Dispersal, Group Formation and Kinship in the Black-Faced Lion Tamarin (*Leontopithecus caissara*)

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Key Words

Demography · Dispersal · Group formation · Callitrichidae · Lion tamarin · *Leontopithecus caissara*

Abstract

We report on (i) new group formation, (ii) sex differences in dispersal and (iii) dispersal distance over 6 years for 3 social groups of the black-faced lion tamarin (*Leontopithecus caissara*) in the vicinity of Ariri, São Paulo state, Brazil. The groups were: Bina (monitored for 74 months), BM5 (52 months) and Teca (13 months). Each group was censused once a week and monitored for 3 days each month. Mating opportunities were found to be the incentive for young adult black-faced lion tamarins to either disperse or remain in their kin group. Young adults show delayed dispersal that is related to the cooperative breeding system characteristic of the Callitrichidae and to a low population density which hinders the formation of new breeding pairs. Our findings suggest that in *L. caissara* (i) both sexes disperse, (ii) successful immigration is related to breeding opportunities in an existing group, (iii) female immigration motivates male emigration and the formation of new groups, and (iv) emigrants tend to form new groups close to their natal groups. These patterns of dispersal and formation of new groups are efficient because the species has been able to avoid loss of genetic diversity despite their small population size.

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Introduction

The black-faced lion tamarin *Leontopithecus caissara* [Lorini and Persson, 1990] is today the only lion tamarin still classified as ‘critically endangered’ on the Red List of Threatened Species of the International Union for Conservation of Nature [IUCN, 2008]. The population of about 400 individuals [Nascimento et al., 2011a] is restricted to approximately 300 km² in the extreme south of the state of São Paulo and north-west of the state of Paraná (fig. 1) [Lorini and Persson, 1994].

This minuscule range of *L. caissara* is today divided into insular and continental populations due to the construction of the Varadouro Canal in 1953. Today 4 separate populations remain: the island population of Superagui (Paraná) and 3 on the mainland, in the valley of the Rio dos Patos and Sebuí region (Paraná), and the other in the vicinity of Ariri to the north (São Paulo; fig. 1). The 4 populations are restricted to lowland mature and continuous forest [Lorini and Persson, 1994; Schmidlin, 2004; Nascimento and Schmidlin, 2011; Nascimento et al., 2011b].

Despite recent advances in our understanding of the behaviour, ecology and genetics of *L. caissara* [Moro-Rios, 2009; Ludwig, 2011; Martins et al., 2011; Nascimento et al., 2011a, b; Nascimento and Schmidlin, 2011; Barriento, 2013], the mechanisms of dispersal and new group formation, an understanding of which is important for conservation management, are still unknown. Dispersal is an important component of population and demographic dynamics – immigration and emigration directly influence population size and structure.

Mating systems are the prime drivers of differences in dispersal patterns among species [Griffin and West, 2002; Dobson, 2013]. All the marmosets, tamarins and lion tamarins of the family Callitrichidae live in groups that breed cooperatively and have a flexible mating system that spans monogamy, polyandry and polygyny [Rylands, 1986; Goldizen, 1987, 1988; Baker, 1991; Digby and Barreto, 1993; Baker et al., 2002] and makes dispersal dynamics more complex [Tomasello and Call, 1997; Cunningham and Jason, 2007].

Lion tamarins are socially monogamous, despite a certain promiscuity, and adult and subadult group members help in the care of the offspring of a, usually single, breeding female [Baker et al. 2002; Anzenberger and Falk, 2012]. In lion tamarins, this cooperative breeding system has played an important role in the evolution of their social behaviour [Baker et al., 2002]. Older siblings learn how to care for their younger kin [Kleiman et al., 1988; Rylands, 1993, 1996; Tardif et al., 2002], and delayed or limited dispersal is to be expected [Hamilton, 1964; Griffin and West, 2002].

Information available for the other lion tamarins, mainly *L. rosalia*, has shown that group dynamics and demography are driven largely by related individuals and that both males and females disperse [Baker, 1991; Dietz et al., 1996; Baker et al., 2002]. Successful immigration in *L. rosalia* has been found to be rare and strongly male biased, and to occur mostly in the context of replacement of individuals in a group [Baker and Dietz, 1996]. Long-term studies have also shown that cooperative polyandry or polygyny occurs in some groups of *L. rosalia* and *L. chrysomelas* [Baker et al., 2002].

Here we report on dispersal patterns in wild *L. caissara* groups observed during a 6-year study in the state of São Paulo. We observed (i) the formation of new groups, (ii) possible sex differences in dispersal rates and (iii) recorded the distance in relation to their natal group at which emigrants established their home range.

Fig. 1. Geographic distribution of the black-faced lion tamarin (*Leontopithecus caissara*).

We expected that existing groups would be composed mainly of related individuals and that dispersal was related to the replacement of the usually single breeding females and their mates. We also supposed that both sexes were equally likely to disperse and that dispersing individuals would establish their range as near as possible

to their natal territory. Both sexes should disperse, since opportunities to occupy the breeding position can become available for both males and females. Both sexes suffer intrasexual competition, and the advantages and disadvantages of either dispersing or remaining in their groups are similar. Those that disperse should try to fix their home on known areas avoiding the risks associated with dispersal.

Methods

Study Area

The study was carried out in the vicinity of the village of Ariri (25°13'04" S; 48°02'22" W) in the Lagamar de Cananeia State Park, in the state of São Paulo; the northernmost locality of the known range of *L. caissara* (fig. 1). The forest in this region is taller and more stratified than is typical of disturbed forest fragments [Roderjan and Kuniyoshi, 1988; Schmidlin, 2004].

Study Groups and Data Collection

We monitored 3 groups of lion tamarins: Bina, BM5 and Teca. They were captured to change radio-collars, take biometric data, and record the age and sex of each individual. The Bina group was captured 9 times over 74 months, BM5 twice over 52 months and Teca once during 13 months. Each group was generally censused at least once a week, and they were monitored for 3 or more days each month to collect systematic data on use of space. The long-term data on ranging behaviour will be reported in a separate paper [Nascimento et al., in preparation].

Initially, the groups were composed of 3 (Bina), 2 (BM5) and 7 individuals (Teca; table 1). We recorded changes in group composition and the behaviour of potentially dispersing individuals in each group, and monitored potential immigrants.

Results

Demographics, Kinship and the Formation of New Groups

The composition of the Bina group ranged from 3 to 9 members during 74 months of monitoring (October 2005 to November 2011; table 1). The BM5 group was formed in September 2007, when a young female FaB, until then unknown to the field research team, entered the Bina group and dispersed in that same month with M05, a radio-collared young male born in October 2005. The group formed by this pair (BM5) increased to 7 over the course of 52 months with the birth of 6 offspring in all, and the dispersal of the first, FB08, in November 2011. The Bina group began to break up when the breeding pair MaEnf and FaBina, each accompanied by an infant, disappeared in April 2011 and October 2011, respectively. It was renamed as Teca group when their daughter, born in October 2008 (F08Teca), became the dominant female, pairing with a male MaF08 that entered the group in November 2011 (table 1).

During 13 months of monitoring, the Teca group varied from 7 to 9 individuals, initially having 4 descendants of the Bina group – F08Teca's siblings – but one of which (M08) dispersed in December 2011. Two infants were born in November 2011 (NT1.11 and NT2.11) and another 2 (NT1.12 and NT2.12) in December 2012. A sibling of F08Teca (F10.1) dispersed in April 2012, and a male (MF10.2) entered the Teca group in November 2012.

FaBina, the breeding female of the Bina group from October 2005 to October 2011, had 5 sets of twins and 2 single births during the study period (74 months). She did not give birth in 2009 but produced twins twice in 2010, in January and October.

Table 1. Demographic events in the groups Bina, Teca and BM5 over the course of the study

Group	Year	Offspring	Probable death	Death or dispersal	Dispersal	Age at dispersal (emigrants), months	Total individuals	Total kin	Individuals in the group
Bina	Oct 2005	1 (Oct)	–	–	–	–	3	3	FaBina, MaEnf, M05
	2006	2 (Nov)	–	–	–	–	5	5	FaBina, MaEnf, M05, M06, F06
	2007	1 (Oct)	–	–	I (FaB) + E (M05) ¹	24	5	5	FaBina, MaEnf, M06, F06, F07
	2008	2 (Oct)	–	F06	–	–	6	6	FaBina, MaEnf, M06, F07, F08Teca, M08
	2009	–	–	–	I (FemaleUnknownM06 ²)	–	6	6	FaBina, MaEnf, M06, F07, F08Teca, M08
	2010	4 (2 Jan, 2 Oct)	–	F07	–	–	9	9	FaBina, MaEnf, M06, F08Teca, M08, F10, F10.1, F10.2, M10
	Nov 2011	2 (Feb)	4 (MaEnf + N1-11/Apr, FaBina + N2-11/Oct)	–	E (M06 + F10/Jul)	56 and 18	5	5	F08Teca, M08, F10.1, F10.2, M10
Teca	Nov 2011	2 (Nov)	–	–	I (MaF08/Nov); E (M08/Dec)	38	7	6	MaF08, F08Teca, F10.1, F10.2, M10, NT1.11, NT2.11
	Dec 2012	2 (Dec)	–	–	E (F10.1/Apr); I (MF10.2/Nov)	22	9	7	MaF08, F08Teca, MF10.2, F10.2, M10, NT1.11, NT2.11, NT1.12, NT2.12
BM5	Sep 2007	–	–	–	–	–	2	2	FaB, M05a
	2008	1 (Nov)	–	–	–	–	3	3	FaB, M05a, FB08
	2009	1 (Dec)	–	–	–	–	4	4	FaB, M05a, FB08, FB09
	2010	2 (Oct)	–	–	–	–	6	6	FaB, M05a, FB08, FB09, NB1.10, NB2.10
	Dec/2011	2 (Dec)	–	–	E (FB08/Nov)	36	7	7	FaB, M05a, FB09, NB1.10, NB2.10, NB1.11, NB2.11

I = Immigrant; E = emigrant.
¹ Founded group BM5. ² This female probably died since M06 returned to the Bina group 2 weeks after dispersal.

Two of the infants (F06 and F07) disappeared; their fate was not ascertained. Three of the infants emigrated: M05 paired with a female FaB and formed a new group BM5; and M06 and F10 emigrated together (table 1).

Two pairs of twins were born to F08Teca during the course of 13 months; the first in November 2011 and the second in December 2012. The first was soon after MaF08 had entered the group, meaning that conception, presuming he was the father, must have occurred during intergroup encounters of the Bina group. The breeding pair of BM5 produced its first infant in November 2008, 14 months after forming the group. The 4 births in 52 months were in October, November and December; the first 2 were singletons and the following 2 were twins. All but 2 of the 13 births recorded in the 3 groups were between October and December. The 2 exceptions were one in January (Bina group in 2010) and another in February (also the Bina group in 2011).

During the study we registered 4 deaths, all in the Bina group in 2011: FaBina, MaEnf, N1–11 and N2–11. These deaths we believe to have been the result of predation, probably when each of the 2 adults was carrying offspring; MaEnf and N1–11 in April and FaBina and N2–11 in October (table 1). Two of the Bina infants (F06 and F07) may have been killed.

Table 2. Dispersal events observed for the black-faced lion tamarin groups Bina, BM5 and Teca

Individual	Group	Dispersal	Age at dispersal, months	Notes
M05	Bina	E	24	Paired with FaB to form the BM5 group; took over the range of the Bina group
M06 + F10	Bina	E	56, 18	Siblings of different ages; set up a group adjacent to the Bina group
FB08	BM5	E	36	Paired with an unknown male; set up a group near the BM5 group
M08	Teca	E	38	Forced emigration (kin competition); entered the same group as that of M06 and F10
F10.1	Teca	E	22	Forced emigration (kin competition); fate unknown
FaB	Bina	I	Unknown	Failed to establish itself in the Bina group, but paired with M05 and emigrated to form the BM5 group; took over the range of the Bina group
FemaleUnknow M06	Bina	I	Unknown	Failed to enter the Bina group; paired with M06 on an ephemeral dispersal; probably died since M06 returned to the Bina group
MaF08	Bina/Teca	I	Unknown	Entered the Teca group, pairing with F08Teca
MaF10.2	Teca	I	Unknown	Entered the Teca group and may have created an opportunity for polyandry with 2 reproductive pairs

E = Emigration; I = immigration.

Dispersal Patterns and Sex Differences in Dispersal

We observed 9 dispersal events comprising 4 immigrations and 5 emigrations in 3 groups observed over 74 months (tables 1, 2). Events involved both sexes: 5 females and 5 males (tables 1, 2). Over the period of 74 months, 3 individuals dispersed from the Bina group (M05 in 2007, and M06 together with F10 in 2011), and 2 lion tamarins attempted to immigrate but failed (FaB in 2007 and FemaleUnknowM06 in 2009; table 1). The male M05 emigrated when 2 years old, together with the female FaB that had been trying to enter the group but had not been accepted. After a failed attempt to disperse when it was 2.5 years old, following its mating with an ephemeral immigrant to the Bina group (FemaleUnknowM06), male M06 dispersed with his sister F10 two years later (in 2011). His sister was then 1.5 years old. This sibling emigration of M06 + F10 in July 2011 occurred after the breeding male MaEnf had disappeared in April 2011. Two females (F06 and F07) born in the Bina group disappeared; it is not known if they emigrated or died (table 1).

Two females tried, but failed, to enter the Bina group. While doing so, however, they motivated the dispersal of young males: M05 together with FaB, and M06 in his

first unsuccessful attempt to disperse in July 2009. The unknown female that dispersed with M06 in 2009 probably died, since M06 returned to the Bina group 2 weeks later. Marking the transition from the Bina to the Teca group, the male MaF08 successfully entered to take up the position of breeding male with F08Tecaa after the death of the breeding pair of the Bina group (table 1).

There were 2 forced emigrations in the Teca group. The breeding male MaF08 expelled M08 (F08Tecaa's sibling in the Bina group) in December 2011. F08Tecaa and F10.2 expelled the female F10.1 (twin of F10.2) in April 2012. M08 joined his brother M06 and sister F10 in a group (unnamed) near the Teca group, but the fate of F10.1 was not ascertained.

In November 2012, a male MaF10.2, previously unfamiliar to our field team, entered the Teca group. We recorded just 1 dispersal during 52 months monitoring the BM5 group. A female born in 2008 left the group in November 2011 and, when 3 years old, paired up with an unfamiliar male.

Dispersal Distances

Of the 5 observed emigrations (table 2), we were able to monitor the fate of the male M05. In the first month of dispersal (September 2007), M05, alongside the female FaB, explored the entire territory of his natal group Bina (fig. 2). Over 52 months the pair formed a new group (BM5) that established its range in the area once occupied by the Bina group. The Bina group, meanwhile, moved their home range to the south of their previous range, as illustrated in figure 2. The distance between the core areas of these groups was about 2,400 m. During 22 months of simultaneous field data collection on the two groups Bina and BM5, we did not observe any home range overlap between them.

Although we monitored only the dispersal of M05 and FaB (BM5 group), we were able to confirm that emigrants M06 and his sister F10 (Bina group) and FB08 (BM5 group) also established their home ranges close to their natal groups (table 2, notes). M08, forced to leave the Teca group, entered the group of his brother (M06) and sister (F10) that was a neighbour of the Teca group. The fate of F10.1 was not ascertained. It is worth emphasizing that the Teca group inherited the territory previously occupied by the Bina group and remained there during the subsequent 13 months of field monitoring.

Discussion

Our findings suggest that in *L. caissara* both sexes disperse. Dispersal, especially successful male immigration, appears to be related to the appearance of breeding opportunities in an existing group. Three females – FaB, FemaleUnknownM06 and FB08 – tried to enter existing groups and motivated (or at least were associated with) the emigration of mature males, promoting the formation of new groups.

The age of dispersal emigrants varied from 1.5 to 4 years and 8 months (tables 1, 2). Of the 5 emigrants, 1 male (M06) co-emigrated with a younger individual that it helped to raise (F10). Sibling dispersal is a common occurrence in *L. rosalia*, but in all cases they have been of male siblings dispersing together rather than male and female [Baker, 1991; Baker et al., 2002]. The emigration of M08 and F10.1 from the Teca group was motivated by intragroup competition, following the replacement of the

Fig. 2. Movement pattern of M05 after dispersal from the Bina group and formation of a new group (BM5).

breeding pair of the Bina group by the immigrant MaF08 and F08Tecaa. This may also have influenced the emigration of M06 alongside F10, who left their kin group after the disappearance of their father (MaEnf) from the Bina group. Forced emigrations comprise a substantial portion of the recorded dispersal events in *L. rosalia* [Baker, 1991; Baker et al., 2002].

Two of the 4 immigrants encountered strong resistance (FaB and the unknown female that first dispersed with M06), the third (MaF08) was opportunistic and the fourth (MaF10.2) was readily accepted by the new group. The entry of MaF10.2 into

the Teca group is noteworthy because it may have created an opportunity for cooperative polyandry or 2 reproductive pairs in the same group (MaF10.2 mating with the female F10.2). Cooperative polyandry and polygyny have been previously reported in *L. rosalia* [Baker et al., 1993; Dietz and Baker, 1993; Baker and Dietz, 1996; Baker et al., 2002], and our findings suggest they may also occur in *L. caissara*. Polygyny and polyandry have been related to habitat saturation and limited mating opportunities [Dietz and Baker, 1993; Digby and Ferrari, 1994; Rylands, 1996; Baker et al., 2002].

Baker and Dietz [1996] reported that in *L. rosalia*, immigration is highly male biased because adult daughters inherit their breeding positions and female immigrants face intersexual as well as intrasexual aggression. The probability of male and female black-faced lion tamarins immigrating appears to be similar, but females evidently face greater resistance, as was also reported by Baker and Dietz [1996]. In the case of *L. caissara*, female immigration may be an important incentive for young males to leave their parental groups and establish new family groups. Our finding that F08Teca inherited the breeding position and home range from the Bina group after competition for sexual dominance and space is similar to situations observed in *L. rosalia* by Baker and Dietz [1996].

As was also observed for *L. rosalia* by Baker and Dietz [1996] and for *Saguinus oedipus* by Savage et al. [1996], our data indicate that in *L. caissara* successful immigration into established groups is infrequent and generally occurs in the context of changes in the breeding pair through senescence or death (as observed in the Teca group). Although monitoring was restricted to only 3 groups, our data suggest that black-faced lion tamarins live in kin groups very largely composed of related individuals, as has been reported for *L. rosalia* [Kleiman, 1977; Baker and Dietz, 1996; Baker et al., 2002] and other callitrichids [Epplé, 1975; Savage et al., 1996].

Mating opportunities stimulate young adult black-faced lion tamarins to either disperse or remain in their kin group. This study shows that *L. caissara* show delayed dispersal related to the species' cooperative breeding system and low population density, which hinders the formation of new breeding pairs. The spatial association of close kin is the basis for cooperation and the evolution of the social behaviour [Dobson et al., 1998; Goldizen, 2003; Hatchwell, 2009; Viblanc et al., 2010; Dobson et al., 2012] characteristic of the lion tamarins and all of the callitrichids studied to date [Rylands, 1996]. The turning point determining philopatry or emigration in *L. caissara* may be group stability and changes in breeding positions associated with kin competition that motivate dispersal.

That the newly formed BM5 group occupied the area previously occupied by the Bina group, the remnants of which ceded its home range and moved south (fig. 2), is unsurprising because staying in familiar areas tends to have high adaptive value. During the course of our field study, we never observed agonistic encounters between the two groups, possibly the consequence of the kin-selected advantage of altruism toward relatives [Griffin and West, 2002; Platt and Bever, 2009]. Our observation that the established group Bina moved their home range to accommodate a dispersing relative (M5) can be interpreted as cooperative in that it increases the local carrying capacity and reduces inbreeding depression and loss of genetic diversity.

Except for the female F10.1 expelled from the Teca group (fate unknown), all emigrants established their home ranges close to their parental groups. Staying in a familiar area is adaptive due to familiarity with travel routes, sleeping sites, food re-

sources and potential predators. The interpretation of these results from the perspective of a dispersing lion tamarin allows us to understand the energy saved and the greater safety involved in residing in familiar areas. Leaving the natal group for reproduction is a moment of high risk in itself, whereas encounters with neighbouring groups are opportunities to identify possible sexual partners, and incursions beyond home range boundaries configure new possibilities in the cognitive map. Throughout the dispersal process, in which the goal was to search for sexual partners, food and overnight shelter, moving into familiar areas seemed to be the best route to follow.

We conclude that in *L. caissara* (i) both sexes disperse, (ii) successful immigration is related to the opening of breeding opportunities in an existing group, (iii) female immigration to existing groups can motivate males to emigrate and can result in the formation of new groups, and (iv) emigrants tend to form new groups that are close to their parental families.

These patterns of dispersal and formation of groups are efficient in terms of fitness because the species has been able to avoid detrimental effects and inbreeding despite its low genetic diversity [Martins et al., 2011] and small population size of about 400 individuals [Nascimento et al., 2011a]. The maintenance of these strategies over time depends on the integrity in terms of quantity and quality of the species habitat [Dietz and Baker, 1993; Digby and Ferrari, 1994; Rylands, 1996; Baker et al., 2002], a challenge that goes far beyond research and involves local and international conservation strategies and public policies.

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