



High rates of pregnancy loss by subordinates leads to high reproductive skew in wild golden lion tamarins (*Leontopithecus rosalia*)

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ABSTRACT

Across taxa, cooperative breeding has been associated with high reproductive skew. Cooperatively breeding golden lion tamarins (*Leontopithecus rosalia*) were long thought to have a monogynous mating system in which reproduction was limited to a single dominant female. Subordinates with few reproductive opportunities delayed dispersal and remained in the natal group to provide alloparental care to siblings, thus allowing dominant reproductive females to meet the energetic needs associated with high rates of reproduction and successful infant rearing. The goal of this study was to re-assess monogyny in wild golden lion tamarin groups based upon pregnancy diagnoses that used non-invasive enzyme immunoassay for progesterone and cortisol, combined with weekly data on individual weight gain, bi-annual physical examinations noting pregnancy and lactation status and daily behavioral observations. We established quantitative and qualitative criteria to detect and determine the timing of pregnancies that did not result in the birth of infants. Pregnancy polygyny occurred in 83% of golden lion tamarin groups studied. The loss of 64% of subordinate pregnancies compared to only 15% by dominant females limited reproductive success mainly to dominant females, thus maintaining high reproductive skew in female golden lion tamarins. Pregnancy loss by subordinate adults did not appear to result from dominant interference in subordinate hormonal mechanisms, but more likely resulted from subordinate abandonment of newborn infants to mitigate dominant aggression.

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Introduction

In cooperatively breeding species, reproduction is commonly limited to one or a few dominant individuals of each sex (Clutton-Brock, 2009). The young born to breeding females are reared by all group members, including non-reproductive helpers. Several mechanisms have been suggested to explain high reproductive skew in female cooperative breeders, including lower concentrations of reproductive hormones in subordinates (Creel et al., 1992; Faulkes and Bennett, 2001; Mays et al., 1991; Schoech et al., 1991), suppression of subordinate ovulation (Abbott, 1984; Faulkes and Bennett, 2001; French, 1997; Solomon et al., 2001), dominant interference in subordinate mating (Abbott, 1984), behavioral

suppression of subordinate reproduction (Clutton-Brock et al., 2008; De Vleeschouwer et al., 2001; Inglett et al., 1989; Kleiman, 1979; Kutsukake and Clutton-Brock, 2006), stress-induced infertility and pregnancy loss (Gilchrist, 2006a; Pottinger, 1999; Wasser and Barash, 1983; Young et al., 2006), infanticide (Clutton-Brock et al., 1998a; Gilchrist, 2006a; Hoogland, 1985; Saltzman et al., 2009) and ecological constraints on subordinate reproduction (Clutton-Brock et al., 2001a; Creel and Creel, 1991; Emlen, 1982; Hatchwell and Komdeur, 2000; Kleiman, 1977b). If multiple females produce litters at the same time the amount of help received by the offspring of the dominant female may be reduced, resulting in lower infant growth and/or survival (Clutton-Brock et al., 2001b; Digby, 1995a; Hodge, 2009) and reduced dominant fecundity (Clutton-Brock et al., 1998b; Fite et al., 2005; Russell et al., 2003). Therefore, dominant females able to limit subordinate reproduction should have a selective advantage. Indeed, 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 and French, 1997), birds (Mays et al., 1991; Reyer et al., 1986; Schoech et al., 1991), fishes (Fitzpatrick et al., 2008) and invertebrates (Hamilton, 2004).

As long-term field research continues, the presence of multiple breeding females within cooperatively breeding groups originally

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described as monogynous or singular breeding has been observed in an increasing number of species including blue tits (*Parus caeruleus* (Kempnaers, 1994)), wolves (*Canis lupus* (Mech, 2000)), naked mole-rats (*Heterocephalus glaber* (Faulkes and Abbott, 1997)), dwarf mongooses (*Helogale parvula* (Creel and Waser, 1991)), common marmosets (*Callithrix jacchus* (Arruda et al., 2005; Digby, 1995b; Digby and Ferrari, 1994; Hubrecht, 1984)), pygmy marmosets (*Cebuella pygmaea* (Soini, 1982)), cotton-top tamarins (*Saguinus oedipus* (Savage et al., 1996)), saddle-back tamarins (*Saguinus fuscicollis* (Goldizen et al., 1996)) and mustached tamarins (*Saguinus mystax* (Garber et al., 1993, 1984; Ramirez, 1984; Smith et al., 2001)). Though multiple breeding females may be present, high reproductive skew remains, with subordinates having lower reproductive success than dominant females in banded mongooses (*Mungos mungo* (Gilchrist, 2006a, 2006b)), dwarf mongooses (Creel and Waser, 1997), meerkats (*Suricata suricatta* (Clutton-Brock et al., 2008; Young et al., 2006)), marmosets (Arruda et al., 2005; Digby, 1995a; Saltzman et al., 2008, 2009; Sousa et al., 2005) and tamarins (Garber, 1997; Goldizen et al., 1996). In 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 and McGrew, 1991; Savage et al., 1996). Non-invasive hormonal assays to determine the reproductive status of all group members can be used to reassess mating patterns in cooperatively breeding species as well as illuminate the mechanisms responsible for maintaining high reproductive skew in spite of the presence of multiple breeding females.

Marmosets and tamarins, neotropical primates in the family Callitrichidae (genera *Callithrix*, *Cebuella*, *Saguinus* and *Leontopithecus*), were long thought to have a monogynous mating system in which reproduction was limited to a single dominant female (Goldizen, 1987; Sussman and Garber, 1987). Golden lion tamarins (GLTs, *Leontopithecus rosalia*) are cooperative breeders that display a high degree of reproductive skew, with reproduction limited to one or a few dominant individuals of each sex even in groups containing as many as 13 individuals (Dietz and Baker, 1993). Dietz and Baker (1993) described the mating system in GLTs as monogyny with about a 10% incidence of polygyny. However, when examining only those groups containing more than one potentially reproductive female, 44.3% showed pregnancy polygyny (i.e. more than one female was confirmed to be pregnant within the same breeding season) and 26.2% showed rearing polygyny (more than one female reared offspring to weaning) (Baker et al., 2002; Dietz and Baker, 1993). Lion tamarin offspring typically delay dispersal and reproduction, and remain in their natal group to help with the care of infant siblings (Dietz and 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 (Baker et al., 1993; Dietz and Baker, 1993; Kleiman, 1977a; Sussman and Garber, 1987). Therefore, lion tamarins represent a good candidate species for evaluating the occurrence of, and mechanisms underlying, singular vs. plural breeding in a cooperatively breeding mating system.

The goal of this study was to re-assess the degree of polygyny in wild GLT groups based upon pregnancy diagnoses that used non-invasive hormonal enzyme immunoassay for progesterone and cortisol combined with weekly data on individual weight gain, pregnancy and lactation status from bi-annual capture records and behavioral observations. We collected the following data on females residing within seven groups of GLTs over three reproductive years: group demography, dominance status, reproductive status and reproductive success defined as pregnancies that resulted in the birth of live offspring. We tested two competing predictions derived from the hypothesis that reproduction is limited to a single dominant female in the majority of GLT groups. To the extent that dominant females fully 'control' reproduction in subordinates, we predicted that subordinate adult female GLTs would not become pregnant while residing within their natal group. In the case where dominant female control was incomplete, we predicted that

pregnancies by dominant adult female GLTs would result in the birth of live offspring; whereas pregnancies by subordinate adult female GLTs would not. We also examined two alternative methods by which dominant females may control subordinate reproduction to maintain high reproductive skew. If dominant females suppress subordinate reproduction via hormonal mechanisms, we predicted that subordinates would not get pregnant, or at the least, that hormonal patterns during subordinate pregnancy would be abnormal, resulting in higher rates of subordinate pregnancy loss. Alternatively, if dominant females suppress subordinate reproduction via behavioral mechanisms, we predicted that subordinates might become pregnant, but that dominant aggression and harassment of pregnant subordinates would result in higher rates of pregnancy loss. We also predicted that the offspring of subordinate females might not survive because they would not receive infant care from group members attempting to avoid dominant aggression.

Methods

Study site and species

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 and Dietz, 2006). PDA holds the largest remaining population of GLTs in the wild, with an estimated 350 GLTs in the secondary forests protected by the reserve (Ruiz-Miranda et al., 2008; Rylands et al., 2002).

Individual identification and weighing

The animals under study at PDA are native and non-manipulated 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 and 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).

Group demography

We 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. Data were collected 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, with losses typically filled by immigrants. 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 (Bales et al., 2001; Dietz et al., 1994; French et al., 2003). Adults were defined as individuals older than 18 months of age (Dietz and Baker, 1993), corresponding to the average age of sexual maturation (Dietz et al., 1994; French and

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