

Chapter 16

Eviction and Troop Reconstruction in a Single Matriline of Ring-Tailed Lemurs (*Lemur catta*): What Happened When “Grandmother” Died?

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Abstract Eviction of subordinate females is well known in female-dominated ring-tailed lemur society. In almost all cases, evictions result from a dominant matriline targeting aggression towards subordinate matriline. Here, we report an eviction in a large, single matrilineal troop after the death of the troop’s “Grandmother.” Although the troop contained ≥ 18 individuals and 8 females over several years, no evictions occurred while the Grandmother was alive. After her death, a newly dominant female and her younger sisters evicted their nieces whose higher-ranking mother had already died. The younger relatives of the evicted females did not follow their mother and sisters but stayed in the natal troop. We suggest (1) the presence of certain females like Grandmother may function as a deterrent to eviction among descendants; (2) if eviction occurs within a single matriline, aggressors evict the most distant kin; (3) a newly dominant female may form a subgroup with her younger and subordinate sisters rather than older and higher-ranking ones to circumvent intragroup competition; and (4) the juveniles of evicted female kin do not always follow the nomadic evictees but may choose the safer strategy of remaining within their natal troop.

Resume L’éviction de femelles subordonnées dans des groupes sociaux dominés par les femelles est bien connue chez le Lémur *catta*. Dans presque tous les cas, les évictions font suite à des agressions ciblées dirigées d’une lignée dominante vers une lignée subordonnée. Nous rapportons ici un cas d’éviction dans une troupe constituée d’une seule lignée matrilineaire qui a fait suite à la mort de la « Grand-mère ». Bien que la troupe contienne ≥ 18 individus et 8 femelles depuis plusieurs années, aucun cas d’éviction n’a été observé tant que Grand-mère était en vie. Après sa mort, une nouvelle femelle dominante et ses jeunes sœurs ont évincé leurs nièces dont la mère, de rang élevé, était morte auparavant. Les jeunes apparentés aux

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femelles évincées n'ont pas suivi leurs mères et sœurs mais sont restés dans la troupe natale. Nous suggérons que (1) la présence de certaines femelles telles que Grand-mère pourrait inhiber les évictions entre ses descendants; (2) quand une éviction se produit au sein d'un groupe matrilineaire, les agresseurs évincent les individus qui leur sont le moins apparentés; (3) une nouvelle femelle dominante pourrait former un sous-groupe composé de sœurs plus jeunes qui leur sont subordonnées, plutôt que de femelles de haut rang et plus âgées, afin de diminuer la compétition entre groupes; (4) les jeunes apparentés aux femelles évincées ne suivent pas toujours les femelles évincées, mais peuvent choisir la stratégie plus sûre consistant à demeurer dans leur groupe natal.

Introduction

Female ring-tailed lemurs (*Lemur catta*) are dominant over males (Jolly 1966; Kappeler 1990; Sauther 1993). Eviction of females from their natal troops has been observed in troops with ≥ 16 individuals, at least 7–8 of whom are adult females (Jolly et al. 2002; Ichino and Koyama 2006), as a result of targeting aggression (intense and persistent aggression from one or more females to one or more subordinate individuals; Vick and Pereira 1989; Koyama et al. 2002; Ichino and Koyama 2006).

Almost all previous descriptions of female eviction have involved aggression by dominant kin groups towards subordinate ones, suggesting that female eviction and troop fission occur between matrilineal groups to reduce intratrop competition (Koyama et al. 2002; Ichino and Koyama 2006). We report a sequence of observations from targeting aggression and female eviction to troop fission in a single matriline after the death of their “Grandmother.” In our terminology, *troops* have at least one adult male while *groups* have no adult males (Koyama 1991). The terms *nomadic troop* and *nomadic group* describe troops/groups that do not maintain exclusive core areas (Jolly and Pride 1999). *Troop fission* refers to the separation of troop members into permanent new social troops with secure ranges (Vick and Pereira 1989; Hood and Jolly 1995; Koyama et al. 2002).

Study Site and Troop History

Our study was conducted in the Berenty Private Reserve adjacent to the Mandrare River in southern Madagascar (see Chap. 39). The reserve is approximate 240 ha, and composed of gallery forest, scrub forest, and spiny forest (Jolly 1966; Jolly and Pride 1999). Individuals in the seven study troops have been systematically identified and named by Koyama and his colleagues since 1989 (Chap. 42). Every female has her own code name; e.g., ME89♀ refers to the daughter born to mother ME♀ in the year 1989 and ME8993♀ is the granddaughter of ME♀ born to ME89♀ in 1993.

The composition of C1 troop over 2 years (2004 and 2005) is shown in Table 16.1. Individuals ≥ 3 years of age were considered adult. Rank was determined by submissive behaviors like spat calls. C1 troop split from the original C troop in 1989, sharing its original core area with the neighboring CX troop. When observations commenced in September 2004, C1 comprised 21 individuals including 8 adult females and 5 adult males. Their territory, which they defended in confrontations with other troops, was 4.19 ha, situated in the gallery forest, and included the tourist bungalow area. A map showing the territories of these and adjacent troops can be found in Koyama et al. (2006) and in Chap. 42 (Fig. 42.4).

Methods

The study formed part of a broader investigation into feeding ecology that spanned 13 months (September 16, 2004–February 15, 2005; April 10–November 20, 2005) and focused on two ring-tailed lemur troops, C1 and CX. Observations were conducted from 6:00 to 18:00 in the dry season and from 5:00 to 19:00 in the rainy season. We used focal animal sampling (Altmann 1974) and 5-min instantaneous point sampling to collect data on proximity of individuals (≥ 2 m). When targeting aggression, eviction or other special behaviors occurred, and we collected data ad libitum, including time, behavior, and place.

Results

We observed the following sequence of events.

1. Rank change and emergence of subgroups before September 2004

Troop C1 was composed of the descendants of one female, “Grandmother” ME89♀. She gave birth to 11 offspring, 8 of whom were still living at the time of the study (6 females and 2 males). From September 2000 to 2006, the troop contained 18–21 individuals and 6–8 adult females. The female dominance hierarchy generally reflected birth order, with the older daughters being more dominant. In September 2003, ME89♀’s fourth daughter ME8998♀ became the second-ranked female after her mother. ME89♀ was not very active but still dominant. Both ME89♀ and her second daughter ME8994♀ died sometime between December 2003 and August 2004.

By September 2004, C1 troop contained 21 individuals (Table 16.1). After the death of Grandmother ME89♀, ME8998♀ (6 years old) became the Alpha female. She and her three younger sisters without offspring, ME8900♀, ME8901♀, and ME8999♀, formed a subgroup (proximity rate = 21.6, 18.4, and 10.6 % respectively, $N = 2$ days). The oldest sister (ME8993♀) was Beta-ranked and associated with her two sons, ME899302♂ and ME899303♂ (24.7 and 36.1 %, $N = 2$ days). Older, middle-ranked ME8997♀ associated often with her

Table 16.1 Age-sex composition and names of individuals in C1 troop over the study

Rank	(a) Names of individuals (September 2004)				(b) Names of individuals (September 2005)						
	Order	Class	Female	Age	Male	Age	Female	Age	Male	Age	
1	Ad	ME8998♀	6	TUR♂	Unknown	7	ME8998♀		TUR♂	Unknown	
2		ME8993♀	11	SEN♂	Unknown		ME8997♀	8	SEN♂	Unknown	
3		ME8997♀	7	FUJ♂	Unknown	4	ME8901♀	4	FUJ♂	Unknown	
4		ME8900♀	4	GRZ♂→	Unknown	5	ME8900♀	5	↓GRI♂	Unknown	
5		ME8901♀	3	KTN♂	Unknown	12	ME8993♀		↓FTM♂	Unknown	
6		ME899499♀	5			6	ME8999♀		ME8902♂	3	
7		ME899401♀	3				ME899702♂	3	ME899702♂	3	
8		ME8999♀	5				ME899302♂	3	ME899302♂	3	
9							KTN♂		KTN♂	Unknown	
10							↓TUN♂		↓TUN♂	Unknown	
	Sad	ME899402♀	2	ME899702♂	2	Sad	ME899403♀	2	ME8903♂	2	
				ME899302♂	2				ME899303♂	2	
				ME8902♂	2				ME89949903♂	2	
	J	ME899403♀	1	ME8903♂	1	J			ME890004♂	1	
				ME89949903♂	1						
				ME899303♂	1						
	I	ME899804♀	0	ME890004♂	0	I			ME890005♂	0	
				ME890104♂	0				ME890105♂	0	
				ME89949904♂	0				ME899805♂	0	
	Troop C1 = 21 + 4NI										
	Adult females N = 8										
	→: Emigration										
	↓: Immigration										
	Troop C1 = 21 + 3NI										
	Adult females N = 6										
	Evicted										
	Left C1 troop										
	ME899499♀										
	ME899402♀										
	ME899401♀										

Ad: Adult, Sad: Subadult, J: Juvenile, I: Infant

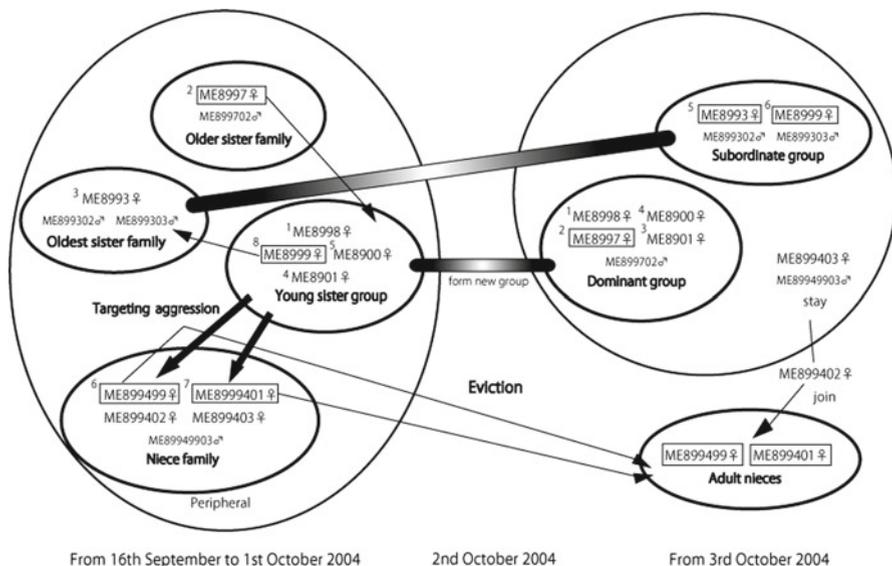


Fig. 16.1 Diagram of social changes in the C1 troop before and after the evictions

subadult son, ME899702♂. ME8994♀'s daughters, ME899499♀, ME899401♀, ME899402♀, and ME899403♀, who had not stayed in the troop center near the Alpha female, kept their distance from the other females on September 17. ME899499♀ had also not remained near the Alpha (0 %) and other females (2.8–6.8 %) but stayed with her sisters (36.8 %) on October 18. Thus, there were four female subgroups in September 2004 (1) the Alpha female and her younger sisters, (2) the older sister family, (3) the oldest sister family, and (4) the niece family (Fig. 16.1).

2. Targeting aggression and eviction, late September to early October 2004

The Alpha female (ME8998♀) and ME8900♀ began targeting aggression at ME8994♀'s adult daughters in mid-September 2004 (5 times in 3 days). ME8998♀, ME8900♀, ME8999♀ (lost on September 18), and ME899401♀ had infants during this period. At 15:00 on October 2, ME899499♀ and ME899401♀ were chased by the Alpha subgroup and ran away, crossing the territories of two other troops into A2 territory. After this eviction, whenever C1 troop encountered ME8994♀'s adult daughters, three of the Alpha subgroup (ME8998♀, ME8900♀, and ME8901♀) pursued their adult nieces aggressively, while ME8993♀, ME8997♀, and ME8999♀ did not.

The older ME8997♀ began to participate in the Alpha female subgroup after the eviction. ME8993♀, the oldest sister, fell in rank from Beta to second lowest female. Subordinate ME8999♀ left the Alpha female group and moved with ME8993♀. The new subgroups were (1) the dominant group, (2) the subordinate group, and (3) the adult nieces outside the troop (Fig. 16.1). The subordinate

group was not aggressive to ME899499♀ and ME899401♀ when they encountered each other on the C1 boundary.

The second daughter of ME8994♀, ME899401♀, had a male infant when the eviction occurred. The infant fell from his mother and was found in a weakened condition near the boundary of the neighboring YF troop on October 3. The dominant group was not aggressive towards the immature ME899402♀ and ME899403♀, and even though their older sisters had been chased, they were allowed to return to C1 troop. ME899402♀ sometimes stayed with her sisters but most often returned to C1 troop. However, she joined her older sisters on October 15 and remained with them.

3. Juveniles remained in their natal troop, early October

There were two juveniles in the evicted niece family. The youngest, ME899403♀, tried to follow her sisters, but when ME899499♀ and ME899401♀ fled, she could not keep up and lost track of them. On October 15, when the C1 troop encountered ME899499♀ and ME899401♀ at the A2/C1 boundary, they were attacked by the Alpha female; ME899402♀ followed her sisters but ME899403♀ could not, emitting loud “lost calls,” and ceased following her sisters from that time. ME899499♀’s son, ME89949903♂, did not follow his mother but stayed in C1 troop. He spent time with his mother outside the C1 territory three times, when he groomed and moved with his family, but returned to C1 in the evening. Although he became less active and lost weight and condition, he survived and was not subjected to aggression by troop members.

4. Formation of a nomadic troop after the mating season, April 2005

From November to December 2004, the adult nieces avoided the C1 home range, although they were seen in the neighboring CX range. However, from the end of January 2005, when the top-ranking food plant *Azadirachta indica* was fruiting, they entered the C1 range several times quietly to feed on fruits. Whenever they were discovered by the dominant group, they were chased vehemently.

In the April 2005 mating season, we frequently found the adult nieces near the C1/A2 boundary with two accompanying males (5 times in 9 days). One A2 male joined them temporarily during the mating season, but another 6-year-old male, CW9094♂ from the neighboring CX troop, remained with them beyond this period. Hence, the adult nieces formed a new troop (Koyama 1991). The dominant group continued to chase them, but the adult nieces resisted their aggression, fighting back on the confrontation line. ME8993♀ and ME8999♀ did not attack the nieces in the absence of the dominant group members. Although they were still nomadic (Ichino and Koyama 2006), they intruded frequently into the C1, A2, and CX home ranges, from April through the dry season to November.

By the September 2005 birth season, the adult nieces had gained a sleeping site on the A1/A2 boundary. However, they did not often win confrontations with other troops, and ME899499♀ dropped her infant when they retreated on October 11. They did not succeed in establishing a territory. On October 31, 2005, their male consort (CW909499♂) was found dead from unidentified causes, and the adult nieces again became a nomadic group.

Discussion

Troop Hierarchy Change After the Death of Grandmother

Almost all cases of eviction described previously at Berenty and Beza Mahafaly were carried out by dominant matrilineal groups against subordinate matrilines (Koyama 1991; Hood and Jolly 1995; Jolly and Pride 1999; Gould et al. 2003; Ichino and Koyama 2006). In the T2 troop, a similar classic eviction occurred in September 2003 ($N=18$, 8 adult females comprised of 6 dominant kin and 2 subordinate kin, 5 adult males, dominant kin group = 11, subordinate kin group = 3). Ichino and Koyama (2006) proposed that female eviction occurred when the troop contained ≥ 16 individuals (mean = 22.5, range 16–28) and the number of adult females was ≥ 7 (mean = 8.4, range 7–10), while Jolly et al. (2002) favored ≥ 8 females. When C1 contained more than two matrilineal groups in 2000, ME89♀ and her daughters evicted another kin group.

In C2A troop, two females were evicted in October 2009 when the number of adult females reached 7; the Alpha female, her daughters, and granddaughter evicted her cousin's daughters. In the A2 troop, which lacked a Grandmother figure, 3 adult females were evicted in October 2012 when the adult female number was 10 (our observations).

In the case we have described, all the females in C1 troop were daughters or granddaughters of Grandmother ME89♀, who retained the Alpha rank until she died. Although C1 troop comprised more than 16 individuals and 8 females, there were no evictions and the dominance hierarchy was stable. After Grandmother's death, hierarchy stability crumbled and targeting aggressions led to evictions. The presence of an old matriarch thus may deter evictions when all the troop's females are her descendants.

Choice of Eviction Targets and Allies

If a dominant female evicts other females within the same matriline to avoid food competition, nieces would be more appropriate targets than sisters because of their more distant relationship; this was the case in our study.

ME8998♀ initially formed a subgroup with her younger sisters rather than the older, stronger ones with offspring. Among cercopithecine monkeys, adult sisters usually rank in inverse order of age (Japanese macaque: Koyama 1970; Nakamichi et al. 1995; long-tailed macaque: Netto and van Hooff 1986), female dominance ranks remain stable over considerable periods, and daughters acquire ranks immediately below those of their mothers (Nakamichi et al. 1995). In ring-tailed lemurs, however, daughters are not invariably ranked immediately below their mothers, and adult sisters are dominant over younger sisters (Nakamichi and Koyama 1997). Moreover, dominance relations change frequently in both sexes (Jolly 1966; Taylor

and Sussman 1985; Nakamichi et al. 1997) and are largely determined by attributes like age, size, fighting ability, and social skills (Nakamichi and Koyama 1997). When ME8998♀ became an adult, her older sisters, ME8993♀ and ME8994♀, were higher ranking. ME8998♀ emitted submissive “spat” calls and was displaced by them, while her younger sisters were not aggressive towards her. She chose to form a subgroup with her more compliant younger sisters in intragroup contests, ultimately depriving her older sisters of their high ranks. Moreover, targeting her nieces for eviction could increase ME8998♀’s inclusive fitness.

Juvenile Strategies to Cope with the Eviction of Close Kin

Although their close kin, including their mothers, were evicted, the juveniles chose to stay in C1 troop. They groomed and moved with their mothers and sisters for a few hours when they met them, indicating they did not forget their close kin.

When a female of CX troop died, her female juvenile did not have any kin with whom to groom and huddle. She did not feed well and died 2 weeks after the death of her mother (Soma 2006). ME89♀’s last offspring, ME8903♂, also became markedly unhealthy after his mother’s death. However, ME899403♀ and ME899403♂ had juvenile ($N=2$) and subadult males ($N=3$) and adult females from the same matriline with whom they could groom and huddle, and the dominant subgroup members were not especially aggressive towards them. The adult females were tolerant and groomed the juveniles. Later, when ME8990♀ was evicted by the returned adult nieces in 2006, her son ME899005♂ did not follow his mother and remained in C1 troop.

Juveniles face potential costs in following nomadic kin as opposed to staying in their natal troops. They might not be able to follow the adults when they intrude into another territory and are chased by the proprietors. Juveniles left alone in unfamiliar territories are vulnerable to predation, and October may be a time of especially high vulnerability for infant ring-tailed lemurs, because this period coincides with the nesting season of both harrier hawks and buzzards, which have increased nutritional needs for egg laying and incubation (Sauther 1989). A subadult male of the T1B troop was preyed upon by a Madagascar buzzard, *Buteo brachypterus*, in September 2003 (Jolly and Soma, personal observation). In May 2005, a male juvenile of CX troop ($N=10$, 5 adult females and 3 adult males) was eaten by a feral dog, even though he was moving with his mother in the troop (Soma, personal observation). Juveniles may be less vulnerable than infants but still face danger moving alone, making it safer for them to stay in the natal troop with its enhanced capacity for predator detection.

When C1 and CX troops split, Koyama et al. (2002) found the juveniles initially stayed in the natal C1 troop and did not follow their mother and sisters. However, once their kin succeeded in establishing a territory, the juveniles joined their kin. Hence, ME899403♀ and ME89949903♂ may join the adult nieces’ troop when they establish a stable territory.

Conclusions

1. The existence of a matriarch like Grandmother in a ring-tailed lemur troop may deter evictions when all the troop's females are her descendants.
2. If eviction occurs within a single matriline, targeting the most distantly related kin could increase the inclusive fitness of the dominant and high-ranking antagonists.
3. The dominant female may form a subgroup with her younger and subordinate sisters rather than the older and higher-ranking ones to circumvent intragroup competition.
4. Juveniles of evicted females may not follow their closest nomadic kin, preferring the relative safety of their natal troops.

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