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Predation rate and future reproductive potential explain home range size in golden lion tamarins

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The ecological constraints hypothesis states that as group size increases, groups travel further and occupy larger home ranges in order to meet basic energetic needs for survival and reproduction. In this paper we used 19 years of demographic and ranging data on a study population of golden lion tamarins, *Leontopithecus rosalia*, to examine this hypothesis. Significant variation in rate of predation on lion tamarins during the study affected group size, membership and population density, which allowed us to test for predicted correlations between these changes and home range size. We found that predation-mediated changes in group composition and population density explained 71% of variation in home range size. Increased predation decreased lion tamarin home ranges because of the effects of decreased group size, fewer adult natal males and fewer reproductive females in the group. The effect of these factors on decreased ranging was offset somewhat by lower population density during high predation, which resulted in range expansion due to reduced pressure from neighbouring groups. We also found that groups with high future reproductive potential (i.e. with multiple breeding females) increased their range size. This effect was independent of group size. We propose a new hypothesis, that taxa with high rates of reproduction, such as lion tamarins, will increase home range size to accommodate future energy needs, rather than current needs, as would be predicted by the ecological constraints hypothesis. No or low production of infants and litters on the smallest lion tamarin ranges in our study supports this new hypothesis.

Animals are thought to occupy the smallest home ranges adequate to provide energy sufficient for survival and reproduction (Maynard Smith, 1974; Wilson, 1975), a hypothesis supported by the relationship between body size, energetic demands and home range size (Mace, Harvey, & Clutton-Brock, 1983; McNab, 1963; Milton & May, 1976). Extending this logic to use of space in social animals, food availability may limit group size when a group must travel farther than an individual forager to meet its energetic needs (Chapman, 1990; Clutton-Brock & Harvey, 1977; Milton, 1984; Terborgh, 1983; Wrangham, Gittleman, & Chapman, 1993). This ecological constraints model has been the dominant explanation of the relationship between group size and travel patterns for the last 25 years, with support for the model coming from many studies (Barton, Whiten, Strum, Byrne, & Simpson, 1992; Dias & Strier, 2003; Gillespie & Chapman, 2001; Herrera & MacDonald, 1989; Isbell, 1991; Teichroeb & Sicotte, 2009; Watts, 1998), and exceptions from others (Butynski, 1990; Isbell, 1983, 2012; Struhsaker & Leland, 1987; Yeager & Kirkpatrick, 1998). The ecological constraints model has been used to predict, for example, increases in day range, travel rate, time spent travelling, time spent feeding and home range size (Chapman, Wrangham, & Chapman, 1995; Clutton-Brock & Harvey, 1977; Gillespie & Chapman, 2001; Janson & Goldsmith, 1995; Milton, 1984; Milton & May, 1976).

However, an interaction of food availability and group size may be insufficient to predict travel patterns in some group-living species (Adams, 2001; Isbell, 2012). Space use may reflect the combined effects of several factors acting at different levels (Chapman & Chapman, 2000a), including breeding system (Clutton-Brock & Harvey, 1977; Maher & Burger, 2011), social factors (Chapman & Pavelka, 2005; Isbell, 1983), human-altered landscapes (Gurarie, Suutarinen, Kojola, & Ovaskainen, 2011; Isbell, 2012; Rich, Mitchell, Gude, & Sime, 2012) and population density (Benson, Chamberlain, & Leopold, 2006; Horiuchi, 2006; Maher & Burger, 2011). Independent of the effect of group size, home range size may be related to the number of adult males or females in a group. More adult males may increase home range size

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because of heightened defence capabilities (Lehmann & Boesch, 2003; Peres, 1989; Ramos-Fernandez, Smith Aguilar, Schaffner, Vick, & Aureli, 2013), with adult females contributing to group defence in some taxa (Isbell, 1991; Lehmann & Boesch, 2003). In addition to defence, the assessment of potential breeding vacancies in neighbouring groups, such as during intergroup encounters (Baker & Dietz, 1996; Garber, Pruetz, & Isaacson, 1993; Lazaro-Perea, 2001), may also affect ranging patterns. Finally, Huxley (1934) postulated that when density increases, heightened pressure from neighbouring groups results in a decrease in home range size. A negative relationship between population density and home range size has been found in several taxa: birds (Holmes, 1970; Huxley, 1934), social carnivores (Benson et al., 2006), ungulates (Kjellander et al., 2004), bears (Dahle & Swenson, 2003), pigs (Saunders & McLeod, 1999) and primates (Horiuchi, 2006).

To our knowledge, no study has examined the effects of all these factors on home range size. We use 19 years of data collected on golden lion tamarins, *Leontopithecus rosalia*, at Poço das Antas Reserve, Brazil to test four nonmutually exclusive hypotheses explaining variation in home range size: group size, adult male presence, adult female presence and population density. We also examine the impact of changes in the level of predation across the study period.

Summary of Golden Lion Tamarin Social Organization in Poço das Antas Reserve

Golden lion tamarins are small, cooperative breeding primates that feed on fruits and insects, live in groups ranging in size from 3 to 14 individuals, and defend partially overlapping territories (Lapenta, de Oliveira, & Nogueira-Neto, 2007; Miller & Dietz, 2005; Peres, 1989) that range in size from 17.4 to 87.7 ha (Hankerson, 2008). In a 10-year study including 22 territorial groups habituated to the presence of observers and tracked for 1749 group-months (reviewed in Baker, Bales, & Dietz, 2002), most golden lion tamarin groups contained one reproductive female. In all cases in which two females successfully reared young in the same season (and the female–female relationship was known), the two females were mother and daughter. In nearly half the documented group-months, golden lion tamarin groups in this population were potentially polyandrous (i.e. contained two or occasionally more adult males unrelated to the current breeding female). Natal males were not observed copulating with reproductive females, typically their mother or sister. Behavioural and demographic data support the conclusion that potentially polyandrous groups typically were genetically monoandrous, with a single behaviourally dominant male monopolizing paternity.

Group Size Hypothesis

In this study we examine the relationship between group size and home range by testing two predictions. First, if space use is determined by current energetic demands of group members competing among themselves or with other groups for food (Isbell, 1991), there will be a positive relationship between group size, or biomass, and home range size. Second, groups in high-quality habitat will have smaller home ranges than groups in poor-quality habitat.

Male Presence Hypothesis

The presence of multiple adult males in a social group may increase home range size for two reasons: (1) additional males increase the group's defensive capabilities, or (2) additional males require the group to increase its range to find additional breeding positions in neighbouring groups ('prospecting'). We examine the male presence hypothesis by looking at the impact of the number of males, both potentially breeding and natal, on home range size.

Female Presence Hypothesis

The presence of more than one adult female in a group may increase home range size for three reasons: (1) additional reproductive females may result in increased reproductive output and, thus, the need for additional resources; (2) as for males, the presence of multiple reproductive females or adult natal females requires increased travel to 'prospect' for breeding opportunities; or (3) additional reproductive or adult natal females allow the group to defend a larger area and, therefore, more resources. A difference in home range size between groups containing one versus two reproductive females, but no difference between groups with versus without adult natal females would support the reproductive output explanation.

Population Density

We also examine the effect of population density on home range size. If small home ranges are the result of crowding under high population density we predict that lion tamarin ranges will contract during periods of high population density and expand when density is reduced.

Predation

In this and other studies on social mammals, predation has been identified as the cause of large and inconsistent changes in population and group demography (Anderson, 1986; Caine, 1993; Isbell, 1990; Isbell, Young, Jaffe, Carlson, & Chandellor, 2009; Stanford, 1998). Starting in the mid-1990s, the rate of predation on lion tamarins in Poço das Antas Reserve increased dramatically (Franklin, Hankerson, Baker, & Dietz, 2007; Franklin, Miller, Baker, & Dietz, 2007). Prior to this time, the majority of predation events involved the loss of single individuals, with only an occasional event involving multiple lion tamarins. In contrast, from May 1996 through March 2004, partial or whole groups commonly fell victim to predators in the reserve (Franklin, Hankerson, et al., 2007; Franklin, Miller, et al., 2007). While the exact predator(s) was unknown, researchers strongly suspected the role of the of tayra, *Eira barbara*, in these events. The predation rate prior to 1996 was 0.18 golden lion tamarins per group per year, increasing to 0.55 lion tamarins per group per year from 1996 to 2004 (Franklin, Hankerson, et al., 2007; Franklin, Miller, et al., 2007). This variation in predation rate resulted in changes in group size, membership, population density, and ultimately, in home range size. Predation has been reported to alter population density and demography but its impact on home range size is unclear. In general, home range sizes have been predicted to decrease with decreasing group size and increase with decreasing population density. The strength of each of these inputs on home range size will be evaluated through this research.

METHODS

Study Site and Data Collection

We collected data on group composition and movement of golden lion tamarins in Poço das Antas Biological Reserve (22°30–33′S, 42°15–19′W), Rio de Janeiro State, Brazil from January 1987 through January 2006. The reserve is a 6300 ha