

Genetic Evidence for Male and Female Dispersal in Wild *Lemur catta*

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Key Words

Dispersal · *Lemur catta* · Madagascar · Population genetics · Relatedness · Ring-tailed lemur

Abstract

Lemur catta has traditionally been considered a species with male-biased dispersal; however, occasional female dispersal occurs. Using molecular data, we evaluated dispersal patterns in 2 *L. catta* populations in southwestern Madagascar: Tsimanampeso-tse National Park (TNP) and Bezà Mahafaly Special Reserve (BMSR). We also investigated the genetic differentiation between the populations and dispersal partner relatedness. Results showed minor genetic differentiation between the populations ($\Theta_{ST} = 0.039$), which may indicate gene flow historically occurring in this region, made possible by the presence of *L. catta* groups between the sites. Different patterns of sex-biased dispersal were found between the sites using corrected assignment indices: male-biased dispersal in TNP, and a lack of sex-biased dispersal in BMSR. Observational evidence of female dispersal in BMSR supports these results and may imply intense female resource competition in and around BMSR, because small groups of 2–3 females have been observed dispersing within BMSR and entering the reserve from outside. These dispersing groups largely consisted of mothers transferring with daughters, although we have an aunt-niece pair transferring together. Genetic data suggest that males also transfer with relatives. Our data demonstrate that dispersal partners consist of same-sexed kin for *L. catta* males and females, highlighting the importance of kin selection.

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Introduction

Whether or not sex-biased dispersal is found in a population depends on how resource competition affects each of the sexes. Generally, female philopatry occurs where females can defend high-quality resources with relatives [Wrangham, 1980]. Intrasexual competition for mates [Jack, 2003] and/or inbreeding avoidance [Pusey, 1987] often drives males to disperse in such species. Conversely, where females disperse, they often do so due to local resource competition [Greenwood, 1980].

In this study, we set out to evaluate dispersal patterns in 2 wild populations of ring-tailed lemurs (*Lemur catta*) [Sauther et al., 1999; Jolly et al., 2006] by using a combination of observational and genetic data. Genetic methods are increasingly being used to study dispersal [Di Fiore, 2003]. When paired with observational data, molecular data can help provide a more nuanced understanding of a species' social structure and behavior [Lawler et al., 2003; Bradley et al., 2004; Di Fiore et al., 2009; Harris et al., 2009; Baden et al., 2014].

Historically, *L. catta* males have been viewed as the sex that disperses, and they usually transfer between groups in pairs or triplets rather than alone [Jones, 1983; Sussman, 1991, 1992; Gould, 1994, 1997; Koyama et al., 2002; Gould, 2006; Kelley, 2013]. Observations from at least 2 research sites, however, have suggested that female dispersal can also occur in *L. catta* [Sauther et al., 1999; Koyama et al., 2002]. These observations pose the question of whether evidence for female dispersal will be revealed by molecular data. Results from this evaluation can potentially indicate the level of resource competition facing females in different *L. catta* habitats. As part of our molecular evaluation of dispersal patterns, we also sought to determine the level of genetic differentiation between our study sites. Low differentiation, if found, would indicate that the 2 locations may have historically experienced gene flow. The degree of relatedness of transfer partners was also determined with molecular data. Such information can be helpful in indicating the importance of kin selection in the dispersal of this species or whether individuals travel between groups with unrelated individuals. No study has previously evaluated the level of genetic differentiation between wild *L. catta* populations, used genetics to test for sex biases in dispersal in this species or measured the degree of relatedness between dispersing individuals using genetics.

Material and Methods

Study Sites and Sample Collection

We studied *L. catta* in 2 areas of southwestern Madagascar: Bezà Mahafaly Special Reserve (BMSR) and Tsimanampesotse National Park (TNP) [Parga et al., 2012]. TNP is located approximately 135 km southwest of BMSR [Cuozzo et al., 2008]. *L. catta* groups are present in the region between TNP and BMSR [Sauther, pers. observation]. Although there is an absence of major geographic barriers to dispersal (i.e. rivers [Guschanski et al., 2007; Quéméré et al., 2010]) between the 2 locations, potential anthropogenic barriers to dispersal exist, such as deforested patches [Brinkmann et al., 2014].

Hair and blood samples were collected from BMSR (n = 243) between the years of 1987 and 2006 as part of a long-term monitoring of this population [Sussman et al., 2012]. Blood samples were collected at TNP (n = 25) in 2006. Individuals were captured using a Telinject blow dart system and were administered a drug mixture of ketamine and/or ketamine and diazepam, based

Table 1. Heterozygosity and allele number for each locus

Locus	BMSR			TNP		
	k	H _O	H _E	k	H _O	H _E
Lc5	9	0.750	0.778	7	0.800	0.782
Lc6	8	0.750	0.734	6	0.720	0.708
Lc7	10	0.900	0.838	11	0.800	0.835
Lc8	7	0.733	0.757	–	–	–
Lc10	10	0.807	0.794	–	–	–
69HDZ267 ^a	10	0.800	0.816	10	1.000	0.866
69HDZ299	7	0.700	0.795	8	0.760	0.802
Efr02	10	0.741	0.758	–	–	–
Efr09 ^a	12	0.800	0.740	7	0.680	0.772
L-2	12	0.850	0.825	10	0.760	0.804
Em7	5	0.588	0.621	–	–	–
Em12 ^a	17	0.850	0.864	14	0.880	0.818
Pv1	13	0.841	0.869	–	–	–
Average	10.0	0.778	0.784	9.1	0.800	0.798

k = Number of alleles; H_O = observed heterozygosity; H_E = Nei's [1978] unbiased estimate of expected heterozygosity. ^a Not in Hardy-Weinberg equilibrium.

on protocols developed over the past 25 years and 360 captures [Sauther et al., 2006]. All animal handling was conducted with Institutional Animal Care and Use Committee approval from the University of Colorado and/or the University of North Dakota. Regular monthly censuses began in BMSR in the latter half of 2005. Prior to this, instances of dispersal were documented yearly. Dispersal events involving pairs or small groups of individuals in BMSR were included in this study only if genetic information was available for one or more of the dispersing individuals. A dispersal event was noted when an individual entered a new group for at least 6 months.

Genetic Analyses

A standard phenol-chloroform extraction [Sambrook et al., 1989] was used to obtain genomic DNA from hair and blood samples. For blood samples collected on Schleicher & Schuell IsoCode cards, PCR amplification of microsatellites was performed as described in Parga et al. [2012]. Both species-specific and heterologous microsatellites were used: Lc5, Lc6, Lc7, Lc8, Lc9, Lc10 [Pastorini et al., 2005], 69HDZ267, 69HDZ299 [Zaonarivelo et al., 2007], Efr09 [Jekielek and Strobeck, 1999], Efr02 [Wimmer, 2000], L-2 [Merenlender, 1993], Em7 [Pastorini et al., 2004], Em12 [Pastorini, this study; forward: gaacctgggtggctacattc, reverse: gtttgattaggcttgctgc], and Pv1 [Lawler et al., 2001]. Approximately 10–100 ng template DNA was amplified in 12.5- or 20- μ l reactions (see Pastorini et al. [2005] and Parga et al. [2012]). A total of 243 samples were analyzed from BMSR, gathered across 6 collection years and 11 different groups between 1987 and 2006. From TNP, 25 samples from 4 different groups were analyzed from a single year, 2006.

MICRO-CHECKER version 2.2.3 [van Oosterhout et al., 2004] was used to evaluate the data for null alleles and scoring errors. One microsatellite (Lc9) showed evidence of scoring errors and null alleles, so was discarded. POPGENE version 1.31 [Yeh et al., 1999] was used to test each locus for Hardy-Weinberg equilibrium within each population. Loci not in Hardy-Weinberg equilibrium (table 1) were excluded from the calculation of Θ_{ST} , tests of population differentiation, F_{IS} and tests of sex-biased dispersal.

FSTAT version 2.9.3 [Goudet, 2001] was used to calculate Θ_{ST} and F_{IS} following Weir and Cockerham [1984]. The test for population differentiation in FSTAT uses the log likelihood statistic G [Goudet et al., 1996] and was run using 1,000 permutations, testing the value for Θ_{ST} against the null hypothesis of an absence of population differentiation ($\Theta_{ST} = 0$). Only samples collected in 2006 were used to test for population differentiation and to generate F_{IS} values, as that was the single year in which samples were available from both TNP and BMSR.

Assignment indices (AI) [Paetkau et al., 1995] use an individual's multilocus genotype to identify the likelihood that the individual was born into a particular population. We used GenAEx 6.5 [Peakall and Smouse, 2012] to calculate the corrected AI (AI_c), for use in sex-biased dispersal tests. AI_c values were calculated by subtracting the population mean AI as calculated per analyzed year from each individual's AI, with positive AI_c values indicating that an individual is likely philopatric (resident to the area), while strongly negative values indicate rare genotypes and likely immigrant status [Favre et al., 1997; Mossman and Waser, 1999]. Tests for sex-biased dispersal were run separately within each population, and were run for BMSR samples per collection year. Only years in which genotypes were available for ≥ 20 individuals (males plus females) were included in sex-biased dispersal tests. Mann-Whitney U tests in GenAEx were used to determine if there was a significant difference in the AI_c values of males versus females in each population.

ML-Relate was used to estimate pairwise relatedness using maximum likelihood methods [Kalinowski et al., 2006]. The putative relationship (parent-offspring, full-sibling, half-sibling, unrelated) identified as most likely was tested against the second most likely alternative using likelihood ratio tests, with a 0.05 significance level. Overall within-sex relatedness estimates were also calculated per site.

In some cases, CERVUS 3.0.3 [Marshall et al., 1998; Kalinowski et al., 2007] was used to help clarify the relationship between individuals transferring together via the identification of those individuals' parents [for details, see Lawler et al., 2003].

Results

For all microsatellites used, heterozygosity ranged between 0.588 and 0.900 (table 1). Genetic differentiation between the 2 populations, BMSR and TNP, was low ($\Theta_{ST} = 0.039$) but significantly different from 0 ($p < 0.001$), as calculated across all loci. When calculated separately for each sex, significance was again reached ($p < 0.001$), with females ($\Theta_{ST} = 0.056$) showing greater genetic differentiation than males ($\Theta_{ST} = 0.035$).

The mean F_{IS} (averaged across all loci) was positive for both populations (BMSR: 0.024; TNP: 0.018). When calculated per sex, BMSR males showed a positive mean F_{IS} (0.047), whereas females showed a negative mean F_{IS} (-0.004). At TNP, both males and females showed positive mean values of F_{IS} (0.019 and 0.102, respectively).

Overall variance in AI_c was greater for males than for females in each year and in both sites; however, when comparing individual male versus female AI_c values per site and sex to assess dispersal trends, only TNP showed significantly more negative scores among males than females (fig. 1; table 2). At BMSR during the same year (2006), males and females showed an extensive overlap in AI_c values, and no significant sex bias in dispersal was detected (fig. 1; table 2). This lack of sex bias in dispersal in BMSR held consistently for all 5 study years tested (table 2).

Genetic data were available for 5 dispersal events by pairs or small groups of individuals at BMSR (table 3). In the first event, 2 adult and 1 subadult female immigrated as a small group into BMSR from outside of the reserve. Genetic data revealed that these 2 adults were most likely a mother-daughter pair (no genetic information was available for the subadult female). The conditions under which these 3 females

Table 2. Variance in corrected assignment indices (vAI_c) and mean assignment indices (mAI_c) per site and per year, with Mann-Whitney U results for sex-biased dispersal tests

Population	Year	Male vAI _c	Female vAI _c	Male mAI _c	Female mAI _c	n _{males}	n _{females}	Z	p
BMSR	1995	1.127	1.028	0.1	-0.095	17	18	0.6	0.55
	2003	1.72	1.314	0.073	-0.06	41	50	0.74	0.46
	2004	1.152	0.99	0.039	-0.39	44	44	0.47	0.64
	2005	1.446	0.845	0.002	-0.002	40	49	-0.26	0.8
	2006	1.158	0.54	-0.1	0.097	20	20	0.568	0.57
TNP	2006	1.65	0.807	-0.64	0.97	15	10	3.2	0.002

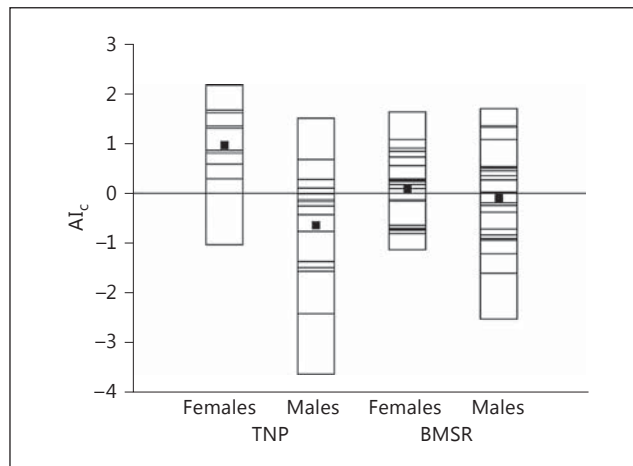


Fig. 1. The range of AI_c scores in 2006 per sex and per site, representing each individual as a horizontal line. Note that TNP shows a significant male bias in dispersal ($p = 0.002$), while BMSR shows no sex bias in dispersal ($p = 0.57$; table 2). Positive values are associated with population residents, while negative scores indicate rare genotypes more likely to be associated with immigrants. Filled squares indicate mean AI_c values.

left their original group were unknown, but they were in poor physical condition and injured upon entry into BMSR. The group they transferred into had recently lost half of their reproductive females (2 of 4). Within several months of transferring into this group, another original female was killed by a dog and by the end of the next year the remaining original female disappeared, leaving only the immigrant females. In all other instances, females transferred between groups *within* BMSR, and were known to have dispersed because they were forcibly evicted from their social groups. Event 2 was a case of female dispersal with offspring (a daughter and son; table 3). Our data also show that 2 females dispersing between groups together (event 3, table 3) shared an aunt-niece relationship. The mothers of these 2 females were determined to have

Table 3. Dispersal events by pairs or small groups in BMSR for which genetic data were available

Sex	Event	Year of dispersal	Sex ratio in group of origin	Sex ratio in group of entry	Individuals dispersing together, listed by age class and study ID	Estimates of relatedness	Putative relationship
F	1	2006	unknown	6:2	2 AF (106, 105), 1 SF ¹ (103)	$r = 0.50$	mother-daughter*
	2	2006	3:4	n.a.	2 AF (459, 34), 1 SM (275)	459 and 34: $r = 0.53$ 459 and 275: $r = 0.50$ 34 and 275: $r = 0.16$	mother-daughter* mother-son* half-siblings
	3	2008	10:8	5:2	2 AF (231, 364)	$r = 0.096$	aunt and niece* ²
M	4	2004	9:5	unknown	2 AM (160, 161)	$r = 0.26$	half-siblings*
	5	2007	3:4	n.a.	2 AM (253, 330)	$r = 0$	same-aged 2nd cousins ³

AF = Adult female; AM = adult male; SF = subadult female; SM = subadult male. Sex ratios for males:females (subadult and older), not including the emigrants/immigrants; unknown = group of origin or entry was outside of the study area; n.a. = not applicable – emigrants formed a new group. * $p < 0.05$: statistically significant.

¹ No genetic data currently available for this individual.

² The mothers of these two dispersing females were parent-offspring themselves, as determined by CERVUS.

³ CERVUS determined that these 2 males dispersing from the same natal group had different fathers; however, their mothers were matrilineally related at the level of first cousins ($r = 0.121$).

a parent-offspring relationship via CERVUS and were no longer present in the group at the time of the joint dispersal of their daughters, although both dispersing females had other female relatives present in the group (i.e. sister, aunts) at the time of their departure.

For males, dispersal partners were also related. In event 4 (table 3), 2 adult males transferring between 2 nonnatal groups appeared to be related at the level of half-siblings. In event 5, a pair of same-aged males dispersing from their natal group together were distantly related enough to return an r value of 0 (table 3). CERVUS, however, was used to determine these males' mothers, who were related at the level of first cousins – making the same-aged dispersing natal males related at the level of second cousins.

Although it was unknown where some groups of dispersing individuals immigrated to or originated from (e.g. event 1, table 3), dispersing pairs/groups of females generally left groups because they were aggressively evicted by other female residents (events 2 and 3, table 3), and either joined other established groups (event 1, table 3) or formed the basis of a new group (event 2, table 3). In contrast, dispersing males left groups of their own volition to create new groups or enter other fully formed groups.

A comparison of relatedness values of dispersal partners in table 3 with estimates of average relatedness calculated within each sex at each site (BMSR: males, $r = 0.074$, females, $r = 0.071$; TNP: males, $r = 0.0497$, females, $r = 0.067$) shows that on average, dispersal partners were more related than were random individuals of the same sex in the population. A consideration of average relatedness within each sex also shows that only in TNP was the average female relatedness greater than male relatedness, as would be expected in a species with female philopatry and male dispersal. Conversely, BMSR males and females showed nearly the same average relatedness, which would be consistent with both male and female dispersal occurring in BMSR.

Discussion

L. catta at BMSR and TNP showed only minor genetic differentiation (as measured by θ_{ST}), but the difference was significant. The area between the 2 habitats contains mixed dry scrub and dry forest, and there are *L. catta* groups present along the road between Ambatry and TNP [Sauther, Cuozzo, pers. observation]. Given sufficient mobility and interbreeding with the *L. catta* groups living in the area between BMSR and TNP, the 2 populations may have historically experienced gene flow, which could have resulted in our finding of low genetic differentiation between the sites.

Repeating tests for genetic differentiation (θ_{ST}) within each sex separately showed that greater differentiation existed among females than among males, as would be expected where males are the dispersing sex [Favre et al., 1997]. The variance in AI_c values was also consistently higher for males than for females across all years and in both sites, which is the pattern expected with male-biased dispersal [Goudet et al., 2002]. These results suggest that gene flow among females has been more restricted than gene flow among males, which is in agreement with behavioral data on intergroup movement showing male-biased dispersal in *L. catta* (BMSR [Sussman, 1991, 1992; Gould, 1994, 1997, 2006]; Berenty, Madagascar [Jones, 1983; Koyama et al., 2002]).

The mean F_{IS} was slightly positive for both populations. Rather than indicating inbreeding, this positive mean F_{IS} likely resulted from the sampling of structured populations consisting of distinct social groups having nonrandom mating [Sugg et al., 1996]. When calculated per sex in each site, only males in BMSR showed the expected result of the dispersing sex having a mean F_{IS} value that is positive and higher than that of females [Lawson Handley and Perrin, 2007].

Tests to detect sex-biased dispersal comparing individual corrected assignment indices between males and females per year revealed evidence for male-biased dispersal at TNP, but not at BMSR. There was no significant difference between males and females in corrected assignment indices for all of the study years tested at BMSR, suggesting that female dispersal occurs in addition to male dispersal at this site. Observational data on pairs and small groups of females entering BMSR also support this result [Sauther et al., 1999; this study].

In sum, although there are several indicators of male-biased dispersal in both sites, the AI_c sex-biased dispersal test results, within-sex relatedness measures at each site, and observational evidence support female dispersal in BMSR. Why female dispersal appears to occur in BMSR but not TNP is unclear. Because 2 instances of observed female dispersal in BMSR were driven by female eviction, it is possible that the factors which lead to increased competition among females and group fission [Koyama et al., 2002] may be the primary driver of female dispersal in *L. catta*. Indeed, in the single case of female dispersal in BMSR where group sex ratio was known for pre- and posttransfer groups, the dispersing females transferred into a group with fewer females than were in their original group (8 and 2, respectively). In addition, for the case of the 2 females and a subadult transferring from outside of BMSR, the females joined a group that had recently lost half of their adult females and within a year they were the only females remaining in the group. Interestingly, female dispersal in *L. catta* has also been documented in at least 1 other wild research site (Berenty [Koyama et al., 2002]). To reach any solid conclusions about why female dispersal appears

to happen in some, but not all, populations of this species, further research is needed on how variables related to resource competition, such as habitat quality or population density, might be affecting dispersal patterns.

Although based on a small sample size, our genetic data show that individuals of both sexes disperse with kin who are markedly more related to them than other random same-sex individuals in the population. Among 3 groups of dispersing females, genetic data reveal a parent-offspring bond in 2 cases, and in a third, a likely aunt-niece relationship. One pair of adult males transferring between groups together was related at the level of half-siblings. Parallel dispersal [Schoof et al., 2009] of relatives has been found in a few other primates, e.g. vervets (*Cercopithecus aethiops*) [Cheney and Seyfarth, 1983] and white-faced capuchins (*Cebus capucinus*) [Jack and Fedigan, 2004]. This strategy can have many advantages. In addition to inclusive fitness benefits, practicing parallel dispersal with a relative can provide several direct benefits, such as partnership in affiliative interactions and aiding in the detection of predators or aggressive conspecifics during the transfer process [Sussman, 1992; Gould, 1994, 1997, 2006]. Hence, dispersing with kin can offer fitness gains, and this strategy appears to be used by both male and female *L. catta*. One interesting avenue for future research would be to assess the extent to which individuals disperse with relatives at other *L. catta* study sites, and to evaluate whether males ever transfer between groups with their male offspring.

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