reserve (Rylands et al., 2002; Ruiz-Miranda et al., 2008).

The GLT diet includes fruits, seeds, flowers, nectar, gum, insects, and small vertebrate prey (Dietz et al., 1997; Miller, 2002; Procópio de Oliveira, 2002; Miller & Dietz, 2006; Procópio de Oliveira et al., 2008a). In this study, I focused only on the calories provided from fruit and nectar species occurring within GLT home ranges.

Individual identification and weighing

The animals under study at PDA are native and unmanipulated except for bi-annual live captures necessary for replacing radio collars to facilitate group location. During these routine captures, usually in May or early June and again in December or January, individuals are given identifiable markings (hair dye and tattoos), weighed, and evaluated for growth and body condition including notes regarding female nipple length (reflecting parity), lactation, and pregnancy (Dietz & Baker, 1993; Dietz et al., 1994). During the current study weights were also obtained weekly from August through December of each year using baited scales in the field (Bales, 2000; Bales et al., 2002; Siani, 2009).

Behavioral observations

I collected data on 7 groups of wild GLTs at PDA, each containing 2 to 13 individuals and 1 to 3 adult females. All individuals were habituated to the presence of human observers. I collected data over three reproductive years: 2004-2005, 2005-2006, and 2006-2007. A reproductive year was defined as the 1st of March through the 28th of February in order to encompass the mating period, pregnancy, and the first annual peak in infant births (October through November (Dietz et al., 1994)) as well as post-partum ovulation, mating, and pregnancy that lead to the second annual peak in infant births (February (Dietz et al., 1994)). Six of these groups were observed from March 2004 through February 2007. Another group was added to the study in June of 2005, and was observed until the end of the study in February of 2007. Group sizes fluctuated but losses typically were filled by colonizers. Field assistants performed randomly alternated daily behavioral observations on these seven study groups. Focal observations included observed reproductive behavior, fights, infant care, and food species consumed. Group scans recorded position, habitat type, and activity every 20 minutes. Group composition was recorded daily including all births, deaths, emigrations, and immigrations.

The ages of individuals born within study groups are known from long-term demographic data or estimated to year based upon weight, the eruption of permanent teeth, and degree of tooth wear and discoloration noted at semi-annual captures (Dietz et al., 1994; Bales et al., 2001; French et al., 2003). Adults were defined as individuals older than 18 months of age (Dietz & Baker, 1993) corresponding to the average age of sexual maturation (French & Stribley, 1987; French et al., 1989; Dietz et al., 1994;

French et al., 2002). The average life span for captive tamarins is nine years of age (Dyke et al., 1993).

Each group contained one adult female who was behaviorally dominant to other females in the group. Dominance was assigned to the predominant aggressor based upon archwalks, mounts, and chases and winner of fights (Dietz & Baker, 1993; Bales et al., 2005).

Fecal sample collection

I collected 1176 fecal samples from individually identified female GLTs in 7 free-ranging social groups from March 2004 through February 2007. Feces were collected from a total of 21 GLT females including 14 adults, 4 females that passed from subadult to adult, 1 from juvenile to adult, 1 from juvenile to subadult, and 1 from infant to subadult (Table 3.1). I collected samples year-round during reproductive and non-reproductive months of the year. I collected fecal samples from each female once or twice per week as they left their sleeping locations or during subsequent observations. I attempted to restrict fecal collection to the morning hours to reduce diurnal variation in concentrations of fecal progesterone metabolites (Sousa & Ziegler, 1998; French et al., 2003). As a result, 28% of samples were collected before 0900h, and 83% by 1200h. No more than 10 hours passed between fecal sample collection and storage in a freezer. Samples remained frozen until analysis at the Callitrichid Research Center, University of Nebraska at Omaha.

Pregnanediol-3-glucuronide (PdG) and cortisol extraction from feces

Pregnanediol-3-glucuronide (PdG) is a metabolite of the hormone progesterone excreted in the feces and has been validated as a reliable indicator of circulating

progesterone concentrations (Bales, 2000; French et al., 2003). Cortisol is excreted directly into the feces. PdG and cortisol were extracted simultaneously from fecal samples. Fecal samples were thawed at room temperature, processed by removing large plant and insect fragments, and dried prior to weighing in a drying oven at 37 ° C. Extraction of both PdG and cortisol was performed by briefly vortexing and then shaking 0.125 g of dried fecal matter in 2.5 ml of solubilizing extraction buffer (40% methanol (MeOH):60% phosphate buffered saline (PBS)) for 12-16 hours on a shaker rack. Samples were then briefly vortexed to remove residue along the tube walls and centrifuged for 15 min at 2000 rpm at 6 ° C. The supernatant was decanted into a clean test tube and refrozen for storage until further diluted for assay.

Enzyme immunoassay (EIA) for PdG

PdG was measured using an assay previously described (Chapter 1, this dissertation), validated against circulating hormone levels and tested for accuracy (Bales, 2000; French et al., 2003). Extracted fecal samples were diluted 1:5 in PBS prior to assay. PdG standards ranged from 10,000 to 78 pg/well and were prepared using halving dilutions in 1:5 extraction buffer:PBS. Controls were 1:5 extraction buffer:PBS. Internal quality control pools consisted of female Geoffroy's marmoset (*Callithrix geoffroyi*) urine. They were run at high concentrations (1:80 in 1:5 extraction buffer:PBS) and low concentrations (1:640 in 1:5 extraction buffer:PBS). PdG concentrations were determined through standardized enzyme immunoassay techniques (EIA) and calculations resulting from a four-parameter sigmoidal curve-fitting function. The intra- and inter-assay coefficients of variation for high and low concentrations of a urine quality

control pool for the PdG assay were 9.1% and 19.9% (high), and 7.4% and 26.7% (low), respectively.

Enzyme immunoassay (EIA) for cortisol

Fecal cortisol was measured using an assay previously described (Chapter 1, this dissertation), validated against circulating hormone levels and tested for accuracy (Bales, 2000; Bales et al., 2005). Extracted fecal samples were diluted 1:10 in PBS prior to assay. Cortisol standards ranged from 1,000 to 7.8 pg/well and were prepared using halving dilutions in 1:10 extraction buffer:PBS. Controls were 1:10 extraction buffer:PBS. Internal quality control pools consisted of female Geoffroy's marmoset urine. They were run at high concentrations (1:2560 in 1:10 extraction buffer:PBS) and low concentrations (1:20,480 in 1:10 extraction buffer:PBS). Cortisol concentrations were determined through standardized EIA techniques and calculations resulting from a four-parameter sigmoidal curve-fitting function. The intra- and inter-assay coefficients of variation for high and low concentrations of a urine quality control pool for the cortisol assay were 3.9% and 11.4% (high), and 3.9% and 20.7% (low), respectively.

Detection of ovulation, pregnancy, parturition, and abortion

I plotted PdG and cortisol concentrations over time to help visualize reproductive patterns for individual GLT females. Variation in progesterone levels corresponds to ovulation, the formation of the *corpus luteum*, and placental development (Ojeda, 1996; Nelson, 2005) and has been used to trace ovarian cycles and pregnancy in GLTs (French & Stribley, 1985; French & Stribley, 1987; Bales, 2000; French et al., 2002; French et al., 2003). I examined progesterone profiles of subordinate adult GLT females from 18 months of age until conception of their first pregnancy. Subordinate adult females were

considered ovulatory if non-pregnant progesterone profiles showed cyclical elevation in PdG concentrations averaging 20 days in periodicity (French et al., 2002).

Pregnancy was diagnosed primarily by the prolonged elevation of PdG concentrations (Bales, 2000; French et al., 2002; French et al., 2003). Cortisol, a glucocorticoid responsible for mobilizing fat and protein reserves for use by the body in times of food deprivation or stress (Nelson, 2005), also shows a significant increase in concentration during the 3rd trimester of GLT pregnancy (Bales, 2000; Bales et al., 2005), so can be used as a late pregnancy diagnostic. In addition, pregnant GLT females demonstrate steady and considerable weight gain beginning in their 2nd trimester of pregnancy and continuing throughout gestation (Bales et al., 2001; Hankerson, 2008). Parturition was diagnosed by a sudden drop in PdG concentrations to baseline levels (Bales, 2000; French et al., 2002; French et al., 2003) accompanied by a rapid and large amount of weight loss (mean=112.7 g; range 73 to 142 g; n=12 full term pregnancies for which immediate pre- and post-partum weights were available (Siani, 2009)). I defined successful pregnancies as those that were carried to full term and that resulted in observations of new infants carried and nursed during the first week after birth by the female I identified as the mother. Birth dates were recorded within one or two days of parturition for most infants and within one week for all observed infants born during this study. To establish a calendar for each successful pregnancy I divided the 125-day gestation period (French et al., 2002) into trimesters. Trimesters were assigned by counting back from known parturition dates: 84-125 days (3rd trimester), 42-83 days (2nd), and 0-41 days (1st) (French & Stribley, 1985; French et al., 2002). Because hormone profiles are highly individualized, for each reproductive female I calculated

average PdG concentrations during each trimester of pregnancy and during non-pregnant periods to provide “typical” values for successful pregnancies. These trimester averages were used as a guide in diagnosing suspected pregnancies for which infants were not observed and to determine the probable trimester in which pregnancies were aborted.

Pregnancy diagnoses and assignment of trimesters when no infants were observed were made by consulting multiple sources of information on a case by case basis as described previously (Chapter 1, this dissertation). First, I consulted average trimester PdG values for successful pregnancies. Mean PdG concentrations of 1500 ng PdG/g feces, 3500 ng/g, 5000 ng/g, and 10,000 ng/g were indicative of an adult female that was either non-pregnant or in her 1st, 2nd, or 3rd trimester of pregnancy, respectively. Consistently high levels of PdG that suddenly dropped to titer levels indicated pregnancy loss or parturition depending on when concentrations returned to baseline values (Bales, 2000; French et al., 2002; French et al., 2003). Second, a large and consistent rise in cortisol reaching a mean of 15,000 ng cortisol/g feces was used to diagnose pregnancies that had proceeded into the middle to late 3rd trimester. Third, I used patterns of weight gain in females in the current study to establish general guidelines for diagnosing pregnancy from the 2nd trimester onward. Females gaining 5-10% or in excess of 10% of their non-pregnant average weight in a consistently rising pattern were diagnosed as being in their 2nd or 3rd trimester, respectively. Females that gained approximately 20% of their body mass were considered to have reached full term, since neonatal weight for *Leontopithecus* is on average 20% of the mother’s body weight (Tardif et al., 1993). Average weight loss for 12 births during the current study for which immediate pre- and post-partum weights were available was 18.6% of the females’ post-partum weight

(Siani, 2009). Rapid weight loss was considered indicative of parturition or the loss of a 2nd or 3rd trimester pregnancy. Fourth, bi-annual capture records including each female's weight, nipple length, whether a female was lactating or not, and the results of uterus palpation for pregnancy and trimester diagnosis at the time of capture (Dietz & Baker, 1993; Dietz et al., 1994) provided data points during early pregnancy in late May or June when field weights were not available and pregnancy diagnoses were not often possible given hormonal concentrations that remain low during this early stage. *Ad libitum* field observations regarding female appearance and behavioral changes were consulted for additional confirmation, though were not considered diagnostic.

PdG and cortisol averages by trimester

I divided pregnancies that did not result in the observation of live infants, thus did not have known dates of parturition, into trimesters using the guidelines established above and counting either forward or backward from an established trimester to obtain surrounding trimester cut off dates as well as probable conception and projected parturition dates. I then calculated average PdG and cortisol concentrations for each trimester for all pregnancies, successful and non-successful, as well as for non-pregnant adult females.

Interfemale interbirth interval

I defined interfemale interbirth interval (IFIBI) as the number of days between consecutive known or calculated parturition dates by different females within the same group that were pregnant at the same time during the same reproductive year whether both pregnancies were carried through to parturition or not.

Home range and habitat type quantification

I defined a home range as the area within which a group of GLTs could be found 95% of the time (Kernohan et al., 2001), using ArcView 3.2 with fixed kernel density to map ranges based on GLT group locations collected at 20 min intervals during daily follows. Home ranges were calculated separately for each reproductive year. Once I had mapped the home ranges for each reproductive year I categorized the habitats contained within each home range as either hillside, lowland transitional, or swamp forest (refer to definitions of hilltop/hillside forest, corridor, and swamp forest/gingers in Dietz et al. (1997)). I distinguished these habitat types based upon their topography, vegetation structure and composition, degree of moisture, and soil properties (James & Shugart Jr., 1970; Peres, 1994; Dietz et al., 1997; Brugiere et al., 2002; Procópio de Oliveira, 2002; Raboy et al., 2004; Procópio de Oliveira et al., 2008b). By layering the habitat map on top of annual home ranges in ArcView 3.2, I was able to quantify the area of each GLT home range occupied by hill, lowland transitional, and swamp habitat for each reproductive year as previously described (Chapter 1, this dissertation).

Caloric availability

To quantify monthly caloric availability from fruit and nectar within GLT home ranges, I established in each of six ranges three transects (one of each habitat type), each 195 m in length and 10 m wide. At monthly intervals I evaluated all individuals of plant species that were identified as being eaten by GLTs occurring within these transects for the presence of edible fruit and nectar-producing flowers. I ranked the quantities of flowers, unripe fruit, and ripe fruit present in each monitored tree on a scale from 0 (absence) to 4 (100%) based on the percentage of the tree crown covered in flowers,

unripe fruit, and/or ripe fruit (Peres, 1994). I then counted the number of edible unripe fruits, ripe fruits, and nectar-producing flowers per m³ present in GLT food trees and extrapolated over fruit-bearing tree crown volume to estimate total fruits available in the tree as previously described (NRC, 1981; Chapman et al., 1992; Miller & Dietz, 2004) (Chapter 1, this dissertation).

I quantified the number of edible fruits and nectar-producing flowers of each species present within sampled transects each month using the fruit counts performed on individual trees and extrapolations from standard curves for those trees that were given rankings but fruits were not counted as previously described (Chapter 1, this dissertation). Briefly, I produced nine standard curves by plotting ordinal rankings (0-4) on the x axis and their corresponding fruit and flower counts on the y axis for all individuals within the same group of species. Species were grouped according to similarities in life form, fruit size, and fruiting arrangement such that all members of a given group with a similar ordinal fruit and flower ranking also had similar quantities of fruit or flowers present in their crowns. I used nonlinear regression to fit a power curve to the data. I estimated the number of edible fruits and nectar-producing flowers present within trees that were given only rankings by extrapolating from the appropriate standard curve.

I then converted estimates of edible fruits and nectar-producing flowers into estimates of edible calories. For edible fruits I multiplied the number of fruits of each species present during each phenological sample by the dry weight of a single fruit of that species (obtained from Miller & Dietz (2004) and Miller (unpublished data)). I multiplied that product by the number of calories per gram of dry matter of that species (obtained from Miller (2002), Miller & Dietz (2006), and Miller (unpublished data)).

I estimated calories available from *Symphonia globulifera* nectar, the only species of nectar that I saw GLTs consume, by multiplying the calories from nectar present in each flower by the quantity of *S. globulifera* flowers present in each sampled transect. I used methods reported by Kearns & Inouye (1993) and Dafni et al. (2005) to estimate cal/flower based upon the following information. Gill Jr et al. (1998) reported that each flower contained a median amount of 66.5 μ l of nectar with a mean total sugar concentration of 10%. Dafni et al. (2005) reported an energetic value of 4 cal/mg of sugar (sucrose) in nectar.

For those species within transects that produced edible fruit during the course of this study, but for which dry weights or caloric values were not available (n=11 species), I substituted values of those fruits most similar to the unknown in terms of size, consistency, taste, portion eaten, and typically within the same genera. Where commonalities with a fruit species of known dry weight and caloric content did not exist (n=2 species), I substituted the average dry weight and caloric content for all members of the species group to which the unknown was previously assigned. These calculations provided an estimate of the average number of calories from fruit and nectar per hectare available within each habitat type during each month of the reproductive year for 2004-2005, 2005-2006, and 2006-2007. I extrapolated to estimate the available calories from fruit and nectar each month in each home range during the three reproductive years.

STATISTICAL ANALYSES

Stress in subordinate females

I used logistic regression analyses to test for a statistical relationship between circulating maternal cortisol concentrations (during the non-pregnant period just prior to

pregnancy, the 1st trimester of pregnancy, the 2nd trimester of pregnancy, and/or the 3rd trimester of pregnancy) and the likelihood that the pregnancy would result in live infants (SAS 9.2, SAS Institute, Cary, North Carolina). Using cortisol concentrations at each of the four stages of reproduction as potential predictor variables, I performed backward selection eliminating the least significant potential predictor variable (the variable with the largest p-value>0.05) one at a time. The full dataset of 37 pregnancies was reduced to 25 detected pregnancies (20 successful and 5 non-successful) for which hormonal averages were available for all four states of pregnancy. To control for multiple pregnancies by some females I included individual female identity (FEMID) as a covariate in the model. The backward selection process resulted in a model containing only non-significant predictor variables and which neither met the assumptions required of a logistic regression model nor provided a good fit to the data. Therefore, I used the Score Chi-Square prior to analysis to select a reduced number of hormonal explanatory variables that were more likely to predict a successful pregnancy. I chose the model with the smallest number of variables explaining the largest amount of variation between successful and non-successful pregnancies. To predict successful pregnancies based upon cortisol, I chose a model including the 1st, 2nd, and 3rd trimester cortisol averages as explanatory variables and FEMID as a covariate. Thirty pregnancies (23 successful and 7 non-successful) for which cortisol averages for all three trimesters were available were considered in the analyses. I performed the logistic regression procedure again using the reduced model including only the explanatory variables selected above to determine whether a successful pregnancy could be predicted based upon 1st, 2nd, and 3rd trimester cortisol levels. Using this alternate method all assumptions were met for the model.

To determine whether cortisol profiles differed for successful vs. non-successful pregnancies I performed a series of linear mixed model analyses of variance (ANOVA), one for each stage of pregnancy (non-pregnant, 1st, 2nd, and 3rd trimester), using Proc GLIMMIX in SAS 9.2. I included 32 pregnancies (23 successful and 9 non-successful) for which hormonal data were collected just prior to the pregnancy in question, 36 pregnancies (26 successful and 10 non-successful) for which hormonal data were collected during the 1st trimester, 35 pregnancies (25 successful and 10 non-successful) for which hormonal data were collected during the 2nd trimester, and 31 pregnancies (23 successful and 8 non-successful) for which hormonal data were collected during the 3rd trimester. GLIMMIX allows for the assignment of both random and repeated effects, such as individual female identity, thus addressing the problem of pseudoreplication that occurs when multiple observations are drawn from a single female or from multiple females occupying a single home range by accounting for correlations within the data (Diggle et al., 1999; Bales et al., 2001; Bales et al., 2002). FEMID was included as the subject within the random home range effect (HR) as a covariate in the model. HR(FEMID) was removed as a covariate if the covariance parameter associated with it was 0 thereby treating each reproductive attempt for a given female within a given home range as independent (Bales et al., 2001; Bales et al., 2002). I controlled for individual non-pregnant baseline differences in cortisol among females in this analysis by including baseline cortisol concentrations (AVG_NP_CORT) in the model when testing for differences between successful and non-successful pregnancies during the three trimesters of pregnancy, but not during non-pregnant periods. I defined the baseline cortisol concentration for each adult female as the average cortisol concentration of all

samples collected from that female while she was non-pregnant. Where necessary I used a log transformation to meet normality requirements prior to analysis.

Effect of dominance, maternal age, and group size on reproduction

I used logistic regression analyses to test for a statistical relationship between the demographic variables associated with each pregnancy and the likelihood that the pregnancy would result in live infants. Explanatory variables included whether the pregnant female was dominant or subordinate, her age in years, and the average number of individuals in her group at the time of the pregnancy. Non-significant variables were removed by backward selection as described above. The full dataset of 37 pregnancies conceived by 14 dominant and subordinate adult females (26 successful to 10 females and 11 non-successful to 7 females) was used in this analysis. FEMID was included as a covariate in the model. The final model was accepted when every variable remaining in the model was significant, the model as a whole was significant, and all assumptions for the model were met.

Effect of age of dominant female, timing of subordinate reproduction, and group size on reproduction

To identify variables useful in predicting a successful pregnancy to a subordinate female pregnant at the same time as the dominant female in her group I used the logistic regression procedure with removal of non-significant effects one at a time through backward selection as described above. Explanatory variables included the age of the dominant female, whether the subordinate female conceived while the dominant female was heavily pregnant with her first litter of the year and prior to conception of the second litter by the dominant female, interfemale interbirth interval (IFIBI), and group size. The

dataset consisted of 11 cases of simultaneous pregnancies in 2 females within the same group (4 cases where both the dominant and subordinate females were successful and 7 cases in which only the dominant female was successful). FEMID was again included in the model, but removed from the model when the effect was non-significant such that each reproductive attempt by the same female was treated as an independent observation (Bales et al., 2001; Bales et al., 2002). All assumptions were met for this model.

Effect of caloric availability on reproduction

I used logistic regression analyses to test for a statistical relationship between average number of calories per month of pregnancy in the home range and the likelihood that the pregnancy would result in live infants. All 37 pregnancies detected during the study were included in this analysis. FEMID was included as a covariate in the model. All assumptions were met for this model.

RESULTS

Hormonal and behavioral control of subordinate reproduction

Subordinate females between 18 months of age and the conception of their first pregnancy showed cyclical elevation in PdG concentrations from less than 500 ng PdG/g feces to an average of 1000 ng PdG/g feces with 15-30 day periodicity consistent with ovulatory patterns observed in adult GLTs (Chapter 2, this dissertation). Age of first conception ranged from 2.5 to 3.9 (mean=3.1 ± 0.2 standard error) years for 8 GLT females conceiving for the first time during this study (Table 3.1). All females over 3.9 years of age became pregnant. Of the 21 GLT females sampled, only 5 adult females did not conceive. Four of the five were younger than three years of age but did show cyclical elevations in PdG concentrations. The fifth female was of unknown age and remained

within a habituated study group for just three months during which time she did not become pregnant.

Dominant females conceived 26 pregnancies, 22 successful and 4 non-successful (Table 3.1). Subordinate females conceived 11 pregnancies, 4 successful and 7 non-successful. Pregnancy polygyny occurred in five GLT groups. Three of these five polygynous groups were mother-daughter reproductive pairs, whereas the other two were sisters transferring together to neighboring groups. Four pregnancies by two subordinate adult females in two groups resulted in the birth of live young. Seven pregnancies by five subordinate adults in five groups failed to produce live young. Both successful subordinates were daughters reproducing alongside their dominant mothers while remaining within their natal group. One of these females reproduced successfully three times while remaining subordinate to her mother. The other reproduced successfully once while subordinate to her mother and twice after she became dominant to her mother.

Stress in subordinate females

A logistic regression model including average cortisol levels during all three trimesters of pregnancy and controlling for FEMID was marginally significant (Likelihood Ratio Chi-Square=8.73, df=4, p=0.0681) (Table 3.2). By knowing the average 1st, 2nd and 3rd trimester cortisol concentrations of a pregnant female, I could correctly predict a successful pregnancy 81.4% of the time. My analyses indicated that lower cortisol levels during the 1st trimester of pregnancy and higher cortisol levels during the 2nd and 3rd trimesters were loosely associated with successful pregnancies. Though cortisol levels during a single trimester alone were each non-significant predictors of successful pregnancies (1st trimester Wald Chi-Square=0.47, df=1,

$p=0.4914$; 2nd trimester Wald Chi-Square=0.63, $df=1$, $p=0.4274$), higher cortisol levels during the 3rd trimester alone were the most useful in predicting pregnancy success when data for all three trimesters were not available (Wald Chi-Square=2.31, $df=1$, $p=0.1284$).

In concordance with results from my logistic regression analyses, the linear mixed model ANOVA indicated a non-significant trend toward higher levels of cortisol for successful pregnancies when compared to non-successful pregnancies during both the 2nd (successful mean=3310.31 \pm 616.89 vs. non-successful mean=1429.67 \pm 977.01 ng cortisol/g feces; F-value=2.68, $ddf=32$, $p=0.1113$) and 3rd trimester of pregnancy (successful mean=18688.00 \pm 5121.92 vs. non-successful mean=9652.59 \pm 5923.39 ng cortisol/g feces; F-value=2.59, $ddf=16$, $p=0.1269$) (Figure 3.1). Cortisol levels during the 2nd and 3rd trimesters of successful pregnancies were approximately double those of non-successful pregnancies.

Effect of dominance, maternal age and group size on reproduction

Both dominance status of the pregnant female (Wald Chi-Square=7.69, $df=1$, $p=0.0055$) and the number of individuals in her group (Wald Chi-Square=4.52, $df=1$, $p=0.0335$) were significant predictors of a successful pregnancy according to a significant logistic regression model that also controlled for FEMID (Likelihood Ratio Chi-Square=15.37, $df=3$, $p=0.0015$) (Table 3.2). A pregnant female holding dominant status in her group during her pregnancy was 40.4 (95% confidence limits=3.0-552.1) times as likely to give birth to live young as a pregnant female holding a subordinate ranking. Pregnant females residing in larger groups also had a greater likelihood of having successful pregnancies. For every additional group member, pregnant females increased their chances of success by 1.7 (95% confidence limits=1.0–2.9) times. Given

information on the dominance status of the pregnant female and the number of individuals residing within her group, I was able to classify a pregnancy correctly as successful 88.5% of the time. The effect of maternal age was not significant (Wald Chi-Square=2.12, df=1, p=0.1452) (Table 3.2).

Effect of age of dominant female, timing of subordinate reproduction, and group size on reproduction

A logistic regression model including both the age of the dominant female (Wald Chi-Square=1.32, df=1, p=0.2499) and whether the subordinate female conceived while the dominant female was heavily pregnant with her first litter of the year and prior to conception of the second litter by the dominant female (Wald Chi-Square=2.23, df=1, p=0.1353) as predictors of reproductive success to a subordinate female whose pregnancy overlapped with that of a dominant female was marginally significant (Likelihood Ratio Chi-Square=4.98, df = 2, p=0.0829) (Table 3.2). Though neither of these pieces of information was a significant predictor of subordinate success, knowing both of these pieces of information provided an 85.7% likelihood of correctly predicting a successful pregnancy to a subordinate female. As the age in years of the dominant female increased, the likelihood of success by a subordinate female increased. Under this model, for every year of age of the dominant female, a pregnancy by the subordinate female was 2.0 times as likely to be successful (95% confidence interval was 0.6-6.6). The mean age of the dominant female during a non-successful pregnancy by a subordinate was 6.4 years compared to 10.9 years during a successful pregnancy by a subordinate. All four successful pregnancies by subordinate females occurred when the dominant female in each of the two groups was 10 years old or older. In comparison, pregnancies by

subordinates were only 0.06 times as likely to be successful (95% confidence interval was 0.001-2.4) if the subordinate female was pregnant before the dominant female became pregnant with her second litter of the year. All four successful pregnancies by subordinate females were conceived prior to overlapping pregnancies of the dominant female (Figures 3.2 and 3.3). Three successful subordinate pregnancies were conceived while the dominant female was heavily pregnant with her first litter of the year and prior to the conception of the second annual litter by the dominant female. One successful subordinate pregnancy was conceived just three days prior to the conception of the dominant female's first litter of the year. Seven of eight pregnancies conceived by subordinate females while the dominant female was either non-pregnant or in her 1st trimester of pregnancy failed. Interfemale interbirth interval (Wald Chi-Square=0.24, df=1, p=0.6275) (Table 3.2) and group size (Wald Chi-Square=0.79, df= 1, p=0.3755) were removed from the model as non-significant predictor variables in the order stated. Continuing past this point with backward selection of non-significant terms resulted in a non-significant model (Likelihood Ratio Chi-Square=2.28, df=1, p=0.1307) without any statistically significant predictor variables.

Effect of caloric availability on reproduction

Average monthly caloric availability (Wald Chi-Square=1.14, df=1, p=0.2866) (Table 3.2) was a non-significant predictor of a successful pregnancy, and the logistic regression model containing caloric availability as an explanatory variable was non-significant (Likelihood Ratio Chi-Square=0.11, df=1, p=0.7446).

DISCUSSION

Hormonal control of subordinate reproduction

As predicted by the hypothesis of incomplete control, reproduction in subordinate adult female GLTs was not limited by hormonal suppression. Whereas subordinate females younger than 2.5 years of age ovulated but did not become pregnant, all GLT females older than 3.9 years of age became pregnant. Saltzman et al. (1996, 1997a) suggested that older subordinate females may be released from hormonal suppression. If so, progesterone concentrations should increase with age. Progesterone controls cyclical follicular development leading to ovulation and maintains the uterine lining for implantation after conception (Ojeda, 1996). In pregnant females, placental progesterone maintains pregnancy by inhibiting uterine contractions, inhibiting prostaglandin (thereby inhibiting parturition), and blocking the cellular immune response that would otherwise attack the fetus residing within the uterus as a foreign body (Carr, 1996). Thus, an increase in circulating progesterone concentrations in older subordinate females may increase the likelihood of conception and successful pregnancy. To test the relationship statistically between age and progesterone concentrations while non-pregnant and during each of the three trimesters of pregnancy, I performed a *post hoc* linear mixed model ANOVA (GLIMMIX procedure) in SAS 9.2. I included dominance status, maternal age, age of the dominant female in the group, and group size as explanatory variables. I removed non-significant variables one at a time by backward selection. The dataset consisted of monthly average PdG concentrations while non-pregnant (n=179 PdG averages, from 18 females), during the 1st (n=65, 14), 2nd (n=65, 14), and 3rd (n=58, 14) trimester of pregnancy. FEMID was included as the subject within the random home

range effect (HR(FEMID)) as a covariate in the model, but removed if the covariance parameter associated with it was 0. I also controlled for the possible correlation between data points from the same pregnancy by including the identity of each pregnancy by an individual female as a covariate in the model (PREGID(FEMID)). I controlled for individual non-pregnant baseline differences in PdG among females in this analysis by including baseline PdG concentrations (AVG_NP_PDG) in the model when testing for effects during the three trimesters of pregnancy, but not during non-pregnant periods. A log transformation was performed as necessary to meet normality requirements prior to analysis. Maternal age did not significantly affect either non-pregnant or pregnant progesterone concentrations in adult GLT females.

The switch from non-reproductive to reproductive status in subordinate GLT females around three years of age was not due to an age-related release from hormonal suppression. Since subordinate GLT females experience normal ovulatory cycles typical of reproductive females beginning at approximately 18 months of age (French, 1987; French & Stribley, 1987; French et al., 1989; Inglett, 1993; Monfort et al., 1996; French et al., 2002) (Chapter 2, this dissertation) and progesterone levels did not increase with age, subordinate females were apparently physiologically capable of reproducing well before three years of age. These results combined with the non-significant effect of maternal age on the likelihood of a pregnancy resulting in the birth of infants suggest that once normal ovulatory cycles have been established in GLT females, hormonal competence to conceive and maintain a pregnancy does not change with age. Subordinate adult females from 1.5-3 years of age do not reproduce though they appear to have the endocrine basis to do so. In chapter two of this dissertation I present evidence

supporting the idea that young subordinate GLT females restrain their own reproduction in response to the threat of eviction posed by a young dominant female and to avoid inbreeding.

Behavioral control of subordinate reproduction

As predicted by the hypothesis of incomplete dominant control and consistent with the findings of French et al. (2003), older subordinate GLT daughters conceive within their natal groups and some reproduce successfully. All subordinate daughters over 3.9 years of age mated and became pregnant regardless of the age of the dominant female or the presence of a non-related male in the group (Dietz & Baker, 1993; Baker et al., 2002). Four pregnancies by two subordinate adult females in two groups resulted in the birth of live young. Pregnancy loss among older subordinate females ultimately limited the production of live offspring to a single dominant female in the majority of GLT groups. Unable to prevent ovulation and conception by older subordinate daughters, dominant females may interfere in some subordinate pregnancies. In polygynous groups, only subordinate females lost pregnancies. A pregnancy by a dominant female was 40 times more likely to result in the birth of live infants than a pregnancy by a subordinate female, and 7 of 11 pregnancies by subordinate females failed to produce live young. Higher reproductive success in dominant individuals has been repeatedly documented in cooperatively breeding birds (Koenig & Dickinson, 2004) and mammals (Digby, 1995a; Solomon & French, 1997a; Hodge et al., 2008; Saltzman et al., 2008; Saltzman et al., 2009), but the mechanisms responsible for maintaining high reproductive skew vary.

Stress in subordinate females

Chronic stress as the result of aggression by the dominant female directed toward the subordinate does not appear to be the cause of abortions in either captive or wild callitrichids (Smith & French, 1997b; Saltzman et al., 1998; Bales et al., 2005; Saltzman et al., 2009). In contrast with the ICM prediction that subordinates must win a struggle with the dominant female in order to reproduce successfully, subordinate female GLTs did not appear to be under high levels of social stress as measured by non-pregnant and 1st trimester cortisol concentrations. Instead, subordinates that succeeded in reproducing may have been allowed to do so by dominant females without a fight as predicted under the hypothesis of optimal skew. Lower cortisol concentrations during the 1st trimester (an indicator of reduced stress (Smith & French, 1997a)) combined with higher cortisol concentrations during both the 2nd and 3rd trimesters (characteristic of normal fetal development (Bales et al., 2005; Tardif et al., 2005; Power et al., 2006)) were loosely predictive of a successful pregnancy. Failed pregnancies did not differ significantly from successful pregnancies in their starting non-pregnant cortisol levels, nor in cortisol concentrations during the 1st trimester (Figure 3.1). Data from my study provide no evidence in support of the hypothesis that dominant aggression culminated in pregnancy loss in subordinate GLT females.

To test for a statistical relationship between dominance status and circulating cortisol concentrations, I performed another *post hoc* linear mixed model ANOVA. The analysis was identical to the GLIMMIX procedure with backward selection described above for PdG, but the dataset consisted of monthly average cortisol concentrations while non-pregnant (n=176 cortisol averages, from 18 females), during the 1st (n=65, 14), 2nd

(n=65,14), and 3rd (n=58, 14) trimester of pregnancy. In contrast to predictions derived from ICM where subordinate females should be under high levels of social stress (Abbott et al., 2003), I found that monthly average cortisol concentrations in subordinate females were not significantly different than cortisol concentrations in dominant females while non-pregnant or during any trimester of pregnancy. Though some species intensify the aggression directed toward subordinates upon attempts to reproduce (Wasser & Starling, 1988; Margulis et al., 1995; Scheibler et al., 2006; Young et al., 2006), this does not appear to be true for wild GLTs. My results are consistent with previous reports whose authors concluded that subordinate females attempting to breed alongside a dominant were not subject to chronic stress due to receipt of aggression from the dominant (GLTs: (Bales et al., 2005); saddle-back tamarins: (Goldizen et al., 1996); common marmosets: (Saltzman et al., 1997c; Abbott et al., 2003; Saltzman et al., 2004; Alencar et al., 2006; Saltzman et al., 2008; Saltzman et al., 2009); mandrills: (Setchell et al., 2008); and meerkats: (Young et al., 2008)).

An increasing number of studies of cooperative breeders have revealed that glucocorticoid concentrations in subordinates are either similar to or lower than that of dominant individuals (cotton-top tamarins: (Ziegler et al., 1995); common marmosets: (Saltzman et al., 1998); Wied's black tufted-ear marmosets: (Smith & French, 1997b); dwarf mongooses: (Creel et al., 1992; Creel et al., 1996); meerkats: (Carlson et al., 2004); African wild dogs: (Creel et al., 1996; Creel et al., 1997); gray wolves: (Sands & Creel, 2004); Harris' hawks: (Mays et al., 1991); and Florida scrub jays: (Schoech et al., 1991)). Many of the species that do not show elevated hypothalamo-pituitary-adrenal (HPA) activity in the form of elevated glucocorticoid concentrations in subordinates are

cooperative breeders that exhibit high reproductive skew (Solomon & French, 1997b). Where constraints upon subordinates are expected to be high, reduced HPA sensitivity may be an adaptation (Solomon & French, 1997b; Saltzman et al., 1998) that allows non-reproductive helpers to avoid the costs and potentially harmful consequences associated with mounting a chronic stress response (Munck et al., 1984; Sapolsky, 1992; Wingfield, 1994; Sapolsky, 2000; Sapolsky, 2002; Nelson, 2005). An alternative explanation worthy of consideration is that dominant females may also experience high levels of stress as a consequence of imposing reproductive restrictions upon subordinates (Creel, 2005). If asserting dominance is as stressful as being dominated, then cortisol concentrations between dominants and subordinates would not differ.

Age of the dominant female affects subordinate reproduction

In support of hypotheses of incomplete control and optimal skew, successful reproduction by subordinate female GLTs occurred only in groups where the dominant female was at least 10 years old. The likelihood of a pregnancy by a subordinate female resulting in the birth of live young doubled with each year of age of the dominant female. The mean age of the dominant female during a non-successful pregnancy by a subordinate was 6.4 years as compared to 10.9 years during a successful pregnancy by a subordinate. One assumption of incomplete control models is that elderly dominant females are either behaviorally or hormonally unable to prevent subordinate reproduction (Barrett et al., 1990; Abbott et al., 1993; Barrett et al., 1993; Smith & Abbott, 1995; Abbott et al., 1997; Abbott et al., 1998; Clutton-Brock et al., 2001a; French et al., 2003; Clutton-Brock et al., 2008; Hodge et al., 2008; Tardif et al., 2008). Based upon a reduction in GLT body mass with age (Dietz et al., 1994; Bales et al., 2002) and

increased incidences of subordinate reproduction in groups with an elderly dominant female, French et al. (2003) suggested that an elderly dominant female may be physically unable to control subordinate reproduction either through eviction or aggressive harassment. However, results from my study as well as those from Bales et al. (2005) indicate that stress and inter-group aggression are low among wild GLT groups, and fighting between dominant and subordinate females does not appear to limit subordinate reproduction. In the *post hoc* linear mixed model ANOVA testing for demographic effects on maternal cortisol described above, I found that the age of the dominant female in the group had a significant effect on cortisol concentrations of non-pregnant females in the same group (F-value=6.35, ddf=15.68, p=0.0230). As the dominant female in the group aged, her non-pregnant cortisol concentrations as well as those of other adult females in the group decreased significantly. These results suggest that conditions are less stressful among females when the dominant female is old, perhaps because elderly dominants lose the ability to evict their daughters from the natal group.

The ability of elderly dominant females to exert hormonal control over the outcome of subordinate pregnancies already in progress may also be reduced. Significant reductions in progesterone during late pregnancy can lead to pre-term abortion (Carr, 1996), as demonstrated by the fact that failed GLT pregnancies had significantly lower concentrations of PdG during the 3rd trimester than did pregnancies that resulted in the birth of live young (Chapter 1, this dissertation). According to the *post hoc* linear mixed model ANOVA designed to examine demographic effects on maternal PdG concentrations, age of the dominant female in a group had a marginally significant effect on PdG concentrations during the 3rd trimester of pregnancies within the group (F-value=

3.19, $ddf=21.32$, $p=0.0883$). Pregnant subordinate GLT females occupying groups with older dominant females tended to have higher 3rd trimester PdG concentrations. This relationship may result from the reduced ability of elderly dominants to interfere with subordinate pregnancy via this hormonal pathway.

In contrast with OSM predictions, my data suggest that elderly dominant females that allow subordinate reproduction to secure a breeding position for their daughter and that provide allocare for their grandoffspring do not increase their inclusive fitness. In those species where reproductive senescence renders females of advanced age incapable of reproducing, providing care for offspring as well as grandoffspring may be their only means of further increasing their inclusive fitness (Hawkes et al., 1997). However, in the current study and that of Bales et al. (2001) elderly GLT females showed no signs of reproductive senescence (but see Caro et al. (1995) for evidence of decreased fertility in older captive GLTs). Neither progesterone concentrations nor the likelihood of having a successful pregnancy decreased with age. The two eldest females in the study (GLT720=12.3 and GLT539=13.3 years old at the end of the study) conceived and carried their pregnancies to full term throughout the study (Figures 3.2 and 3.3). However, after a single reproductive season during which both the subordinate daughter and the dominant mother successfully reproduced, the 13.3 year old female was replaced as the dominant reproductive female by her daughter (Figure 3.3). Though the elderly female carried two more endocrinologically healthy pregnancies to full-term, both pregnancies were lost near the projected parturition date. Following the loss of her own infants, the elderly female carried and nursed her daughter's infants. This elderly female capable of reproduction should have received a larger fitness benefit by reproducing

rather than by foregoing her own reproduction and assisting in her daughter's reproductive efforts (Emlen, 1995).

Timing of subordinate reproduction

Successfully reproducing subordinate daughters staggered the arrival of their single annual litter between the two annual litters of their dominant mother by conceiving while their mother was heavily pregnant with her first litter of the year (Figures 3.2 and 3.3). Subordinate females were not more likely to conceive while the dominant female was heavily pregnant as predicted if subordinate females were temporarily released from hormonal suppression when the dominant female was in late pregnancy (Puffer et al., 2004) or if heavily pregnant dominant females were physically unable (Evans & Poole, 1984; Price, 1992b; Miller et al., 2006) to interfere with conceptions at this time.

However, if a subordinate conceived while the dominant female was heavily pregnant with her first litter of the year and prior to conception of the second litter by the dominant female, her pregnancy was more likely to result in the birth of live young. Though subordinates conceived eight pregnancies while the dominant female was either non-pregnant or in her 1st trimester of pregnancy, only one of these pregnancies resulted in the birth of live infants. In contrast, all three subordinate pregnancies conceived while the dominant female was heavily pregnant (in her 3rd trimester) produced live young.

Pregnancies by subordinate females conceived while the dominant female was heavily pregnant with her first litter of the year and prior to conception of her second litter of the year may have succeeded because they were protected from dominant aggression during the most vulnerable stages. Two successful pregnancies by one subordinate female were conceived 9 days prior to the birth of the dominant female's first

litter of the year, and 17 days prior to the conception of the second pregnancy of the year by the dominant female (Figure 3.2). In another group, a subordinate daughter conceived her pregnancy 26 days prior to the birth of the dominant female's first litter of the year, and 35 days prior to the conception of the second pregnancy of the year by the dominant female (Figure 3.3). Thus, the infants of these subordinate females were born 17, 17, and 35 days (IFIBIs) prior to the infants of the second litter of the dominant female. Timed as such the embryonic and early fetal phases of subordinate pregnancies, when the risk of prenatal mortality is highest in callitrichids (Windle et al., 1999), overlapped with late pregnancy in the dominant female. Perhaps more important in ensuring that a subordinate pregnancy resulted in the birth of live young was that the dominant female was also heavily pregnant during late pregnancy and parturition by the subordinate female. At this late stage when the subordinate female may have been less able to defend herself or her newborn offspring, the dominant female was also carrying a heavy energetic burden and suffers increased risks of injury or pregnancy loss upon fighting (Leutenegger, 1973; Lunn, 1983; Evans & Poole, 1984; Kirkwood & Underwood, 1984; Price, 1992b; Miller et al., 2006).

Alternatively, subordinate pregnancies staggered between those of the dominant female may succeed because they present little competition for resources and allocare for the dominant's litter (Digby, 1995a; Goldizen et al., 1996; Clutton-Brock et al., 2008). Upon the birth of appropriately timed subordinate litters, the dominant's first litter of the year has already been weaned and is largely independent in terms of nutrition and locomotion (Baker, 1991; Ruiz-Miranda et al., 1999; Tardif et al., 2002; Siani, 2009). The second litter by the dominant will be cared for almost entirely by their mother for the

first three weeks of life (Hoage, 1978; Baker, 1991; Santos et al., 1997; Tardif et al., 2002). By the time the second litter by the dominant relies heavily upon allocaregivers, the subordinate female's litter will be five to eight weeks old. At eight weeks of age infants are capable of independent movement and the amount of time allocaregivers spend in transporting infants drops by at least half (Hoage, 1978; Baker, 1991; Santos et al., 1997; Tardif et al., 2002). Timed as such, allocaregivers are not overburdened with the transport of four completely dependent infants at the same time (Goldizen et al., 1996).

Subordinate pregnancies fail when they are not timed appropriately. Seven of the eleven pregnancies detected in subordinate females failed to produce live infants. In three cases, births to subordinates would have occurred less than two weeks prior to births by dominant females (within one day for two failed pregnancies, and within eight days for one failed pregnancy). Additionally, two subordinate pregnancies were lost that would have resulted in the birth of infants during the post-partum estrus of the dominant female. The litter of the subordinate female would have arrived just as the dominant mother relinquished her leading role in infant care to other group members. Competition for allocare would have been extremely high if these five subordinate pregnancies had succeeded. A single subordinate pregnancy was lost that would have resulted in infant birth in July when cold temperatures increase the energetic demands of pregnancy and thermoregulation (Thompson et al., 1994).

Ecological constraints on subordinate reproduction

Group size limits the number of females that successfully reproduce in a reproductive season. Group size was a significant predictor of a successful pregnancy,

but not in the direction predicted by OSM. Rather than dominant females offering reproduction to subordinates more often when there were fewer potential allocaregivers and the relative contribution made by each additional member to dominant fitness was higher (Dietz & Baker, 1993; Reeve & Emlen, 2000; Dietz, 2004; Clutton-Brock et al., 2008), polygyny was more common in large GLT groups. With the addition of each group member, the likelihood of a successful pregnancy increased 1.7 times. Female breeding success in cooperatively breeding meerkats also increases with group size, as group size is positively related to fecundity and pup survival (Hodge et al., 2008). The only subordinate female to reproduce successfully within her natal group for more than a single reproductive season resided within the largest GLT group studied (mean of 9.3 individuals compared to a mean of 4.3 individuals for all other groups). Both the dominant mother and her subordinate daughter reproduced successfully throughout the study (Figure 3.2). Multiple breeding females lead to larger groups, but larger groups also provide the support necessary to care for four infants that arrive during the same reproductive season. Subordinate females in groups with fewer individuals fail to reproduce. The elderly female replaced by her daughter as the reproductive dominant (Figure 3.3) was not ejected from the group; her reproductive attempts were non-successful as she remained in the group as one of only two potential allocaregivers for her daughter's infants.

When caloric availability is sufficient to support not only reproduction by two breeding females but also the group members necessary to provide allocare for two litters, subordinate females do not abide by a social contract that would limit their reproduction (Chapter 1, this dissertation). Low caloric availability within the home

range was not associated with higher reproductive success in subordinates in contrast with the OSM prediction (Reeve & Nonacs, 1992; Reeve & Ratnieks, 1993). Caloric availability did not significantly affect the likelihood of a successful pregnancy in GLTs perhaps because caloric availability in all home ranges was more than adequate to support GLT reproduction during all months of each of the three reproductive years studied (Chapter 1, this dissertation). Under conditions of high caloric availability both within and outside the GLT ranges studied, dominant females were neither more nor less likely to offer reproduction to subordinates. Instead, older subordinates competed with dominant females for reproduction and succeeded in producing live young if the dominant female was at least 10 years old, if subordinates conceived while the dominant was heavily pregnant resulting in staggered births, and if groups contained more individuals over which to distribute infant care.

ACKNOWLEDGEMENTS

Funding for this project was provided by the American Society of Mammalogists, the Copenhagen Zoo Lion Tamarins of Brazil Fund, the University of Maryland Center for Biodiversity, a Darwin Fellowship from the University of Maryland BEES Program, and a Wylie Dissertation Fellowship from the University of Maryland Graduate School to M. Henry and by the National Science Foundation (SBR-9727687; BCS-0216096) to J. Dietz. I thank the Brazilian Science Council (CNPq), Brazilian Institute for the Environment and Renewable Natural Resources (IBAMA), and Golden Lion Tamarin Association (AMLD) for logistic support and permission to conduct this study. This research complies with the guidelines of the University of Maryland Animal Care and Use Committee and all applicable Brazilian laws. Importation of fecal samples into the

U.S. was conducted under the auspices of CITES, USDA, and CDC. Special thanks to Jim Dietz and Jeff French for their guidance and support throughout this project. I thank Ecología research assistants Otávio Narciso, Synval de Melo, Jadir Ramos, and Andréia Martins for help with data collection in the field. A special thanks to Ademilson de Oliveira who taught me to identify Brazilian plant species and helped me set up phenological transects. I thank Jeff Fite, Kate Townley, and Tom Shirazi for assistance with endocrine analyses. Thanks to Jennifer Siani for tamarin weights and Kimran Miller-Buckholz for plant species identifications, dry weights, and caloric values. I sincerely appreciate the work done by Sarah Hankerson mapping habitat data and performing statistical analyses. I thank Karen Bales for setting the precedent for endocrine work in this population of tamarins.

TABLES

Table 3.1. Summary of reproductive and demographic data for 21 GLT females from 7 free-ranging GLT groups sampled from March of 2004 through February of 2007.

Group	Poly-gynous group	Female ID	Dominance status	Relation in group	Age (years) during sample collection	Age (years) at first conception if during study	Successful and failed pregnancies		Fecal samples
3M5	N	782	Dominant	Only female	4.5-6.7		0	1	32
AL	Y	539	Dominant then subordinate	Mother	10.6-13.3		2	2	97
AL	Y	846	Subordinate then dominant	Daughter	2.8-5.3	2.9	3	0	78
AL	Y	1267	Subordinate	Daughter	0.2-1.3	Did not conceive	0	0	21
BO2	Y	720	Dominant	Mother	9.4-12.3		6	0	125
BO2	Y	848	Subordinate	Daughter	2.4-5.3	2.5	3	2	136
BO2/POR	Y/N	880	Subordinate/dominant	Daughter/sister	1.4-4.1	2.8	3	0	88
BO2/POR	Y/N	899	Subordinate	Daughter/sister	1.1-2.4	Did not conceive	0	0	39
BO2/POR	Y/N	1227	Subordinate	Daughter/sister	0.7-2.9	Did not conceive	0	0	68
BO2/POR	Y/N	1241	Subordinate	Daughter/sister	0.8-2.0	Did not conceive	0	0	52
GF	Y	766	Dominant	Mother	5.6-6.9		2	0	35
GF	Y	889	Subordinate	Daughter	1.6-3.0	2.5	0	1	18
GF	N	1266	Dominant	Only female	2.9-4.0	3.4	1	0	32
PA	Y	869	Dominant	Sister	4.7-7.3		4	0	98
PA	Y	884	Subordinate	Sister	1.7-3.3	2.7	0	1	60
PA	Y	1271	Subordinate	Daughter	0.4-1.4	Did not conceive	0	0	32
PP3	N	750	Dominant	Mother	8.7-10.5		1	3	77
PP3	N	1238	Subordinate	Daughter	0.3-1.9	Did not conceive	0	0	56
PP3	Y	1264	Dominant	Sister	4.0-4.3	3.9	1	0	12
PP3	Y	1265	Subordinate	Sister	3.3-4.2	3.9	0	1	10
PP3	N	T0PP3	Dominant	Unknown	Unknown (adult)	Did not conceive	0	0	10
						$\bar{x} = 3.1 \pm 0.2$	$\Sigma = 26$	$\Sigma = 11$	$\Sigma = 1176$

Table 3.2. Summary of the predictions generated by reproductive skew models and empirical findings in golden lion tamarins. (Bold italics indicate predictions consistent with findings in golden lion tamarins. See text for explanations and additional details.)

Predictions	Incomplete control	Optimal skew	Findings in golden lion tamarins
Subordinate adult females ovulate.	yes	few	yes, all ovulate beginning at approximately 18 months of age
Subordinates adult females conceive.	yes	few	yes, all conceive by 3.9 years of age (mean age at first conception=3.1 ± 0.2 years)
Pregnancies by dominant females are more likely to succeed than pregnancies by subordinates.	yes	yes	yes, dominants are 40.4x as likely to have successful pregnancies (Wald Chi-Square=7.69, df=1, p=0.0055)
Pregnancies with lower cortisol levels just prior to conception and during the 1 st trimester are more likely to succeed.	no, higher	yes	yes, lower 1 st trimester cortisol combined with higher 2 nd and 3 rd trimester cortisol were marginally significant predictors of success (Likelihood Ratio Chi-Square=8.73, df=4, p=0.0681)
Pregnancies by older subordinate females are more likely to succeed.	yes	no prediction	no, conceptions are more common after 3.1 years of age, but once pregnant the age of the female does not affect the likelihood of her giving birth to live young (Wald Chi-Square=2.12, df=1, p=0.1452)
Pregnancies in groups containing an older dominant female are more likely to succeed.	yes	yes	yes, likelihood of subordinate success doubles with each year of age of the dominant female (Likelihood Ratio Chi-Square=4.98, df=2, p=0.0829 when model also includes a heavily pregnant dominant female)
Pregnancies conceived while the dominant female is heavily pregnant with her first litter of the year are more likely to succeed.	yes	no prediction	yes (Likelihood Ratio Chi-Square=4.98, df=2, p=0.0829 when model also includes an elderly dominant female)
Pregnancies with longer interfemale interbirth intervals are more likely to succeed.	no prediction	yes	no (Wald Chi-Square=0.24, df=1, p=0.6275)
Pregnancies under lower caloric availability are more likely to succeed.	no prediction	yes	no (Wald Chi-Square=1.14, df=1, p=0.2866)
Pregnancies in smaller groups are more likely to succeed.	no prediction	yes	no, larger groups are more successful; for each additional group member the likelihood of a successful pregnancy by a dominant or a subordinate female increases 1.7 times (Wald Chi-Square=4.52, df=1, p=0.0335)

FIGURE LEGENDS

Figure 3.1. Mean (\pm standard error) cortisol concentrations for successful vs. non-successful pregnancies just prior to conception (NP, n=32 pregnancies, 23 successful, 9 non-successful), during the 1st trimester (I, n=36, 26, 10), during the 2nd trimester (II, n=35, 25, 10), and during the 3rd trimester of pregnancy (III, n=31, 23, 8). Differences in means were not statistically significant according to linear mixed model analysis of variance.

Figure 3.2. Progesterone (PdG) profiles for a dominant mother (GLT720) and her subordinate daughter (GLT848) demonstrating that conceptions by the subordinate while the dominant female was heavily pregnant with her first litter of the year and prior to conception of the second litter by the dominant female were more likely to result in the birth of live infants. Green arrows indicate dates of conceptions resulting in the birth of live young (subsequent red arrow). Blue arrows indicate conceptions that resulted in pregnancy loss. Red arrows indicate successful parturition dates. Note that the first two successful infant births by GLT848 (red arrows) occur between the birth of the first (red arrow in September) and second (red arrow in January or February) annual litters by GLT720, resulting in the staggering of successful births to the subordinate daughter between births to the dominant mother.

Figure 3.3. Progesterone (PdG) profiles for the oldest female in the study (GLT539) and her eldest daughter (GLT846). GLT539 was dominant until after the birth of her second litter in February of 2005 when GLT846 became dominant. While subordinate to her mother, GLT846 conceived a successful litter while her mother was heavily pregnant with her first litter of the year. Pregnancies by GLT539 that were conceived at the same

time as those of her dominant daughter were lost at full term. Green arrows indicate dates of conceptions resulting in the birth of live young. Blue arrows indicate conceptions that resulted in pregnancy loss. Red arrows indicate successful parturition dates. Note that successful reproduction (red arrows) by two females during the same reproductive year occurred only when pregnancies were staggered.

FIGURES

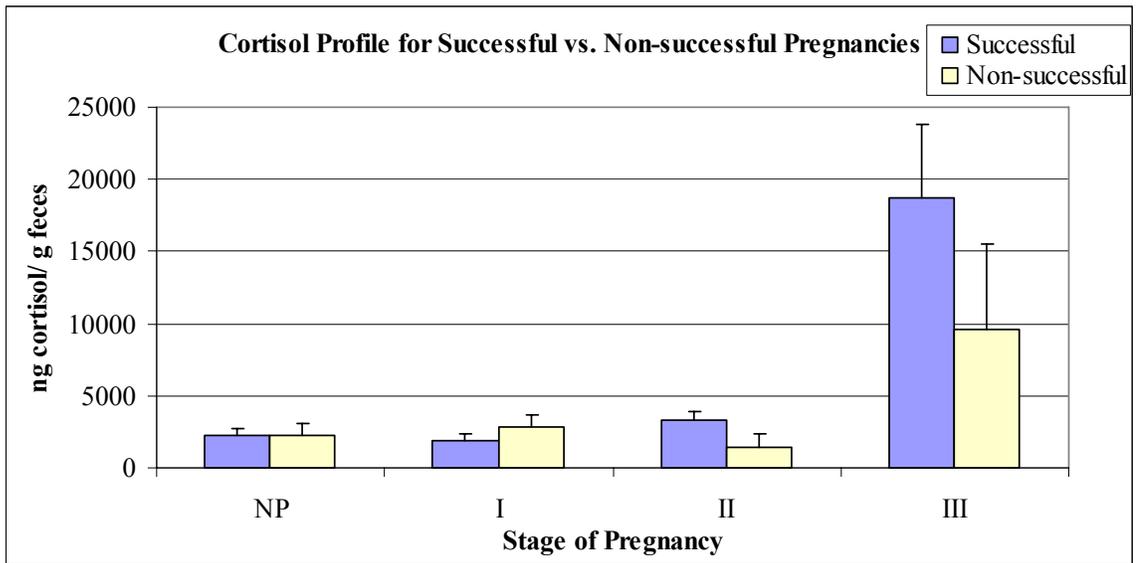


Figure 3.1.

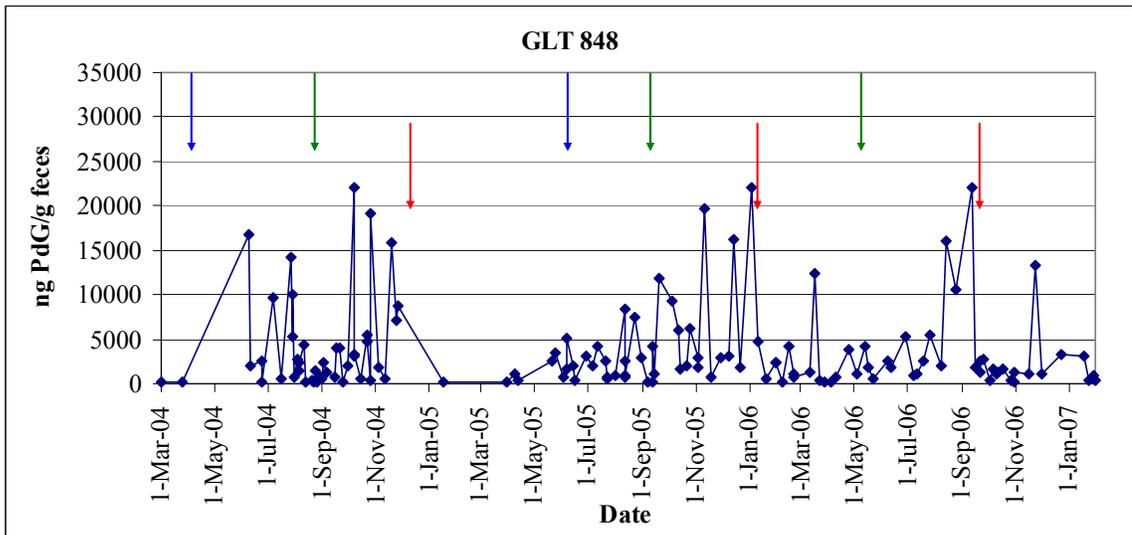
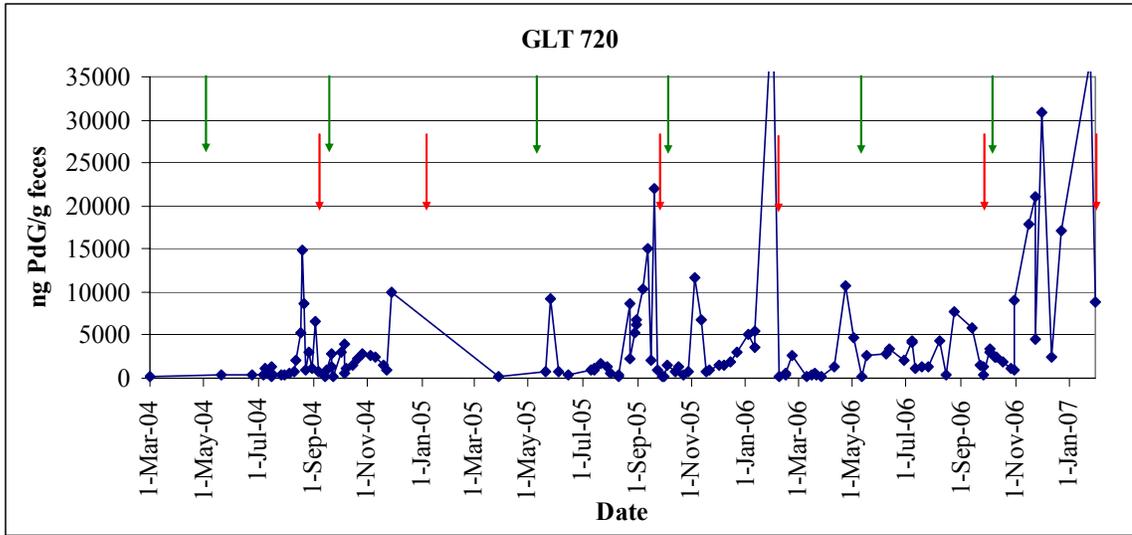


Figure 3.2.

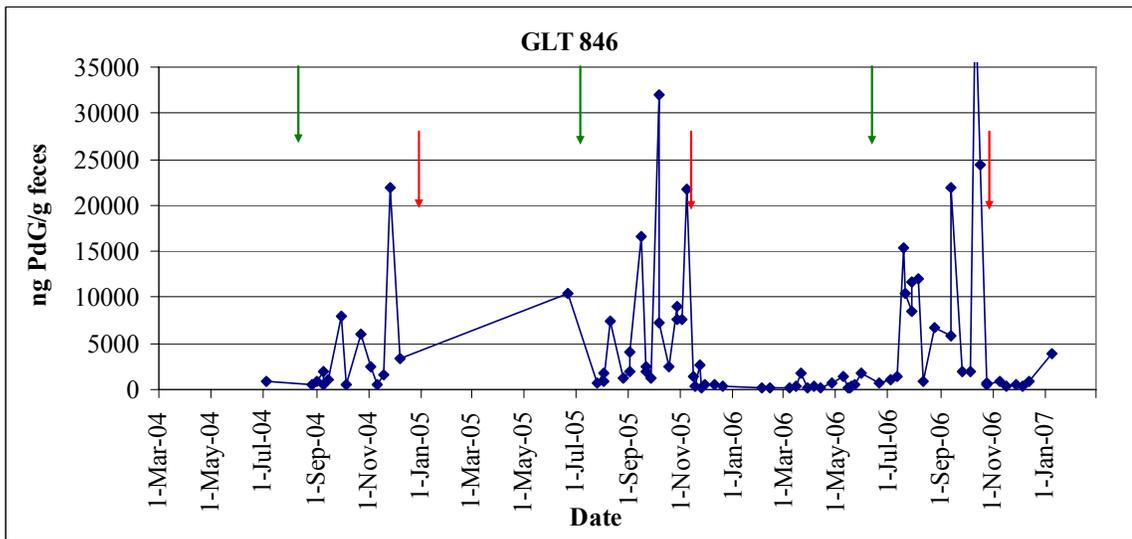
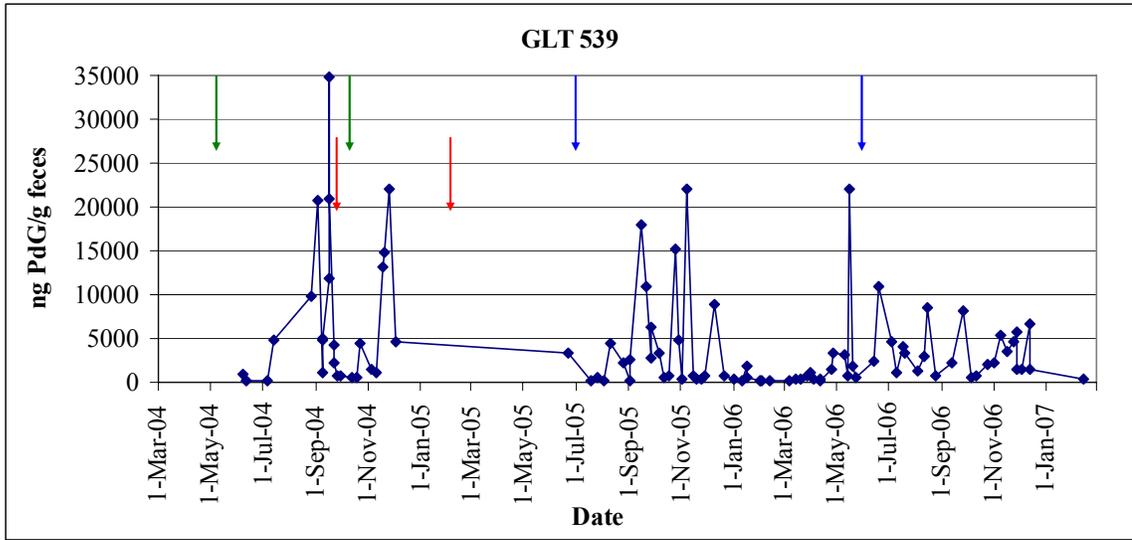


Figure 3.3.

BIBLIOGRAPHY

- Abbott, D. H. 1984. Behavioral and physiological suppression of fertility in subordinate marmoset monkeys. *American Journal of Primatology*, **6**, 169-186.
- Abbott, D. H. 1993. Social conflict and reproductive suppression in marmoset and tamarin monkeys. In: *Primate social conflict* (Ed. by Mason, W. A. & Mendoza, S. P.), pp. 331-372. Albany, NY: State University of New York Press.
- Abbott, D. H., Digby, L. J. & Saltzman, W. 2009. Reproductive skew in female marmosets: contributions of infanticide and subordinate self-restraint. In: *Reproductive skew in vertebrates: proximate and ultimate causes* (Ed. by Hager, R. & Jones, C. B.), pp. 337-368. Cambridge: Cambridge University Press.
- Abbott, D. H., Faulkes, C. G., Barrett, J., Smith, T. E. & Cheesman, D. J. 1993. Social control of female reproduction in marmoset monkeys and naked mole-rats. In: *Endocrine and nutritional control of basic biological functions* (Ed. by Lehnert, H., Murison, R., Weiner, H., Hellhammer, D. & Beyer, J.), pp. 475-489. Seattle, WA: Hogrefe and Huber.
- Abbott, D. H. & George, L. M. 1991. Reproductive consequences of changing social status in female common marmosets. In: *Primate responses to environmental change* (Ed. by Box, H. O.). London, UK: Chapman and Hall.
- Abbott, D. H., George, L. M., Barrett, J., Hodges, K. T., O'Byrne, K., Sheffield, J. W., Sutherland, I. A., Chambers, G. R., Lunn, S. F. & Ruiz de Elvira, M. C. 1990. Social control of ovulation in marmoset monkeys: a neuroendocrine basis for the study of infertility. In: *Socioendocrinology of primate reproduction* (Ed. by Ziegler, T. E. & Bercovitch, F. B.), pp. 135-158. New York, NY: Wiley-Liss.

- Abbott, D. H. & Hearn, J. P. 1978. Physical, hormonal, and behavioural aspects of sexual development in the marmoset monkey, *Callithrix jacchus*. *Journal of Reproduction and Fertility*, **53**, 155-166.
- Abbott, D. H., Hodges, J. K. & George, L. M. 1988. Social status controls in LH secretion and ovulation in female marmoset monkeys (*Callithrix jacchus*). *Journal of Endocrinology*, **117**, 329-339.
- Abbott, D. H., Keverne, E. B., Bercovitch, F. B., Shively, C. A., Mendoza, S. P., Saltzman, W., Snowdon, C. T., Ziegler, T. E., Banjevic, M., Garland, T. & Sapolsky, R. M. 2003. Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. *Hormones and Behavior*, **43**, 67-82.
- Abbott, D. H., McNeilly, A. S., Lunn, S. F., Hulme, M. J. & Burden, F. J. 1981. Inhibition of ovarian function in subordinate female marmoset monkeys (*Callithrix jacchus jacchus*). *Journal of Reproduction and Fertility*, **63**, 335-345.
- Abbott, D. H., Saltzman, W., Schultz-Darken, N. & Smith, T. E. 1997. Specific neuroendocrine mechanisms not involving generalized stress mediate social regulation of female reproduction in cooperatively breeding marmoset monkeys. *Annals of the New York Academy of Sciences*, **807**, 219-238.
- Abbott, D. H., Saltzman, W., Schultz-Darken, N. & Tannenbaum, P. L. 1998. Adaptations to subordinate status in female marmoset monkeys. *Comparative Biochemistry and Physiology Part C Pharmacology Toxicology Endocrinology*, **119**, 261-274.

- Alberts, S. C., Watts, H. E. & Altmann, J. 2003. Queuing and queue-jumping: long-term patterns of reproductive skew in male savannah baboons, *Papio cynocephalus*. *Animal Behaviour*, **65**, 821-840.
- Albuquerque, A. C. S. R., Sousa, M. B. C., Santos, H. M. & Ziegler, T. E. 2001. Behavioral and hormonal analysis of social relationships between oldest females in a wild monogamous group of common marmosets (*Callithrix jacchus*). *International Journal of Primatology*, **22**, 631-645.
- Alencar, A. I., Sousa, M. B., Abbott, D. H. & Yamamoto, M. E. 2006. Contested dominance modifies the anovulatory consequences of social subordination in female marmosets. *Brazilian Journal of Medical and Biological Research*, **39**, 647-658.
- Altmann, J. 1980. *Baboon mothers and infants*. Cambridge: Harvard University Press.
- Altmann, J. & Alberts, S. C. 2003. Variability in reproductive success viewed from a life-history perspective in baboons. *American Journal of Human Biology*, **15**, 401-409.
- Altmann, J. & Alberts, S. C. 2005. Growth rates in a wild primate population: ecological influences and maternal effects. *Behavioral Ecology and Sociobiology*, **57**, 490-501.
- Anzenberger, G. 1985. How stranger encounters of common marmosets (*Callithrix jacchus jacchus*) are influenced by family members: the quality of behavior. *Folia Primatologica*, **45**, 204-224.

- Arnold, K. E. & Owens, I. P. F. 1998. Cooperative breeding in birds: a comparative test of the life history hypothesis. *Proceedings of the Royal Society of London B*, **265**, 739-745.
- Arruda, M. F., Araujo, A., Sousa, M. B. C., Albuquerque, F. S., Albuquerque, A. C. S. R. & Yamamoto, M. E. 2005. Two breeding females withing free-living groups may not always indicate polygyny: alternative subordinate female strategies in common marmosets (*Callithrix jacchus*). *Folia Primatologica*, **76**, 10-20.
- Atsalis, S. & Margulis, S. W. 2008. Perimenopause and menopause: documenting life changes in aging female gorillas. In: *Primate reproductive aging. Interdisciplinary topics in gerontology* (Ed. by Atsalis, S., Margulis, S. W. & Hof, P. R.), pp. 119-146. Basel: Karger.
- Baanders-Van Halewin, E. A. & de Ward, F. 1968. Menstrual cycles shortly after menarche in European and Bantu girls. *Human Biology*, **40**, 314-322.
- Baker, A. J. 1991. Evolution of the social system of the golden lion tamarin (*Leontopithecus rosalia*): mating, group dynamics, and cooperative breeding. In: *Department of Biology*. College Park, MD: University of Maryland.
- Baker, A. J., Bales, K. L. & Dietz, J. M. 2002. Mating system and group dynamics in lion tamarins. In: *Lion tamarins: biology and conservation* (Ed. by Kleiman, D. G. & Rylands, A. B.), pp. 188-212. Washington, D.C.: Smithsonian Institution Press.
- Baker, A. J. & Dietz, J. M. 1996. Immigration in wild groups of golden lion tamarins (*Leontopithecus rosalia*). *American Journal of Primatology*, **38**, 47-56.

- Baker, A. J., Dietz, J. M. & Kleiman, D. G. 1993. Behavioural evidence for monopolization of paternity in multi-male groups of golden lion tamarins. *Animal Behaviour*, **46**, 1091-1103.
- Bales, K. L. 2000. Mammalian monogamy: dominance, hormones, and maternal care in wild golden lion tamarins. In: *Biology*. College Park, MD: University of Maryland.
- Bales, K. L., French, J. A. & Dietz, J. M. 2002. Explaining variation in maternal care in a cooperatively breeding mammal. *Animal Behaviour*, **63**, 453-461.
- Bales, K. L., French, J. A., Hostetler, C. M. & Dietz, J. M. 2005. Social and reproductive factors affecting cortisol levels in wild female golden lion tamarins (*Leontopithecus rosalia*). *American Journal of Primatology*, **67**, 25-35.
- Bales, K. L., O'Herron, M., Baker, A. J. & Dietz, J. M. 2001. Sources of variability in numbers of live births in wild golden lion tamarins (*Leontopithecus rosalia*). *American Journal of Primatology*, **54**, 211-221.
- Bardi, M., Petto, A. J. & Lee-Parriz, D. E. 2001. Parental failure in captive cotton-top tamarins (*Saguinus oedipus*). *American Journal of Primatology*, **54**, 159-169.
- Barrett, J., Abbott, D. H. & George, L. M. 1990. Extension of reproductive suppression by pheromonal cues in subordinate female marmoset monkeys, *Callithrix jacchus*. *Journal of Reproduction and Fertility*, **90**, 411-418.
- Barrett, J., Abbott, D. H. & George, L. M. 1993. Sensory cues and the suppression of reproduction in subordinate female marmoset monkeys, *Callithrix jacchus*. *Journal of Reproduction and Fertility*, **97**, 301-310.

- Bartholomew, G. A. & Rainey, M. 1971. Regulation of body temperature in the rock hyrax (*Heterohyrax brucei*). *Journal of Mammalogy*, **52**, 81-95.
- Bauwens, D. & Thoen, C. 1981. Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. *Journal of Animal Ecology*, **50**, 733-743.
- Beekman, M., Komdeur, J. & Ratnieks, F. L. W. 2003. Reproductive conflicts in social animals: who has the power? *Trends in Ecology and Evolution*, **18**, 277-282.
- Bekoff, M. & Wells, M. C. 1982. The behavioral ecology of coyotes: social organization, rearing patterns, space use, and resource defense. *Zeitschrift der Tierpsychologie*, **60**, 281-305.
- Bennett, N. C. & Faulkes, C. G. 2000. *African mole-rats: ecology and eusociality*. Cambridge: Cambridge University Press.
- Bernasconi, G. & Strassmann, J. E. 1999. Cooperation among unrelated individuals: the ant foundress case. *Trends in Ecology and Evolution*, **14**, 477-482.
- Boinski, S. 1987. Birth synchrony in squirrel monkeys (*Saimiri oerstedii*). *Behavioral Ecology and Sociobiology*, **21**, 393-400.
- Bojilen, K. & Bentzoin, M. 1968. Influence of climate and nutrition on age at menarche: a historical review and a modern hypothesis. *Human Biology*, **40**, 69-85.
- Borries, C. & Koenig, A. 2008. Reproductive and behavioral characteristics of aging in female Asian colobines. In: *Primate reproductive aging. Interdisciplinary topics in gerontology* (Ed. by Atsalis, S., Margulis, S. W. & Hof, P. R.), pp. 80-102. Basel: Karger.

- Bourke, A. F. G. 1999. Colony size, social complexity and reproductive conflict in social insects. *Journal of Evolutionary Biology*, **12**, 245-257.
- Brodie III, E. D. 1989. Behavioral modification as a means of reducing the cost of reproduction. *The American Naturalist*, **134**, 225-238.
- Bronson, F. H. 1989. *Mammalian reproductive biology*. Chicago, IL: University of Chicago Press.
- Brown, J. L. 1987. *Helping and communal breeding in birds*. Princeton: Princeton University Press.
- Brown, P. E. 1966. The age at menarche. *British Journal of Preventative and Social Medicine*, **20**, 9-14.
- Brugiere, D., Gautier, J.-P., Mounrazi, A. & Gautier-Hion, A. 2002. Primate diet and biomass in relation to vegetation composition and fruiting phenology in a rain forest in Gabon. *International Journal of Primatology*, **23**, 999-1024.
- Buston, P. M., Reeve, H. K., Cant, M. A., Vehrencamp, S. L. & Emlen, S. T. 2007. Reproductive skew and the evolution of group dissolution tactics: a synthesis of concession and restraint models. *Animal Behaviour*, **74**, 1643-1654.
- Bygott, J. D., Bertram, B. C. R. & Hanby, J. P. 1979. Male lions in large coalitions gain reproductive advantages. *Nature*, **282**, 838-840.
- Caine, N. G. 1987. Vigilance, vocalizations and cryptic behavior at retirement in captive groups of red-bellied tamarins (*Saguinus labiatus*). *American Journal of Primatology*, **12**, 241-250.
- Cant, M. A., Hodge, S. J., Bell, M. B. V., Gilchrist, J. S. & Nichols, H. J. 2010. Reproductive control via eviction (but not the threat of eviction) in banded

- mongooses. *Proceedings of the Royal Society Biological Sciences*, **277**, 2219-2226.
- Carey, J. R. 2001. Demographic mechanisms for the evolution of long life in social insects. *Experimental Gerontology*, **36**, 713-722.
- Carlson, A. A., Young, A. J., Russell, A. F., Bennett, N. C., McNeilly, A. S. & Clutton-Brock, T. H. 2004. Hormonal correlates of dominance in meerkats (*Suricata suricatta*). *Hormones and Behavior*, **46**, 141-150.
- Caro, T. M., Sellen, D. W., Parish, A., Frank, R., Brown, D. M., Volland, E. & Borgerhoff Mulder, M. 1995. Termination of reproduction in nonhuman and human female primates. *International Journal of Primatology*, **16**, 205-220.
- Carr, B. R. 1996. Fertilization, implantation, and endocrinology of pregnancy. In: *Textbook of endocrine physiology* (Ed. by Griffin, J. E. & Ojeda, S. R.), pp. 223-243. Oxford: Oxford University Press.
- Carter, C. S. & Roberts, R. L. 1997. The psychobiological basis of cooperative breeding in rodents. In: *Cooperative breeding in mammals* (Ed. by Solomon, N. G. & French, J. A.), pp. 231-266. Cambridge: Cambridge University Press.
- Cavigelli, S. A. 1999. Behavioural patterns associated with faecal cortisol levels in free-ranging female ring-tailed lemurs, *Lemur catta*. *Animal Behaviour*, **57**.
- Cavigelli, S. A., Dubovick, T., Levash, W., Jolly, A. & Pitts, A. 2003. Female dominance status and fecal corticoids in a cooperative breeder with low reproductive skew: ring-tailed lemurs (*Lemur catta*). *Hormones and Behavior*, **43**, 166-179.
- Challis, J. R. G., Matthews, S. G., Gibb, W. & Lye, S. J. 2000. Endocrine and paracrine regulation of birth at term and preterm. *Endocrine Reviews*, **21**, 514-550.

- Chapman, C. A. 1988. Patterns of foraging and range use by three species of neotropical primates. *Primates*, **29**, 177-194.
- Chapman, C. A., Chapman, L. J., Wrangham, R., Hunt, K., Gebo, D. & Gardner, L. 1992. Estimators of fruit abundance and tropical trees. *Biotropica*, **24**, 527-531.
- Charles-Dominique, P. 1977. Ecology and behaviour of nocturnal primates. In: *Prosimians of equatorial West Africa*. London: Duckworth.
- Chivers, D. J. & Raemaekers, J. J. 1980. Long -term changes in behaviour. In: *Malayan forest primates* (Ed. by Chivers, D. J.), pp. 209-260. New York: Plenum Press.
- Chrousos, G. P. & Gold, P. W. 1992. The concepts of stress and stress system disorders: overview of physical and behavioral homeostasis. *Journal of the American Medical Association*, **267**, 1244-1252.
- Clarke, F. M. & Faulkes, C. G. 1997. Dominance and queen succession in captive colonies of the eusocial naked mole-rat, *Heterocephalus glaber*. *Proceedings of the Royal Society of London B*, **264**, 993-1000.
- Clarke, F. M., Miethe, G. H. & Bennett, N. C. 2001. Reproductive suppression in female Damaraland mole-rats *Cryptomys damarensis*: dominant control or self-restraint? *Proceedings of the Royal Society of London B*, **268**, 899-909.
- Clutton-Brock, T. H. 1998. Reproductive skew, concessions and limited control. *Trends in Ecology and Evolution*, **13**, 288-292.
- Clutton-Brock, T. H. 2006. Cooperative breeding in mammals. In: *Cooperation in primates and humans* (Ed. by Kappeler, P. M. & Van Schaik, C. P.), pp. 173-190. Berlin: Springer Verlag.

- Clutton-Brock, T. H. 2009. Structure and function in mammalian societies. *Philosophical Transactions of the Royal Society of Biological Sciences*, **364**, 3229-3242.
- Clutton-Brock, T. H., Brotherton, P. N. M., Russell, A. F., O'Riain, M. J., Gaynor, D., Kansky, R., Griffin, A., Manser, M., Sharpe, L., McIlrath, G. M., Small, T., Moss, A. & Monfort, S. L. 2001a. Cooperation, control, and concession in meerkat groups. *Science*, **291**, 478-481.
- Clutton-Brock, T. H., Brotherton, P. N. M., Smith, R., McIlrath, G. M., Kansky, R., Gaynor, D., O'Riain, M. J. & Skinner, J. D. 1998a. Infanticide and expulsion of females in a cooperative mammal. *Proceedings of the Royal Society of London, Series B*, **265**, 2291-2295.
- Clutton-Brock, T. H., Gaynor, D., Kansky, R., MacColl, A. D. C., McIlrath, G. M., Chadwick, P., Brotherton, P. N. M., O'Riain, J. M., Manser, M. & Skinner, J. D. 1998b. Costs of cooperative behaviour in suricates (*Suricata suricata*). *Proceedings of the Royal Society of London B*, **265**, 185-190.
- Clutton-Brock, T. H., Hodge, S. J. & Flower, T. P. 2008. Group size and the suppression of subordinate reproduction in Kalahari meerkats. *Animal Behaviour*, **76**, 689-700.
- Clutton-Brock, T. H., Hodge, S. J., Spong, G., Russell, A. F., Jordan, N. R., Bennett, N. C., Sharpe, L. L. & Manser, M. B. 2006. Intrasexual competition and sexual selection in cooperative mammals. *Nature*, **444**, 1065-1068.
- Clutton-Brock, T. H., Russell, A. F., Sharpe, L., Brotherton, P. N. M., McIlrath, G. M., White, S. & Cameron, E. Z. 2001b. Effects of helpers on juvenile development and survival in meerkats. *Science*, **293**, 2446-2449.

- Coimbra-Filho, A. F. 1977. Natural shelters of *Leontopithecus rosalia* and some ecological implications (Callitrichidae: Primates). In: *The biology and conservation of the Callitrichidae* (Ed. by Kleiman, D. G.), pp. 79-89. Washington, D.C.: Smithsonian Institution Press.
- Comuzzie Crowell, D. K. & Owens, D. W. 1990. A quantitative analysis of courtship behavior in captive green sea turtles (*Chelonia mydas*). *Herpetologica*, **46**, 195-202.
- Contreras, L. C. 1984. Bioenergetics of huddling: test of the psycho-physiological hypothesis. *Journal of Mammalogy*, **65**, 256-262.
- Corbett, L. K. 1988. Social dynamics of a captive dingo pack: population regulation by dominant female infanticide. *Ethology*, **78**, 177-198.
- Coulter, C. L. & Jaffe, R. B. 1998. Functional maturation of the primate fetal adrenal in vivo: 3. Specific zonal localization and developmental regulation of CYP21A2 (P450c21) and CYP11B1/CYP11B2 (P450c11/aldosterone synthase) lead to integrated concept of zonal and temporal steroid biosynthesis. *Endocrinology*, **139**, 5144-5150.
- Creel, S. R. 2005. Dominance, aggression, and glucocorticoid levels in social carnivores. *Journal of Mammalogy*, **86**, 255-264.
- Creel, S. R. & Creel, N. M. 1991. Energetics, reproductive suppression and obligate communal breeding in carnivores. *Behavioral Ecology and Sociobiology*, **28**, 263-270.
- Creel, S. R. & Creel, N. M. 2001. *The African wild dog: behavior, ecology and conservation*. Princeton, NJ: Princeton University Press.

- Creel, S. R., Creel, N. M., Mills, G. L. & Monfort, S. L. 1997. Rank and reproduction in cooperatively breeding African wild dogs: behavioral and endocrine correlates. *Behavioral Ecology*, **8**, 298-306.
- Creel, S. R., Creel, N. M. & Monfort, S. L. 1996. Social stress and dominance. *Nature*, **379**, 212.
- Creel, S. R., Creel, N. M., Wildt, D. E. & Monfort, S. L. 1992. Behavioral and endocrine mechanisms of reproductive suppression in Serenge dwarf mongooses. *Animal Behaviour*, **43**, 231-245.
- Creel, S. R. & Waser, P. M. 1991. Failures of reproductive suppression in dwarf mongooses (*Helogale parvula*): accident or adaption. *Behavioral Ecology*, **2**, 7-15.
- Creel, S. R. & Waser, P. M. 1997. Variation in reproductive suppression among dwarf mongooses: interplay between mechanisms and evolution. In: *Cooperative breeding in mammals* (Ed. by Solomon, N. G. & French, J. A.), pp. 150-198. Cambridge: Cambridge University Press.
- Crockett, C. M. & Rudran, R. 1987. Red howler monkey birth data I: seasonal variation. *American Journal of Primatology*, **13**, 347-368.
- Curry, R. L. 1988. Group structure, within-group conflict and reproductive tactics in cooperatively breeding Galápagos mockingbirds, *Nesomimus parvulus*. *Animal Behaviour*, **36**, 1708-1728.
- Cuvillier-Hot, V., Gadagkar, R., Peeters, C. & Cobb, M. 2002. Regulation of reproduction in a queenless ant: aggression, pheromones, and reduction in conflict. *Proceedings of the Royal Society of London B*, **269**, 1295-1300.

- Cuvillier-Hot, V., Lenoir, A., Crewe, R., Malosse, C. & Peeters, C. 2004. Fertility signaling and reproductive skew in queenless ants. *Animal Behaviour*, **68**, 1209-1219.
- Czaja, J. A. & Goy, R. W. 1975. Ovarian hormones and food intake in female guinea pigs and rhesus monkeys. *Hormones and Behavior*, **6**, 923-928.
- Dafni, A., Kevan, P. G. & Husband, B. C. 2005. Practical pollination biology. pp. 312-313. Cambridge, Ontario: Enviroquest, Ltd.
- Dailey, R. A. & Neill, J. D. 1981. Seasonal variation in reproductive hormones of rhesus monkeys: anovulatory and short luteal phase menstrual cycles. *Biology of Reproduction*, **25**, 560-567.
- Dawson, G. A. 1979. The use of time and space by the Panamanian tamarin, *Saguinus geoffroyi*. *Folia Primatologica*, **31**, 253-284.
- De Vleeschouwer, K., Leus, K. & Van Elsacker, L. 2003. Characteristics of reproductive biology and proximate factors regulating seasonal breeding in captive golden-headed lion tamarins. *American Journal of Primatology*, **60**, 123-137.
- De Vleeschouwer, K., Van Elsacker, L. & Leus, K. 2001. Multiple breeding females in captive groups of golden-headed lion tamarins (*Leontopithecus chrysomelas*): causes and consequences. *Folia Primatologica*, **72**, 1-10.
- Di Bitetti, M. & Janson, C. H. 2000. When will the stork arrive? Patterns of birth seasonality in Neotropical primates. *American Journal of Primatology*, **50**, 109-130.

- Dietz, J. M. 2004. Kinship structure and reproductive skew in cooperative breeding primates. In: *Kinship and behavior in primates* (Ed. by Chapais, B. & Berman, C.), pp. 233-241. New York, NY: Oxford University Press.
- Dietz, J. M. & Baker, A. J. 1993. Polygyny and female reproductive success in golden lion tamarins, *Leontopithecus rosalia*. *Animal Behaviour*, **46**, 1067-1078.
- Dietz, J. M., Baker, A. J. & Ballou, J. D. 2000. Demographic evidence of inbreeding depression in wild golden lion tamarins. In: *Genetics, demography and viability of fragmented populations* (Ed. by Young, A. G. & Clarke, G. M.), pp. 204-211. Cambridge: Cambridge University Press.
- Dietz, J. M., Baker, A. J. & Miglioretti, D. 1994. Seasonal variation in reproduction, juvenile growth, and adult body mass in golden lion tamarins (*Leontopithecus rosalia*). *American Journal of Primatology*, **34**, 115-132.
- Dietz, J. M., Peres, C. A. & Pinder, L. 1997. Foraging ecology and use of space in wild golden lion tamarins (*Leontopithecus rosalia*). *American Journal of Primatology*, **41**, 289-305.
- Digby, L. J. 1995a. Infant care, infanticide, and female reproductive strategies in polygynous groups of common marmosets (*Callithrix jacchus*). *Behavioral Ecology and Sociobiology*, **37**, 51-61.
- Digby, L. J. 1995b. Social organization in wild population of *Callithrix jacchus*. II. Intragroup social behavior. *Primates*, **36**, 361-375.
- Digby, L. J. 1999. Sexual behavior and extragroup copulations in a wild population of common marmosets (*Callithrix jacchus*). *Folia Primatologica*, **70**, 136-145.

- Digby, L. J. & Ferrari, S. F. 1994. Multiple breeding females in free-ranging groups of *Callithrix jacchus*. *International Journal of Primatology*, **15**, 389-397.
- Digby, L. J., Ferrari, S. F. & Saltzman, W. 2007. Callitrichines: the role of competition in cooperatively breeding species. In: *Primates in perspective* (Ed. by Campbell, C. J., Fuentes, A., MacKinnon, C. K., Panger, M. & Bearder, S. K.), pp. 85-106. Oxford: Oxford University Press.
- Diggle, P. J., Liang, K. & Zeger, S. L. 1999. *Analysis of longitudinal data*. Oxford: Clarendon Press.
- Downing, J. A. & Scaramuzzi, R. J. 1991. Nutrient effects on ovulation rate, ovarian function and the secretion of gonadotrophic and metabolic hormones in sheep. *Journal of Reproduction and Fertility*, **43**, 209-227.
- Dreizen, S., Spirakis, C. N. & Stone, R. E. 1967. A comparison of skeletal growth and maturation in undernourished and well nourished girls before and after menarche. *Journal of Pediatrics*, **70**, 256-263.
- Dufour, D. L. & Sauther, M. L. 2002. Comparative and evolutionary dimensions of the energetics of human pregnancy and lactation. *American Journal of Human Biology*, **14**, 584-602.
- Dunbar, R. I. M. 1988. *Primate social systems*. Ithaca, NY: Comstock Press.
- Dunbar, R. I. M., Hannah-Stewart, L. & Dunbar, P. 2002. Forage quality and the costs of lactation for female gelada baboons. *Animal Behaviour*, **64**, 801-805.
- Dyke, B., Gage, T. B., Ballou, J. D., Petto, A. J., Tardif, S. D. & Williams, L. E. 1993. Model life tables for the smaller New World monkeys. *American Journal of Primatology*, **29**, 269-285.

- Ebensperger, L. A. 1998. Strategies and counter strategies to infanticide in mammals. *Biological Reviews of the Cambridge Philosophical Society*, **73**, 321-346.
- Emlen, S. T. 1982. The evolution of helping. I. An ecological constraints model. *American Naturalist*, **119**, 29-39.
- Emlen, S. T. 1995. An evolutionary theory of the family. *Proceedings of the National Academy of Sciences of the United States of America*, **92**, 8092-8099.
- Emlen, S. T., Reeve, H. K. & Keller, L. 1998. Reproductive skew: disentangling concessions from control. *Trends in Ecology and Evolution*, **13**, 458-459.
- Engelhardt, A., Heistermann, M., Hodges, J. K., Nürnberg, P. & Niemitz, C. 2006. Determinants of male reproductive success in wild long-tailed macaques (*Macaca fascicularis*)-male monopolisation, female mate choice or post-copulatory mechanisms? *Behavioral Ecology and Sociobiology*, **59**, 740-752.
- Epple, G. 1967. Vergleichende untersuchungen über sexual- und sozialverhalten de krallenaffen (Hapalidae). *Folia Primatologica*, **7**, 37-65.
- Epple, G. 1970. Maintenance, breeding, and development of marmoset monkeys (Callitrichidae) in captivity. *Folia Primatologica*, **12**, 56-76.
- Epple, G. 1975. Parental behavior in *Saguinus fuscicollis* spp. (Callitrichidae). *Folia Primatologica*, **24**, 221-238.
- Epple, G. & Katz, Y. 1984. Social influences on estrogen excretion and ovarian cyclicity in saddleback tamarins (*Saguinus fuscicollis*). *American Journal of Primatology*, **6**, 215-227.

- Evans, S. & Hodges, J. K. 1984. Reproductive status of adult daughters in family groups of common marmosets (*Callithrix jacchus jacchus*). *Folia Primatologica*, **42**, 127-133.
- Evans, S. & Poole, T. B. 1984. Long-term changes and maintenance of the pair-bond in common marmosets, *Callithrix jacchus jacchus*. *Folia Primatologica*, **42**, 33-41.
- Fadem, B. H. 1987. Activation of estrus by pheromones in a marsupial: stimulus control and endocrine factors. *Biology of Reproduction*, **36**, 328-332.
- Fairbanks, L. A. 1988. Vervet monkey grandmothers: interactions with infant grandoffspring. *International Journal of Primatology*, **9**, 425-441.
- Fairbanks, L. A. & McGuire, M. T. 1986. Age, reproductive value and dominance-related behaviour in vervet monkey females: cross-generational influences on social relationships and reproduction. *Animal Behaviour*, **34**, 1710-1721.
- Faulkes, C. G. & Abbott, D. H. 1993. Evidence that primer pheromones do not cause social suppression of reproduction in male and female naked mole-rats, *Heterocephalus glaber*. *Journal of Reproduction and Fertility*, **99**, 225-230.
- Faulkes, C. G. & Abbott, D. H. 1997. The physiology of a reproductive dictatorship: regulation of male and female reproduction by a single breeding female in colonies of naked mole-rats. In: *Cooperative breeding in mammals* (Ed. by Solomon, N. G. & French, J. A.), pp. 302-334. Cambridge: Cambridge University Press.
- Faulkes, C. G., Abbott, D. H. & Jarvis, J. U. M. 1990. Social suppression of ovarian cyclicity in captive and wild colonies of naked mole-rats, *Heterocephalus glaber*. *Journal of Reproduction and Fertility*, **88**, 559-568.

- Faulkes, C. G. & Bennett, N. C. 2001. Family values: group dynamics and social control of reproduction in African mole-rats. *Trends in Ecology and Evolution*, **16**, 184-190.
- Faulkes, C. G. & Bennett, N. C. 2007. African mole-rats social and ecological diversity. In: *Rodent societies: an ecological and evolutionary perspective* (Ed. by Wolff, J. O. & Sherman, P. W.). Chicago, IL: Chicago University Press.
- Ferrari, S. F. & Diego, V. H. 1992. Long-term changes in a wild marmoset group. *Folia Primatologica*, **58**, 215-218.
- Fite, J. E., Patera, K. J., French, J. A., Rukstalis, M., Hopkins, E. C. & Ross, C. N. 2005. Opportunistic mothers: female marmosets (*Callithrix kuhlii*) reduce their investment in offspring when they have to, and when they can. *Journal of Human Evolution*, **49**, 122-142.
- Fitzpatrick, J. L., Desjardins, J. K., Milligan, N., Stiver, K. A., Montgomerie, R. & Balshine, S. 2008. Female-mediated causes and consequences of status change in a social fish. *Proceedings of the Royal Society Biological Sciences*, **275**, 929-936.
- Ford, S. M. 1980. Callitrichids as phyletic dwarfs, and the place of the Callitrichidae in Platyrrhini. *Primates*, **21**, 31-43.
- Foster, R. B. 1982. Famine on Barro Colorado Island. In: *The ecology of a tropical forest: seasonal rhythms and long-term changes* (Ed. by Leigh Jr., E. G., Rand, A. S. & Windsor, D. M.), pp. 201-212. Washington, D.C.: Smithsonian Institution Press.

- French, J. A. 1987. Reproductive suppression in marmosets and tamarins-absence of social effects in the lion tamarins (*Leontopithecus rosalia*). *American Journal of Primatology*, **12**, 342.
- French, J. A. 1997. Proximate regulation of singular breeding in callitrichid primates. In: *Cooperative breeding in mammals* (Ed. by Solomon, N. G. & French, J. A.), pp. 34-75. Cambridge: Cambridge University Press.
- French, J. A., Abbott, D. H. & Snowdon, C. T. 1984. The effect of social environment on estrogen excretion, scent marking, and socio-sexual behavior in tamarins (*Saguinus oedipus*). *American Journal of Primatology*, **6**, 155-167.
- French, J. A., Bales, K. L., Baker, A. J. & Dietz, J. M. 2003. Endocrine monitoring of wild dominant and subordinate female *Leontopithecus rosalia*. *International Journal of Primatology*, **24**, 1281-1300.
- French, J. A., De Vleeschouwer, K., Bales, K. L. & Heistermann, M. 2002. Lion tamarin reproductive biology. In: *Lion Tamarins: biology and conservation* (Ed. by Kleiman, D. G. & Rylands, A. B.), pp. 133-156. Washington, DC: Smithsonian Institution Press.
- French, J. A., Inglett, B. J. & Dethlefs, T. M. 1989. The reproductive status of non-breeding group members in captive golden lion tamarin social groups. *American Journal of Primatology*, **18**, 73-86.
- French, J. A., Pissinatti, A. & Coimbra-Filho, A. F. 1996. Reproduction in captive lion tamarins (*Leontopithecus*): seasonality, infant survival, and sex ratios. *American Journal of Primatology*, **39**, 17-33.

- French, J. A. & Stribley, J. A. 1985. Patterns of urinary oestrogen excretion in female golden lion tamarins (*Leontopithecus rosalia*). *Journal of Reproduction and Fertility*, **75**, 537-546.
- French, J. A. & Stribley, J. A. 1987. Synchronization of ovarian cycles within and between social groups in the golden lion tamarin (*Leontopithecus rosalia*). *American Journal of Primatology*, **12**, 469-478.
- Frisch, R. E. 1982. Malnutrition and fertility. *Science*, **215**, 1272-1273.
- Frisch, R. E. 1984. Body fat, puberty and fertility. *Biological Reviews*, **59**, 161-188.
- Frisch, R. E. & Revelle, R. 1971. Height and weight at menarche and hypothesis of critical body weights and adolescent events. *Science*, **169**, 397-399.
- Ganas, J. & Robbins, M. M. 2005. Ranging behavior of the mountain gorillas (*Gorilla beringei beringei*) in Bwindi Impenetrable National Park, Uganda: a test of the ecological constraints model. *Behavioral Ecology and Sociobiology*, **58**, 277-288.
- Garber, P. A. 1997. One for all and breeding for one: cooperation and competition as a tamarin reproductive strategy. *Evolutionary Anthropology*, **5**, 187-199.
- Garber, P. A., Encarnación, F. M. L. & Pruett, J. D. 1993. Demographic and reproductive patterns in moustached tamarin monkeys (*Saguinus mystax*): implications for reconstructing platyrrhine mating systems. *American Journal of Primatology*, **29**, 235-254.
- Garber, P. A., Moya, L. & Malaga, C. 1984. A preliminary field study of the moustached tamarin monkey (*Saguinus mystax*) in northern Peru: questions concerned with the evolution of a communal breeding system. *Folia Primatologica*, **42**, 17-32.

- Garland Jr., T. 1985. Ontogenetic and individual variation in size, shape and speed in the Australian agamid lizard *Amphibolurus nuchalis*. *Journal of Zoology Series A*, **207**, 425-439.
- Gengozian, N., Batson, J. S. & Smith, T. S. 1978. Breeding of marmosets in a colony environment. *Primates in Medicine*, **10**, 71-78.
- Gilchrist, J. S. 2006a. Female eviction, abortion, and infanticide in banded mongooses (*Mungos mungo*): implications for social control of reproduction and synchronized parturition. *Behavioral Ecology*, **17**, 664-669.
- Gilchrist, J. S. 2006b. Reproductive success in a low skew, communal breeding mammal: the banded mongoose, *Mungos mungo*. *Behavioral Ecology and Sociobiology*, **60**, 854-863.
- Gill Jr, G. E., Fowler, R. T. & Mori, S. A. 1998. Pollination biology of *Symphonia globulifera* (Clusiaceae) in central French Guiana. *Biotropica*, **30**, 139-144.
- Gittleman, J. & Thompson, S. 1988. Energy allocation in mammalian reproduction. *American Zoologist*, **28**, 863-875.
- Goland, R. S., Jozak, S. & Conwell, I. 1994. Placental corticotropin-releasing hormone and the hypercortisolism of pregnancy. *American Journal of Obstetrics and Gynecology*, **171**, 1287-1291.
- Goldizen, A. W. 1987a. Facultative polyandry and the role of infant-carrying in wild saddle-backed tamarins (*Saguinus fuscicollis*). *Behavioral Ecology and Sociobiology*, **20**, 99-109.
- Goldizen, A. W. 1987b. Tamarins and marmosets: communal care of offspring. In: *Primate Societies* (Ed. by Smuts, B. B., Cheney, D. L., Seyfarth, R. M.,

- Wrangham, R. & Struhsaker, T. T.), pp. 34-43. Chicago, IL: Chicago University Press.
- Goldizen, A. W., Mendelson, J., van Vlaardingen, M. & Terborgh, J. 1996. Saddle-back tamarin (*Saguinus fuscicollis*) reproductive strategies: evidence from a thirteen-year study of a marked population. *American Journal of Primatology*, **38**, 57-83.
- Goldizen, A. W., Terborgh, J., Cornejo, F., Porras, D. T. & Evans, R. 1988. Seasonal food shortage, weight loss, and the timing of births in saddle-back tamarins (*Saguinus fuscicollis*). *Journal of Animal Ecology*, **57**, 893-901.
- Gouzoules, S. & Gouzoules, H. 1987. Kinship. In: *Primate societies* (Ed. by Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. & Struhsaker, T. T.), pp. 299-305. Chicago, IL: University of Chicago Press.
- Griffin, J. E. 1996. Assessment of endocrine function. In: *Textbook of endocrine physiology* (Ed. by Griffin, J. E. & Ojeda, S. R.), pp. 86-100. Oxford: Oxford University Press.
- Hager, R. 2003. Models of reproductive skew applied to primates. In: *Sexual selection and reproductive competition in primates: new perspectives and directions* (Ed. by Jones, C. B.), pp. 65-101. Norman, OK: American Society of Primatologists.
- Hamilton, I. M. 2004. A commitment model of reproductive inhibition in cooperatively breeding groups. *Behavioral Ecology*, **15**, 585-591.
- Hamilton, W. D. 1966. The moulding of senescence by natural selection. *Journal of Theoretical Biology*, **12**, 12-45.
- Handelmann, G., Ravizza, R. & Ray, W. J. 1980. Social dominance determines estrous entrainment among female hamsters. *Hormones and Behavior*, **14**, 107-115.

- Hankerson, S. J. 2008. Resource and space use in the wild golden lion tamarin, *Leontopithecus rosalia*. In: *Behavior, Ecology, Evolution, and Systematics*, pp. 138. College Park: University of Maryland.
- Hatchwell, B. J. & Komdeur, J. 2000. Ecological constraints, life history traits and the evolution of cooperative breeding. *Animal Behaviour*, **59**, 1079-1086.
- Hauber, M. E. & Lacey, E. A. 2005. Bateman's principle in cooperatively breeding vertebrates: the effects of non-breeding alloparents on variability in female and male reproductive success. *Integrative and Comparative Biology*, **45**, 903-914.
- Hawkes, K., O'Connell, J. F., Blurton Jones, N. G., Gurven, M., Hill, K., Hames, R., Kano, T., Nishida, T., White, F. J., Churchill, S. E. & Worthman, C. M. 1997. Hadza women's time allocation, offspring provisioning, and the evolution of long postmenopausal life spans (and comments and reply). *Current Anthropology*, **38**, 551-577.
- Hearn, J. P. 1983. *Reproduction in New World primates*. Lancaster: MTP Press Ltd.
- Heinsohn, R. & Packer, C. 1995. Complex cooperative strategies in group-territorial African lions. *Science*, **269**, 1260-1262.
- Hilton-Taylor, C. 2000. *2000 IUCN Red List of Threatened Species*. Gland, Switzerland: World Conservation Union (IUCN).
- Hoage, R. J. 1978. Parental care in *Leontopithecus rosalia rosalia*: sex and age differences in carrying behavior and the role of prior experience. In: *The biology and conservation of the Callitrichidae* (Ed. by Kleiman, D. G.), pp. 293-305. Washington, D.C.: Smithsonian Institution Press.

- Hodge, S. J. 2009. Understanding variation in reproductive skew: directions for future empirical research. In: *Reproductive skew in vertebrates: proximate and ultimate causes* (Ed. by Hager, R. & Jones, C. B.), pp. 439-466. Cambridge: Cambridge University Press.
- Hodge, S. J., Bell, M. B. V. & Cant, M. A. 2010. Reproductive competition and the evolution of extreme birth synchrony in a cooperative mammal. *Biology Letters*, **doi:10.1098/rsbl.2010.0555**.
- Hodge, S. J., Manica, A., Flower, T. P. & Clutton-Brock, T. H. 2008. Determinants of reproductive success in dominant female meerkats. *Journal of Animal Ecology*, **77**, 92-102.
- Hoogland, J. L. 1985. Infanticide in prairie dogs: lactating females kill offspring of close kin. *Science*, **230**, 1037-1040.
- Hubrecht, R. C. 1984. Field observations on group size and composition of the common marmoset (*Callithrix jacchus jacchus*), at Tapacura, Brazil. *Primates*, **25**, 13-21.
- Hubrecht, R. C. 1989. The fertility of daughters in common marmoset (*Callithrix jacchus jacchus*) family groups. *Primates*, **30**, 423-432.
- Inglott, B. J. 1993. The role of social bonds and the female reproductive cycle on the regulation of social and sexual interactions in the golden lion tamarin (*Leontopithecus rosalia rosalia*). In: *Psychology*. Omaha, NE: University of Nebraska.
- Inglott, B. J., French, J. A., Simmons, L. G. & Vires, K. W. 1989. Dynamics of intra-family aggression and social reintegration in lion tamarins (*Leontopithecus rosalia*). *Zoo Biology*, **8**, 67-78.

- Isbell, L. A. 1991. Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behavioral Ecology*, **2**, 143-155.
- IUCN. 2010. IUCN Red List of Threatened Species Version 2010.4
<http://www.iucnredlist.org>. IUCN.
- James, F. C. & Shugart Jr., H. H. 1970. A quantitative method of habitat description. *Audubon Field Notes*, **24**, 727-736.
- Janson, C. H. & Goldsmith, M. L. 1995. Predicting group size in primates: foraging costs and predation risks. *Behavioral Ecology*, **6**, 326-336.
- Janson, C. H. & van Schaik, C. P. 1988. Recognizing the many faces of primate food competition. *Behaviour*, **105**, 165-186.
- Jansson, T. & Powell, T. L. 2006. Human placental transport in altered fetal growth: does the placenta function as a nutrient sensor? A review. *Placenta*, **27**, S91-S97.
- Jaquish, C. E., Gage, T. B. & Tardif, S. D. 1991. Reproductive factors affecting survivorship in captive Callitrichidae. *American Journal of Physical Anthropology*, **84**, 291-305.
- Johnson, E. O., Kamilaris, T. C., Carter, C. S., Calogero, A. E., Gold, P. W. & Chrousos, G. P. 1996. The biobehavioral consequences of psychogenic stress in a small, social primate (*Callithrix jacchus jacchus*). *Biology of Psychiatry*, **40**, 317-337.
- Johnson, L. D., Petto, A. J. & Sehgal, P. K. 1991. Factors in the rejection and survival of captive cotton top tamarins (*Saguinus oedipus*). *American Journal of Primatology*, **25**, 91-102.
- Johnstone, R. A. 2000. Models of reproductive skew: a review and synthesis. *Ethology*, **106**, 5-26.

- Johnstone, R. A. & Cant, M. A. 1999. Reproductive skew and the threat of eviction: a new perspective. *Proceedings of the Royal Society Biological Sciences*, **266**, 275-279.
- Kearns, C. A. & Inouye, D. W. 1993. *Techniques for pollination biologists*. Niwot, Colorado: University Press of Colorado.
- Kennedy, G. C. 1969. Interactions between feeding behavior and hormones during growth. *Annals of the New York Academy of Sciences*, **157**, 1049-1061.
- Kernohan, B. J., Gitzen, R. A. & Millspaugh, J. J. 2001. Analysis of animal space use and movements. In: *Radio tracking and animal populations* (Ed. by Millspaugh, J. J. & Marzluff, J. M.), pp. 125-166. San Diego, CA: Academic Press.
- Kierulff, M. C. M., Raboy, B. E., Procópio de Oliveira, P., Miller, K. E., Passos, F. C. & Prado, F. 2002. Behavioral ecology of lion tamarins. In: *Lion tamarins: biology and conservation* (Ed. by Kleiman, D. G. & Rylands, A. B.), pp. 157-187. Washington, D.C.: Smithsonian Institution Press.
- Kirkpatrick-Tanner, M., Aeschlimann, C. & Anzenberger, G. 1996. Occurrence of an infanticide within captive polygynous group of common marmosets, *Callithrix jacchus*. *Folia Primatologica*, **67**, 52-58.
- Kirkwood, J. K. 1983. Effects of diet on health, weight and litter-size in captive cotton-top tamarins *Saguinus oedipus oedipus*. *Primates*, **24**, 515-520.
- Kirkwood, J. K. 1985. Patterns of growth in primates. *Journal of Zoology*, **205**, 123-136.
- Kirkwood, J. K., Epstein, M. A. & Terlecki, A. J. 1983. Factors influencing population growth of a colony of cotton-top tamarins. *Laboratory Animals*, **17**, 35-41.

- Kirkwood, J. K. & Underwood, S. J. 1984. Energy requirements of captive cotton-top tamarins (*Saguinus oedipus oedipus*). *Folia Primatologica*, **42**, 180-187.
- Kirkwood, R. N., Cumming, D. C. & Aherne, F. X. 1987. Nutrition and puberty in the female. *Proceedings of the Nutrition Society*, **46**, 177-192.
- Kleiman, D. G. 1977a. Characteristics of reproduction and sociosexual interactions in pairs of lion tamarins (*Leontopithecus rosalia*) during the reproductive cycle. In: *The Biology and Conservation of the Callitrichidae* (Ed. by Kleiman, D. G.), pp. 181-190. Washington, D.C.: Smithsonian Institution Press.
- Kleiman, D. G. 1977b. Monogamy in mammals. *Quarterly Review of Biology*, **52**, 39-69.
- Kleiman, D. G. 1979. Parent-offspring conflict and sibling competition in a monogamous primate. *American Naturalist*, **114**, 753-760.
- Knott, C. D. 2001. Female reproductive ecology of the apes: implications for human evolution. In: *Reproductive ecology and human evolution* (Ed. by Ellison, P. T.), pp. 429-463. New York: Aldine de Gruyter.
- Koenig, A. 1995. Group size, composition and reproductive success in wild common marmosets (*Callithrix jacchus*). *American Journal of Primatology*, **35**, 311-317.
- Koenig, A. 2002. Competition for resources and its behavioral consequences among female primates. *International Journal of Primatology*, **23**, 759-783.
- Koenig, A., Borries, C., Chalise, M. K. & Winkler, P. 1997. Ecology, nutrition, and timing of reproductive events in an Asian primate, the Hanuman langur (*Presbytis entellus*). *Journal of Zoology*, **243**, 215-235.
- Koenig, W. D. & Dickinson, J. L. 2004. *Ecology and evolution of cooperative breeding in birds*. Cambridge: Cambridge University Press.

- Kohrs, M., Harper, A. E. & Kerr, G. R. 1976. Effects of a low-protein diet during pregnancy of the rhesus monkey. I. Reproductive efficiency. *American Journal of Clinical Nutrition*, **29**, 136-145.
- Kruuk, H. 1989. *The social badger*. Oxford: Oxford University Press.
- Kutsukake, N. & Clutton-Brock, T. H. 2006. Aggression and submission reflect reproductive conflict between females in cooperatively breeding meerkats *Suricata suricatta*. *Behavioral Ecology and Sociobiology*, **59**, 541-548.
- Lazaro-Perea, C., Castro, C. S. S., Harrison, R., Araujo, A., Arruda, M. F. & Snowdon, C. T. 2000. Behavioral and demographic changes following the loss of the breeding female in cooperatively breeding marmosets. *Behavioral Ecology and Sociobiology*, **48**, 137-146.
- Lazaro-Perea, C., Castro, C. S. S., Harrison, R., Araujo, A., Arruda, M. F. & Snowdon, C. T. 2001. Intergroup interactions in wild common marmosets, *Callithrix jacchus*: territorial defense and assessment of neighbors. *Animal Behaviour*, **62**, 11-21.
- Lee, P. C. 1987. Nutrition, fertility and maternal investment in primates. *Journal Zoology, London*, **213**, 409-422.
- Lee, P. C. & Hauser, M. D. 1998. Long-term consequences of changes in territory quality on feeding and reproductive strategies of vervet monkeys. *Journal of Animal Ecology*, **67**, 347-358.
- Leutenegger, W. 1973. Maternal-fetal weight relationships in primates. *Folia Primatologica*, **20**, 280-293.

- Leutenegger, W. 1980. Monogamy in callitrichids: a consequence of phyletic dwarfism? *International Journal of Primatology*, **1**, 95-98.
- Li, R., Haas, J. D. & Habicht, J.-P. 1998. Timing and the influence of maternal nutritional status during pregnancy on fetal growth. *American Journal of Human Biology*, **10**, 529-539.
- Ligon, J. D., Carey, C. & Ligon, S. H. 1988. Cavity roosting, philopatry, and cooperative breeding in the green woodhoopoe may reflect a physiological trait. *Physiological Zoology*, **105**, 123-127.
- Lunn, S. F. 1983. Body weight changes throughout pregnancy in the common marmoset *Callithrix jacchus*. *Folia Primatologica*, **41**, 204-217.
- Magnusson, W. E., de Paiva, L. J., da Rocha, R. M., Franke, C. R., Kasper, L. A. & Lima, A. P. 1985. The correlates of foraging mode in a community of Brazilian lizards. *Herpetologica*, **41**, 324-332.
- Malcolm, J. R. & Marten, K. 1982. Natural selection and the communal rearing of pups in African wild dogs (*Lycaon pictus*). *Behavioral Ecology and Sociobiology*, **10**, 1-13.
- Margulis, S. W., Saltzman, W. & Abbott, D. H. 1995. Behavioral and hormonal changes in female naked mole-rats (*Heterocephalus glaber*) following removal of the breeding female from a colony. *Hormones and Behavior*, **29**, 227-247.
- Martin, R. D. 1973. A review of the behaviour and ecology of the lesser mouse lemur (*Microcebus murinus* J. F. Mill 1777). In: *Comparative ecology and behaviour of primates* (Ed. by Michael, R. P. & Crook, J. H.), pp. 1-68. New York: Academic Press.

- Martin, T. 1984. The meaning of weaning. *Animal Behaviour*, **32**, 1257-1259.
- Mastorakos, G. & Ilias, I. 2003. Maternal and fetal hypothalamic-pituitary-adrenal axes during pregnancy and post partum. *Annals of the New York Academy of Sciences*, **997**, 136-149.
- Mays, N. A., Vleck, C. M. & Dawson, J. 1991. Plasma luteinizing hormone, steroid hormones, behavioral role, and nest stage in cooperatively breeding Harris' hawk (*Parabuteo unicinctus*). *Auk*, **108**, 619-637.
- McClintock, M. K. 1978. Estrous synchrony and its mediation by airborne chemical communication (*Rattus norvegicus*). *Hormones and Behavior*, **10**, 264-276.
- McComb, K., Packer, C. & Pusey, A. E. 1994. Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. *Animal Behaviour*, **47**, 379-387.
- Miller, K. E. 2002. Olfactory communication, feeding behaviors and energy budgets of wild golden lion tamarins (*Leontopithecus rosalia*). In: *Biology*. College Park, MD: University of Maryland.
- Miller, K. E., Bales, K. L., Ramos, J. H. & Dietz, J. M. 2006. Energy intake, energy expenditure, and reproductive costs of female wild golden lion tamarins (*Leontopithecus rosalia*). *American Journal of Primatology*, **68**, 1037-1053.
- Miller, K. E. & Dietz, J. M. 2004. Fruit yield, not DBH or fruit crown volume, correlates with time spent feeding on fruits by wild *Leontopithecus rosalia*. *International Journal of Primatology*, **25**, 27-39.

- Miller, K. E. & Dietz, J. M. 2006. Effects of individual and group characteristics on feeding behaviors in wild *Leontopithecus rosalia*. *International Journal of Primatology*, **27**, 911-939.
- Moehlman, P. D. 1979. Jackal helpers and pup survival. *Nature*, **277**, 382-383.
- Moehlman, P. D. 1986. Ecology of cooperation in canids. In: *Ecological aspects of social evolution in birds and mammals* (Ed. by Rubenstein, D. I. & Wrangham, R. W.), pp. 282-302. Princeton, NJ: Princeton University Press.
- Molteno, A. J. & Bennett, N. C. 2000. Anovulation in non-reproductive female Damaraland mole-rats (*Cryptomys damarensis*). *Journal of Reproduction and Fertility*, **119**, 35-41.
- Monfort, S. L., Bush, M. & Wildt, D. E. 1996. Evaluation of natural and induced ovarian synchrony in golden lion tamarins (*Leontopithecus rosalia*). *Biology of Reproduction*, **55**, 875-882.
- Monnin, T. & Peeters, C. 1999. Dominance hierarchy and reproductive conflicts among subordinates in a monogynous queenless ant. *Behavioral Ecology*, **10**, 323-332.
- Moore, J. 1993. Inbreeding and outbreeding in primates: what's wrong with "the dispersing sex"? In: *The natural history of inbreeding and outbreeding: theoretical and empirical perspectives* (Ed. by Thornhill, N. W.), pp. 392-426. Chicago, IL: University of Chicago Press.
- Motulsky, H. J. & Christopoulos, A. 2003. *Fitting models to biological data using linear and nonlinear regression. A practical guide to curve fitting*. San Diego, California: GraphPad Software, Inc.

- Mumme, R. L., Koenig, W. & Pitelka, F. A. 1983. Mate guarding in the acorn woodpecker: within-group reproductive competition in a cooperative breeder. *Animal Behaviour*, **31**, 1094-1106.
- Munck, A., Guyre, P. M. & Holbrook, N. J. 1984. Physiological functions of glucocorticoids in stress and their relation to pharmacological actions. *Endocrine Reviews*, **5**, 25-44.
- Nash, L. T. 1983. Reproductive patterns in galagos (*Galago zanzibaricus* and *Galago garnettii*) in relation to climatic variability. *American Journal of Primatology*, **5**, 181-196.
- Nelson, R. J. 2005. *An introduction to behavioral endocrinology*. Sunderland, MA: Sinauer Associates, Inc.
- Nievergelt, C. M. & Martin, R. D. 1999. Energy intake during reproduction in captive common marmosets (*Callithrix jacchus*). *Physiology and Behavior*, **65**, 849-854.
- NRC. 1981. *Techniques for the Study of Primate Population Ecology*. Washington, DC: National Academy Press.
- Observatório Nacional. 2004. Efemérides Astronômicas. Anuário Interativo do Observatório Nacional. Rio de Janeiro. <http://euler.on.br/ephemeris/index.php>.
- Observatório Nacional. 2005. Efemérides Astronômicas. Anuário Interativo do Observatório Nacional. Rio de Janeiro. <http://euler.on.br/ephemeris/index.php>.
- Observatório Nacional. 2006. Efemérides Astronômicas. Anuário Interativo do Observatório Nacional. Rio de Janeiro. <http://euler.on.br/ephemeris/index.php>.
- Observatório Nacional. 2007. Efemérides Astronômicas. Anuário Interativo do Observatório Nacional. Rio de Janeiro. <http://euler.on.br/ephemeris/index.php>.

- Ojeda, S. R. 1996. Female reproductive function. In: *Textbook of endocrine physiology* (Ed. by Griffin, J. E. & Ojeda, S. R.), pp. 164-200. Oxford: Oxford University Press.
- Ojeda, S. R. & Griffin, J. E. 1996. Organization of the endocrine system. In: *Textbook of Endocrine Physiology* (Ed. by Griffin, J. E. & Ojeda, S. R.), pp. 3-17. Oxford: Oxford University Press.
- Oliveira, L. d. C. 2010. Ecology and demography of golden-headed lion tamarins (*Leontopithecus chrysomelas*) in *cabruca* agroforest, Bahia state, Brazil. In: *Biology*. College Park, MD: University of Maryland.
- Packer, C., Scheel, D. & Pusey, A. E. 1990. Why lions form groups: food is not enough. *American Naturalist*, **136**, 1-19.
- Packer, C., Tatar, M. & Collins, A. 1998. Reproductive cessation in female mammals. *Nature*, **392**, 807-811.
- Paul, A., Keuster, J. & Podzuweit, D. 1993. Reproductive senescence and terminal investment in female Barbary macaques (*Macaca sylvanus*) at Salem. *International Journal of Primatology*, **14**, 105-124.
- Peres, C. A. 1986. Costs and benefits of territorial defense in golden lion tamarins, *Leontopithecus rosalia*. Gainesville, FL: University of Florida.
- Peres, C. A. 1994. Primate responses to phenological changes in an Amazonian terra firme forest. *Biotropica*, **26**, 98-112.
- Petter, J. J. 1978. Ecological and physiological adaptations of five sympatric nocturnal lemurs to seasonal variations in food production. In: *Recent advances in*

- primatology. 1. Behavior.* (Ed. by Chivers, D. J. & Herbert, J.). London: Academic Press.
- Pliner, P. & Fleming, A. S. 1983. Food intake, body weight, and sweetness preferences of the menstrual cycle in humans. *Physiology and Behavior*, **30**, 663-666.
- Pope, T. R. 1996. Socioecology, population fragmentation, and patterns of genetic loss in endangered primates. In: *Conservation genetics: case histories from nature* (Ed. by Avise, J. C. & Hamrick, J. L.), pp. 119-159. New York, NY: Chapman and Hall.
- Pottinger, T. G. 1999. The impact of stress on animal reproductive activities. In: *Stress physiology in animals* (Ed. by Baum, P. H. M.), pp. 130-177. Boca Raton, FL: CRC Press.
- Power, M. L., Bowman, M. E., Smith, R., Ziegler, T. E., Layne, D. G., Schulkin, J. & Tardif, S. D. 2006. Pattern of maternal serum corticotropin-releasing hormone concentration during pregnancy in the common marmoset (*Callithrix jacchus*). *American Journal of Primatology*, **68**, 181-188.
- Power, M. L., Verona, C. E., Ruiz-Miranda, C. R. & Oftedal, O. T. 2008. The composition of milk from free-living common marmosets (*Callithrix jacchus*) in Brazil. *American Journal of Primatology*, **70**, 78-83.
- Power, R. A., Power, M. L., Layne, D. G., Jaquish, C. E., Oftedal, O. T. & Tardif, S. D. 2001. Relations among measures of body composition, age, and sex in the common marmoset monkey (*Callithrix jacchus*). *Comparative Medicine*, **51**, 218-223.

- Price, E. C. 1992a. The benefits of helpers: effects of group and litter size on infant care in tamarins (*Saguinus oedipus*). *American Journal of Primatology*, **26**, 179-190.
- Price, E. C. 1992b. Changes in the activity of captive cotton-top tamarins (*Saguinus oedipus*) over the breeding cycle. *Primates*, **33**, 99-106.
- Price, E. C. 1992c. The cost of infant carrying in captive cotton-top tamarins. *American Journal of Primatology*, **26**, 23-33.
- Price, E. C. & McGrew, W. C. 1991. Departures from monogamy in colonies of captive cotton-top tamarins. *Folia Primatologica*, **57**, 16-27.
- Procópio de Oliveira, P. 2002. Feeding ecology, diet and home range of translocated golden lion tamarins and their relation to the spatial and temporal distribution of feeding resources in the União Biological Reserve, RJ. pp. 234. Belo Horizonte, MG, Brazil: Federal University of Minas Gerais.
- Procópio de Oliveira, P., Kierulff, M. C. M. & Lapenta, M. J. 2008a. Dieta e área de uso de micos-leões-dourados na Reserva Biológica União, RJ. In: *Conservação do mico-leão-dourado: enfrentando os desafios de uma paisagem fragmentada* (Ed. by Procópio-de-Oliveira, P., Daudt Grativol, A. & Ruiz-Miranda, C. R.), pp. 40-57. Campos dos Goytacazes: Universidade Estadual do Norte Fluminense Darcy Ribeiro.
- Procópio de Oliveira, P., Trindade Nascimento, M., Alvim Carvalho, F., Vilela, D., Martins Kierulff, M. C., Peuerta Veruli, V., Janzanti Lapenta, M. & da Silva, A. P. 2008b. Qualidade do habitat na área de ocorrência do mico-leão-dourado. In: *Conservação do mico-leão-dourado: enfrentando os desafios de uma paisagem fragmentada* (Ed. by Procópio-de-Oliveira, P., Daudt Grativol, A. & Ruiz-

- Miranda, C. R.), pp. 14-39. Campos dos Goytacazes: Universidade Estadual do Norte Fluminense Darcy Ribeiro.
- Puffer, A. M., Fite, J. E., French, J. A., Rukstalis, M., Hopkins, E. C. & Patera, K. J. 2004. Influence of the mother's reproductive state on the hormonal status of daughters in marmosets (*Callithrix kuhlii*). *American Journal of Primatology*, **64**, 29-37.
- Raboy, B. E., Christman, M. C. & Dietz, J. M. 2004. The use of degraded and shade cocoa forests by endangered golden-headed lion tamarins *Leontopithecus chrysomelas*. *Oryx*, **38**, 75-83.
- Ralls, K. & Ballou, J. D. 1982a. Effect of inbreeding on juvenile mortality in some small mammal species. *Laboratory Animals*, **16**, 159-166.
- Ralls, K. & Ballou, J. D. 1982b. Effects of inbreeding on infant mortality in captive primates. *International Journal of Primatology*, **3**, 491-505.
- Ralls, K., Ballou, J. D. & Templeton, A. 1988. Estimates of lethal equivalents and the cost of inbreeding in mammals. *Conservation Biology*, **2**, 185-193.
- Ramirez, M. 1984. Population recovery in the moustached tamarin (*Saguinus mystax*): management strategies and mechanisms. *American Journal of Primatology*, **7**, 245-259.
- Rapaport, L. G. & Ruiz-Miranda, C. R. 2006. Ontogeny of provisioning in two populations of wild golden lion tamarins (*Leontopithecus rosalia*). *Behavioral Ecology and Sociobiology*, **60**, 724-735.

- Rasa, O. A. E. 1994. Altruistic infant care or infanticide: the dwarf mongooses' dilemma. In: *Infanticide and parental care* (Ed. by Parmigiani, S. & Saal, F. S. V.), pp. 301-320. London, UK: Harwood Academic Publishers.
- Ratnieks, F. L. W. & Helanterä, H. 2009. The evolution of extreme altruism and inequality in insect societies. *Philosophical Transactions of the Royal Society B*, **364**, 3169-3170.
- Reeve, H. K. & Emlen, S. T. 2000. Reproductive skew and group size: an n-person staying incentive model. *Behavioral Ecology*, **11**, 640-647.
- Reeve, H. K., Emlen, S. T. & Keller, L. 1998. Reproductive sharing in animal societies: reproductive incentives or incomplete control by dominant breeders? *Behavioral Ecology*, **9**, 267-278.
- Reeve, H. K. & Nonacs, P. 1992. Social contracts in wasp societies. *Nature*, **359**, 823-825.
- Reeve, H. K. & Ratnieks, F. L. W. 1993. Queen-queen conflicts in polygynous societies: mutual tolerance and reproductive skew. In: *Queen number and sociality in insects* (Ed. by Keller, L.), pp. 45-85. Oxford: Oxford University Press.
- Reeve, H. K. & Shen, S. F. 2006. A missing model in reproductive skew theory: the bordered tug-of-war. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 8430-8434.
- Reeve, H. K. & Sherman, P. W. 1991. Intracolony aggression and nepotism by the breeding female naked mole-rat. In: *The biology of the naked mole-rat* (Ed. by Sherman, P. W., Jarvis, J. U. M. & Alexander, R. D.), pp. 384-425. Princeton, NJ: Princeton University Press.

- Reyer, H. U., Dittami, J. P. & Hall, M. R. 1986. Avian helpers at the nest: are they psychologically castrated? *Ethology*, **71**, 216-228.
- Rhine, R. J., Norton, G. W., Roertgen, W. J. & Klein, H. D. 1980. The brief survival of free-ranging baboon infants (*Papio cynocephalus*) after separation from their mothers. *International Journal of Primatology*, **1**, 401-409.
- Riehl, C. 2010. Living with strangers: direct benefits favour non-kin cooperation in a communally nesting bird. *Proceedings of the Royal Society Biological Sciences*, **doi:10.1098/rspb.2010.1752**.
- Rood, J. P. 1986. Ecology and social evolution in the mongooses. In: *Ecological aspects of social evolution* (Ed. by Rubenstein, D. I. & Wrangham, R. W.), pp. 131-152. Princeton, NJ: Princeton University Press.
- Rood, J. P. 1990. Group size, survival, reproduction, and routes to breeding in dwarf mongooses. *Animal Behaviour*, **39**, 566-572.
- Ross, C. 1991. Life history patterns of new world monkeys. *International Journal of Primatology*, **12**, 481-502.
- Ross, C. 1992. Environmental correlates of the intrinsic rate of natural increase in primates. *Oecologia*, **90**, 383-390.
- Ross, C. & MacLarnon, A. 1995. Ecological and social correlates of maternal expenditure on infant growth in haplorhine primates. In: *Motherhood in human and nonhuman primates* (Ed. by Pryce, C. R., Martin, R. D. & Skuse, D.), pp. 37-46. Basel: Karger.
- Rothe, H. 1975. Some aspects of sexuality and reproduction in groups of captive marmosets (*Callithrix jacchus*). *Zeitschrift der Tierpsychologie*, **37**, 255-273.

- Rothe, H. & Koenig, A. 1991. Variability of social organization in captive common marmosets (*Callithrix jacchus*). *Folia Primatologica*, **57**, 28-33.
- Ruiz-Miranda, C. R., Daudt Grativol, A. & Procópio-de-Oliveira, P. 2008. Introdução: A espécie e sua situação na paisagem fragmentada. In: *Conservação do mico-leão-dourado: enfrentando os desafios de uma paisagem fragmentada* (Ed. by Procópio-de-Oliveira, P., Daudt Grativol, A. & Ruiz-Miranda, C. R.), pp. 6-13. Campos dos Goytacazes: Universidade Estadual do Norte Fluminense Darcy Ribeiro.
- Ruiz-Miranda, C. R., Kleiman, D. G., Dietz, J. M., Moraes, E., Gravitol, A. D., Baker, A. J. & Beck, B. B. 1999. Food transfers in wild and reintroduced golden lion tamarins, *Leontopithecus rosalia*. *American Journal of Primatology*, **48**, 305-320.
- Russell, A. F., Brotherton, P. N. M., McIlrath, G. M., Sharpe, L. L. & Clutton-Brock, T. H. 2003. Breeding success in cooperative meerkats: effects of helper number and maternal state. *Behavioral Ecology*, **14**, 486-492.
- Russell, M. J., Switz, G. M. & Thompson, K. 1980. Olfactory influences on the human menstrual cycle. *Pharmacology Biochemistry and Behavior*, **13**, 737-738.
- Rutherford, J. N. 2009. Fetal signaling through placental structure and endocrine function: Illustrations and implications from a nonhuman primate model. *American Journal of Human Biology*, **21**, 745-753.
- Rutherford, J. N. & Tardif, S. D. 2008. Placental efficiency and intrauterine resource allocation strategies in the common marmoset pregnancy. *American Journal of Physical Anthropology*, **137**, 60-68.

- Rylands, A. B. 1986. Ranging behaviour and habitat preference of a wild marmoset group, *Callithrix humeralifer* (Callitrichidae, Primates). *Journal of Zoology, London*, **210**, 489-514.
- Rylands, A. B. 1987. Primate communities in Amazonian forests: their habitats and food resources. *Experientia*, **43**, 265-279.
- Rylands, A. B. & Faria, D. S. 1993. Habitats, feeding ecology, and home range size in the genus *Callithrix*. In: *Marmosets and tamarins: systematics, behaviour, and ecology* (Ed. by Rylands, A. B.), pp. 262-272. Oxford: Oxford University Press.
- Rylands, A. B., Kierulff, M. C. M. & De Souza Pinto, L. P. 2002. Distribution and status of lion tamarins. In: *Lion tamarins: biology and conservation* (Ed. by Kleiman, D. G. & Rylands, A. B.), pp. 42-58. Washington, D.C.: Smithsonian Institution Press.
- Sales Coelho, A., Ruiz-Miranda, C. R., Beck, B. B., Martins, A., de Oliveira, C. R. & Sabatini, V. 2008. Comportamento do mico-leão-dourado (*Leontopithecus rosalia*, Linnaeus 1766) em relação à fragmentação do habitat. In: *Conservação do mico-leão-dourado: enfrentando os desafios de uma paisagem fragmentada* (Ed. by Procópio-de-Oliveira, P., Daudt Grativol, A. & Ruiz-Miranda, C. R.), pp. 58-85. Campos dos Goytacazes: Universidade Estadual do Norte Fluminense Darcy Ribeiro.
- Saltzman, W. 2003. Reproductive competition among female common marmosets (*Callithrix jacchus*): proximate and ultimate causes. In: *Sexual selection and reproductive competition in primates: new perspectives and directions* (Ed. by Jones, C. B.), pp. 197-229. Norman, OK: American Society of Primatologists.

- Saltzman, W., Ahmed, S., Fahimi, A., Wittwer, D. J. & Wegner, F. H. 2006a. Social suppression of female reproductive maturation and infanticidal behavior in cooperatively breeding Mongolian gerbils. *Hormones and Behavior*, **49**, 527-537.
- Saltzman, W., Digby, L. J. & Abbott, D. H. 2009. Reproductive skew in female common marmosets: what can proximate mechanisms tell us about ultimate causes? *Proceedings of the Royal Society Biological Sciences*, **276**, 389-399.
- Saltzman, W., Hogan, B. K. & Abbott, D. H. 2006b. Diminished cortisol levels in subordinate female marmosets are associated with altered central drive to the hypothalamic-pituitary-adrenal axis. *Biology of Psychiatry*, **60**, 843-849.
- Saltzman, W., Hogan, B. K., Allen, A. J., Horman, B. M. & Abbott, D. H. 2006c. Hypoestrogenism does not mediate social suppression of cortisol in subordinate female marmosets. *Psychoneuroendocrinology*, **31**, 692-702.
- Saltzman, W., Liedl, K. J., Salper, O. J., Pick, R. R. & Abbott, D. H. 2008. Post-conception reproductive competition in cooperatively breeding common marmosets. *Hormones and Behavior*, **53**, 274-286.
- Saltzman, W., Pick, R. R., Salper, O. J., Liedl, K. J. & Abbott, D. H. 2004. Onset of plural cooperative breeding in common marmoset families following replacement of the breeding male. *Animal Behaviour*, **68**, 59-73.
- Saltzman, W., Schultz-Darken, N. & Abbott, D. H. 1996. Behavioural and endocrine predictors of dominance and tolerance in female common marmosets, *Callithrix jacchus*. *Animal Behaviour*, **51**, 657-674.

- Saltzman, W., Schultz-Darken, N. & Abbott, D. H. 1997a. Familial influences on ovulatory function in common marmosets (*Callithrix jacchus*). *American Journal of Primatology*, **41**, 159-177.
- Saltzman, W., Schultz-Darken, N., Scheffler, G., Wegner, F. H. & Abbott, D. H. 1994. Social and reproductive influences on plasma cortisol in female marmoset monkeys. *Physiology and Behavior*, **56**, 801-810.
- Saltzman, W., Schultz-Darken, N., Severin, J. M. & Abbott, D. H. 1997b. Escape from social suppression of sexual behavior and of ovulation in female common marmosets. *Annals of the New York Academy of Sciences*, **807**, 567-570.
- Saltzman, W., Schultz-Darken, N., Wegner, F. H., Wittwer, D. J. & Abbott, D. H. 1998. Suppression of cortisol levels in subordinate female marmosets: reproductive and social contributions. *Hormones and Behavior*, **33**, 58-74.
- Saltzman, W., Severin, J. M., Schultz-Darken, N. & Abbott, D. H. 1997c. Behavioral and social correlates of escape from suppression of ovulation in female common marmosets housed with the natal family. *American Journal of Primatology*, **41**, 1-21.
- Sánchez, S., Peláez, F., Gil-Bürmann, C. & Kaumanns, W. 1999. Costs of infant-carrying in the cotton-top tamarin (*Saguinus oedipus*). *American Journal of Primatology*, **48**, 99-111.
- Sands, J. L. & Creel, S. R. 2004. Social dominance, aggression and fecal glucocorticoid levels in a wild population of wolves, *Canis lupus*. *Animal Behaviour*, **67**, 387-396.

- Santos, C. V., French, J. A. & Otta, E. 1997. A comparative study of infant carrying behavior in callitrichid primates: *Callithrix* and *Leontopithecus*. *International Journal of Primatology*, **18**, 889-907.
- Sapolsky, R. M. 1992. Neuroendocrinology of the stress-response. In: *Behavioral endocrinology* (Ed. by Becker, J. B.), pp. 287-324. Cambridge, MA: Massachusetts Institute of Technology Press.
- Sapolsky, R. M. 2000. Stress hormones: good and bad. *Neurobiology of Disease*, **7**, 540-542.
- Sapolsky, R. M. 2002. Endocrinology of the stress-response. In: *Behavioral endocrinology* (Ed. by Becker, J., Breedlove, S., Crews, D. & McCarthy, M.), pp. 409-450. Cambridge, MA: MIT Press.
- Savage, A. 1995. Nutrition. In: *Cotton top tamarin - husbandry manual* (Ed. by Savage, A.). Providence, Rhode Island: Roger Williams Park Zoo.
- Savage, A., Giraldo, L. H., Soto, L. H. & Snowdon, C. T. 1996a. Demography, group composition, and dispersal in wild cotton-top tamarin (*Saguinus oedipus*) groups. *American Journal of Primatology*, **38**, 85-100.
- Savage, A., Snowdon, C. T., Giraldo, L. H. & Soto, L. H. 1996b. Parental care patterns and vigilance in wild cotton-top tamarins (*Saguinus oedipus*). In: *Adaptive radiation of neotropical primates* (Ed. by Norconk, M. A., Rosenberger, A. L. & Garber, P. A.), pp. 187-199. New York, NY: Plenum Press.
- Schaffner, C. M. & French, J. A. 1997. Group size and aggression: 'recruitment incentives' in a cooperatively breeding primate. *Animal Behaviour*, **54**, 171-180.

- Scheibler, E., Weinandry, R. & Gattermann, R. 2006. Male expulsion in cooperative Mongolian gerbils (*Meriones unguiculatus*). *Physiology and Behavior*, **87**, 24-30.
- Schneider, J. E. & Wade, G. N. 1999. Inhibition of reproduction in service of energy balance. In: *Reproduction in context: social and environmental influences on reproduction* (Ed. by Wallen, K. & Schneider, J. E.), pp. 35-82. Cambridge, MA: MIT Press.
- Schoech, S. J., Mumme, R. L. & Moore, M. C. 1991. Reproductive endocrinology and mechanisms of breeding inhibition in cooperatively breeding Florida scrub jays (*Aphelocoma c. coerulescens*). *Condor*, **93**, 354-364.
- Seigel, R. A., Huggins, M. M. & Ford, N. B. 1987. Reduction in locomotor ability as a cost of reproduction in gravid snakes. *Oecologia*, **73**, 481-485.
- Setchell, J. M., Charpentier, M. & Wickings, E. J. 2005. Mate guarding and paternity in mandrills: factors influencing alpha male monopoly. *Animal Behaviour*, **70**, 1105-1120.
- Setchell, J. M., Smith, T., Wickings, E. J. & Knapp, L. A. 2008. Factors affecting fecal glucocorticoid levels in semi-free-ranging female mandrills (*Mandrillus sphinx*). *American Journal of Primatology*, **70**, 1023-1032.
- Sherman, P. W. & Jarvis, J. U. M. 2002. Extraordinary life spans of naked mole-rats (*Heterocephalus glaber*). *Journal of Zoology*, **258**, 307-311.
- Sherman, P. W., Lacey, E. A., Reeve, H. W. & Keller, L. 1995. The eusociality continuum. *Behavioral Ecology*, **6**, 102-108.
- Shine, R. 1980. "Costs" of reproduction in reptiles. *Oecologia*, **46**, 92-100.

- Siani, J. M. 2009. Costs and benefits of cooperative infant care in wild golden lion tamarins (*Leontopithecus rosalia*). In: *Behavior, Ecology, Evolution, and Systematics*, pp. 116. College Park: University of Maryland.
- Small, M. F. & Smith, D. G. 1986. The influence of birth timing upon infant growth and survival in captive rhesus macaques (*Macaca mulatta*). *International Journal of Primatology*, **7**, 289-304.
- Smith, A. C., Tirado Herrera, E. R., Buchanan-Smith, H. M. & Heymann, E. W. 2001. Multiple breeding females and allo-nursing in a wild group of moustached tamarins (*Saguinus mystax*). *Neotropical Primates*, **9**, 67-69.
- Smith, R., Mesiano, S., Chan, E.-C., Brown, S. & Jaffe, R. B. 1998. Corticotropin-releasing hormone directly stimulates dehydroepiandrosterone sulfate excretion by human fetal adrenal cortical cells. *Journal of Clinical Endocrinology and Metabolism*, **83**, 2916-2920.
- Smith, R., Wickings, E. J., Bowman, M. E., Belleoud, A., Dubreuil, G., Davies, J. J. & Madsen, G. 1999. Corticotropin-releasing hormone in chimpanzee and gorilla pregnancies. *The Journal of Clinical Endocrinology and Metabolism*, **84**, 2820-2825.
- Smith, T. E. & Abbott, D. H. 1995. Olfactory cues from unfamiliar dominant female common marmosets fail to maintain ovarian suppression in singly housed subordinates (abstract). *American Journal of Primatology*, **36**, 156.
- Smith, T. E. & Abbott, D. H. 1998. Behavioral discrimination between circumgenital odor from peri-ovulatory dominant and anovulatory female common marmosets (*Callithrix jacchus*). *American Journal of Primatology*, **46**, 265-284.

- Smith, T. E. & French, J. A. 1997a. Psychosocial stress and urinary cortisol excretion in marmoset monkeys (*Callithrix kuhlii*). *Physiology and Behavior*, **62**, 225-232.
- Smith, T. E. & French, J. A. 1997b. Social and reproductive conditions modulate urinary cortisol excretion in black tufted-ear marmosets (*Callithrix kuhlii*). *American Journal of Primatology*, **42**, 253-267.
- Smith, T. E., Schaffner, C. M. & French, J. A. 1997. Social and developmental influences on reproductive function in female Wied's black tufted-ear marmosets (*Callithrix kuhlii*). *Hormones and Behavior*, **31**, 159-168.
- Snowdon, C. T. 1996. Infant care in cooperatively breeding species. *Advanced Study in Behavior*, **25**, 643-689.
- Snowdon, C. T., Ziegler, T. E. & Widowski, T. M. 1993. Further hormonal suppression of eldest daughter cotton-top tamarins following birth of infants. *American Journal of Primatology*, **31**, 11-21.
- Soini, P. 1982. Ecology and population dynamics of the pygmy marmoset, *Cebuella pygmaea*. *Folia Primatologica*, **39**, 1-21.
- Solomon, N. G., Brant, C. L., Callahan, P. A. & Steinly Jr, B. A. 2001. Mechanisms of reproductive suppression in female pine voles (*Microtus pinetorum*). *Reproduction*, **122**, 297-304.
- Solomon, N. G. & French, J. A. 1997a. *Cooperative breeding in mammals*. Cambridge: Cambridge University Press.
- Solomon, N. G. & French, J. A. 1997b. The study of mammalian cooperative breeding. In: *Cooperative breeding in mammals* (Ed. by Solomon, N. G. & French, J. A.), pp. 1-10. Cambridge: Cambridge University Press.

- Sousa, M. B. & Ziegler, T. E. 1998. Diurnal variation on the excretion patterns of fecal steroid in common marmoset (*Callithrix jacchus*) females. *American Journal of Primatology*, **46**, 105-118.
- Sousa, M. B. C., Albuquerque, A. C. S. R., Albuquerque, F. S., Araujo, A., Yamamoto, M. E. & Arruda, M. F. 2005. Behavioral strategies and hormonal profiles of dominant and subordinate common marmoset (*Callithrix jacchus*) females in wild monogamous groups. *American Journal of Primatology*, **67**, 37-50.
- Stein, Z. & Susser, M. 1975. Fertility, fecundity, famine: food rations in the Dutch famine 1944/5 have a causal relationship to fertility and probably to fecundity. *Human Biology*, **47**, 131-154.
- Stewart, K. M., Bowyer, R. T., Dick, B. L., Johnson, B. K. & Kie, J. G. 2005. Density-dependent effects on physical condition and reproduction in North American elk: an experimental test. *Oecologia*, **143**, 85-93.
- Strier, K. B. 1991. Demography and conservation in an endangered primate, *Brachyteles arachnoides*. *Conservation Biology*, **5**, 214-218.
- Strier, K. B. 2000. Food and females. In: *Primate behavioral ecology* (Ed. by Kelbaugh, S. L.), pp. 168-194. Boston, MA: Allyn and Bacon.
- Strier, K. B. 2001. Reproductive ecology of New World monkeys. In: *Reproductive ecology and human evolution* (Ed. by Ellison, P. T.), pp. 351-367. New York, NY: Aldine de Gruyter.
- Strier, K. B., Lynch, J. W. & Ziegler, T. E. 2003. Hormonal changes during the mating and conception seasons of wild northern muriquis (*Brachyteles arachnoides hypoxanthus*). *American Journal of Primatology*, **61**, 85-99.

- Sussman, R. W. & Garber, P. A. 1987. A new interpretation of the social organization and mating system of the Callitrichidae. *International Journal of Primatology*, **8**, 3-92.
- Takahashi, H. 2002. Female reproductive parameters and fruit availability: factors determining onset of estrus in Japanese macaques. *American Journal of Primatology*, **51**, 141-153.
- Tanner, J. M. 1962. *Growth at adolescence*. Philadelphia, PA: Blackwell Scientific.
- Tardif, S. D. 1985. Histologic evidence for age-related differences in ovarian function in tamarins (*Saguinus* sp., primates). *Biology of Reproduction*, **33**, 993-1000.
- Tardif, S. D. 1994. Relative energetic cost of infant care in small-bodied Neotropical primates and its relation to infant care patterns. *American Journal of Primatology*, **34**, 133-143.
- Tardif, S. D. 1997. The bioenergetics of parental behavior and the evolution of alloparental care in marmosets and tamarins. In: *Cooperative breeding in mammals* (Ed. by Solomon, N. G. & French, J. A.). Cambridge: Cambridge University Press.
- Tardif, S. D., Araujo, A., Arruda, M. F., French, J. A., Sousa, M. B. C. & Yamamoto, M. E. 2008. Reproduction and aging in marmosets and tamarins. In: *Primate reproductive aging* (Ed. by Atsalis, S., Margulis, S. W. & Hof, P. R.), pp. 29-48. Basel: Karger.
- Tardif, S. D. & Bales, K. L. 2004. Relations among birth condition, maternal condition, and postnatal growth in captive common marmoset monkeys (*Callithrix jacchus*). *American Journal of Primatology*, **62**, 83-94.

- Tardif, S. D., Harrison, M. L. & Simek, M. L. 1993. Communal infant care in marmosets and tamarins: relation to energetics, ecology and social organization. In: *Marmosets and tamarins: systematics, behaviour, and ecology* (Ed. by Rylands, A. B.), pp. 220-234. Oxford: Oxford University Press.
- Tardif, S. D. & Jaquish, C. E. 1994. The common marmoset as a model for nutritional impacts upon reproduction. *Annals of the New York Academy of Sciences*, **709**, 214-215.
- Tardif, S. D. & Jaquish, C. E. 1997. Number of ovulations in the marmoset monkey (*Callithrix jacchus*): relation to body weight, age and repeatability. *American Journal of Primatology*, **42**, 323-329.
- Tardif, S. D., Power, M. L., Layne, D. G., Smucny, D. & Ziegler, T. E. 2004. Energy restriction initiated at different gestational ages has varying effects on maternal weight gain and pregnancy outcome in common marmoset monkeys (*Callithrix jacchus*). *British Journal of Nutrition*, **92**, 841-849.
- Tardif, S. D., Power, M. L., Oftedal, O. T., Power, R. A. & Layne, D. G. 2001. Lactation, maternal behavior and infant growth in common marmoset monkeys (*Callithrix jacchus*): effects of maternal size and litter size. *Behavioral Ecology and Sociobiology*, **51**, 17-25.
- Tardif, S. D., Richter, C. B. & Carson, R. L. 1984. Effects of sibling-rearing experience on future reproductive success in two species of Callitrichidae. *American Journal of Primatology*, **6**, 377-380.
- Tardif, S. D., Santos, C. V., Baker, A. J., Van Elsacker, L., Feistner, A. T. C., Kleiman, D. G., Ruiz-Miranda, C. R., de A. Moura, A. C., Passos, F. C., Price, E. C.,

- Rapaport, L. G. & de Vleeschouwer, K. 2002. Infant care in lion tamarins. In: *Lion tamarins: biology and conservation* (Ed. by Kleiman, D. G. & Rylands, A. B.), pp. 213-232. Washington, D.C.: Smithsonian Institution Press.
- Tardif, S. D., Smucny, D. A., Abbott, D. H., Mansfield, K., Schultz-Darken, N. & Yamamoto, M. E. 2003. Reproduction in captive common marmosets (*Callithrix jacchus*). *Comparative Medicine*, **53**, 364-368.
- Tardif, S. D. & Ziegler, T. E. 1992. Features of female reproductive senescence in tamarins (*Saguinus* spp.), a New World primate. *Journal of Reproduction and Fertility*, **94**, 411-421.
- Tardif, S. D., Ziegler, T. E., Power, M. L. & Layne, D. G. 2005. Endocrine changes in full-term pregnancies and pregnancy loss due to energy restriction in the common marmoset (*Callithrix jacchus*). *The Journal of Clinical Endocrinology and Metabolism*, **90**, 335-339.
- Terborgh, J. 1983. Five New World primates: a study in comparative ecology. In: *Monographs in behavior and ecology* (Ed. by Krebs, J. R. & Clutton-Brock, T. H.). Princeton, NJ: Princeton University Press.
- Terborgh, J. & Goldizen, A. W. 1985. On the mating system of the cooperatively breeding saddle-backed tamarin (*Saguinus fuscicollis*). *Behavioral Ecology and Sociobiology*, **16**, 293-299.
- Terborgh, J. & Stern, M. 1987. The surreptitious life of the saddle-backed tamarin. *American Scientist*, **75**, 260-269.
- Thompson, K. V. 1995a. Flehmen and birth synchrony among female sable antelope, *Hippotragus niger*. *Animal Behaviour*, **50**, 475-484.

- Thompson, K. V. 1995b. Ontogeny of flehmen in sable antelope, *Hippotragus niger*. *Ethology*, **101**, 213-221.
- Thompson, S. D., Power, M. L., Rutledge, C. E. & Kleiman, D. G. 1994. Energy metabolism and thermoregulation in the golden lion tamarin (*Leontopithecus rosalia*). *Folia Primatologica*, **63**, 131-143.
- Tutin, C. E. G. 1979. Responses of chimpanzees to copulation, with special reference to interference by immature individuals. *Animal Behaviour*, **27**, 845-854.
- Umezaki, H., Hess, D. L., Valenzuela, G. J. & Ducsay, C. A. 2001. Fetectomy alters maternal pituitary-adrenal function in pregnant rhesus macaques. *Biology of Reproduction*, **65**, 1616-1621.
- Van Belle, S., Estrada, A., Ziegler, T. E. & Strier, K. B. 2009. Sexual behavior across ovarian cycles in wild black howler monkeys (*Alouatta pigra*): male mate guarding and female mate choice. *American Journal of Primatology*, **71**, 153-164.
- van Schaik, C. P. & van Noordwijk, M. A. 1985. Interannual variability in fruit abundance and the reproductive seasonality in Sumatran long-tailed macaques (*Macaca fascicularis*). *Journal Zoology, London*, **206**, 533-549.
- Vandenbergh, J. G. & Izard, M. K. 1983. Pheromonal control of the bovine ovarian cycle. In: *Chemical signals in vertebrates* (Ed. by Müller-Schwarze, D. & Silverstein, R. M.), pp. 153-158. New York, NY: Plenum Press.
- Videan, E., Fritz, J., Heward, C. & Murphy, J. 2008. Reproductive aging in female chimpanzees (*Pan troglodytes*). In: *Primate reproductive aging. Interdisciplinary topics in gerontology* (Ed. by Atsalis, S., Margulis, S. W. & Hof, P. R.), pp. 103-118. Basel: Karger.

- Vitt, L. J. 1981. Lizard reproduction: habitat specificity and constraints on relative clutch mass. *The American Naturalist*, **117**, 506-514.
- Vitt, L. J. & Congdon, J. D. 1978. Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. *The American Naturalist*, **112**, 595-608.
- Vitt, L. J. & Price, H. J. 1982. Ecological and evolutionary determinants of relative clutch mass in lizards. *Herpetologica*, **38**, 237-255.
- von Holst, D. 1998. The concept of stress and its relevance for animal behavior. *Advanced Study in Behavior*, **27**, 1-131.
- Wasser, S. K. & Barash, D. P. 1983. Reproductive suppression among female mammals: implications for biomedicine and sexual selection theory. *Quarterly Review of Biology*, **58**, 513-538.
- Wasser, S. K., Norton, G. W., Rhine, R. J., Klein, N. & Kleindorfer, S. 1998. Ageing and social rank effects on the reproductive system of free-ranging yellow baboons (*Papio cynocephalus*) at Mikumi National Park, Tanzania. *Human Reproduction Update*, **4**, 430-438.
- Wasser, S. K. & Starling, A. K. 1988. Proximate and ultimate causes of reproductive suppression among female yellow baboons at Mikumi National Park, Tanzania. *American Journal of Primatology*, **16**, 97-121.
- Weir, J., Dunn Jr., J. E. & Jones, E. G. 1971. Race and age at menarche. *American Journal of Obstetrics and Gynecology*, **111**, 594-596.
- West-Eberhard, M. J. 1975. The evolution of social behaviour by kin selection. *Quarterly Review of Biology*, **50**, 1-35.

- Wieczkowski, J. 2005. Examination of increased annual range of a Tana mangabey (*Cercocebus galeritus*) group. *American Journal of Physical Anthropology*, **128**, 381-388.
- Williams, G. C. 1957. Pleiotropy, natural selection, and the evolution of senescence. *Evolution*, **11**, 398-411.
- Windle, C. P., Baker, H. F., Ridley, R. M., Oerke, A.-K. & Martin, R. D. 1999. Unreared litters and prenatal reduction of litter size in the common marmoset (*Callithrix jacchus*). *Journal of Medical Primatology*, **28**, 73-83.
- Wingfield, J. C. 1994. Modulation of the adrenocortical response to stress in birds. In: *Perspectives in comparative endocrinology* (Ed. by Davey, K. G., Peter, R. & Toby), pp. 520-528. Ottawa, Ontario: National Research Council of Canada.
- Wolanski, N. 1968. Environmental modification of human form and function. *Annals of the New York Academy of Sciences*, **134**, 826-840.
- Wolfe, L. G., Deinhardt, F., Ogden, J. D., Adams, M. R. & Fisher, L. E. 1975. Reproduction of wild-caught and laboratory-born marmoset species used in biomedical research (*Saguinus* sp., *Callithrix jacchus*). *Laboratory Animal Science*, **25**, 802-813.
- Young, A. J., Carlson, A. A., Monfort, S. L., Russell, A. F., Bennett, N. C. & Clutton-Brock, T. H. 2006. Stress and the suppression of subordinate reproduction in cooperatively breeding meerkats. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 12005-12010.

- Young, A. J. & Clutton-Brock, T. H. 2006. Infanticide by subordinates influences reproductive sharing in cooperatively breeding meerkats. *Biology Letters*, **2**, 385-387.
- Young, A. J., Monfort, S. L. & Clutton-Brock, T. H. 2008. The causes of physiological suppression among female meerkats: a role for subordinate restraint due to the threat of infanticide? *Hormones and Behavior*, **53**, 131-139.
- Young, A. J., Spong, G. & Clutton-Brock, T. H. 2007. Subordinate male meerkats prospect for extra-group paternity: alternative reproductive tactics in a cooperative mammal. *Proceedings of the Royal Society Biological Sciences*, **274**, 1603-1609.
- Zahavi, A. 1990. Arabian babblers: the quest for social status in a cooperative breeder. In: *Cooperative breeding in birds* (Ed. by Stacey, P. B. & Koenig, W. D.), pp. 103-130. Cambridge: Cambridge University Press.
- Ziegler, T. E., Scheffler, G. & Snowdon, C. T. 1995. The relationship of cortisol levels to social environment and reproductive functioning in female cotton-top tamarins, *Saguinus oedipus*. *Hormones and Behavior*, **29**, 407-424.
- Ziegler, T. E. & Sousa, M. B. 2002. Parent-daughter relationships and social controls on fertility in female common marmosets, *Callithrix jacchus*. *Hormones and Behavior*, **42**, 356-367.
- Ziegler, T. E., Washabaugh, K. F. & Snowdon, C. T. 2004. Responsiveness of expectant male cotton-top tamarins, *Saguinus oedipus*, to mate's pregnancy. *Hormones and Behavior*, **45**, 84-92.