

## Exploring Social Dominance in Wild Diademed Sifakas (*Propithecus diadema*): Females Are Dominant, but It Is Subtle and the Benefits Are Not Clear

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### Abstract

Rarely observed in mammals, female dominance is documented in several of Madagascar's lemurs. Although dominance affects many aspects of primates' lives, studies have largely focused on dyadic agonistic interactions to characterise relationships. We explored the power structure of three diademed sifaka groups (*Propithecus diadema*) at Tsinjoarivo during the lean season (July–August, 325 h) using social behaviours, group leadership, displacements and feeding outcomes. Two groups had a hierarchy dominated by the breeding female, while the highest rank was held by the breeding male in the third; in dyadic interactions, breeding females dominated males in all groups. Inconsistencies in hierarchies suggest that groups vary, with rank related to kinship ties of breeders. Aggression and grooming were rare; adult females received aggression at lower frequencies than males. Group movements were led more by females and followed more by males, and female feeding priority was evident in displacements during feeding. However, males and females did not differ in feeding outcomes, as expected (particularly in the lean season) if female dominance (and/or male deference) serves to ensure better access for females. This unexpected pattern (female dominance despite rare aggression, clear female leadership and displacement, yet no observable benefit in grooming or feeding outcomes) defies easy explanation, and reinforces the fact that studies examining female power in lemurs should take a multifaceted approach. Further study is needed to understand this pattern, the physiological and reproductive consequences of female dominance (e.g. detecting subtler variation in food quality or intake rates) and exactly how (and when) the benefits of female dominance are manifested.

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## Introduction

The acquisition and maintenance of social status in mammalian females is related to age, body mass and androgen levels (which affect aggressiveness), and is shaped by environmental and social factors such as resource holding potential, reproductive skew, demography, variance in relatedness, costs and likelihood of interventions and resource characteristics [Clutton-Brock and Huchard, 2013; Petty and Drea, 2015]. Over evolutionary time, relationships of gregarious primates were shaped such that selected behavioural strategies increased inclusive fitness [de Waal, 1986; Wright, 1999; Kappeler and van Schaik, 2002]. Dominance relationships within groups are one well-explored social factor, with individuals' rank defining their relationships – including aggression, affiliation and the nature and frequency of services given and received [Waeber and Hemelrijk, 2003; Port et al., 2009]. Positive correlations between female rank and elements of fitness (e.g. breeding success, survival and longevity) have been reported, acting via access to resources and improved health, access to mates, reproductive success (including offspring survival and growth), ability to form social bonds and mitigation of predation and infection [Noë and Sluijter, 1990; Pochron et al., 2003; Hemelrijk and Gygas, 2004; Kappeler and Schäßler, 2008; Mathot and Giraldeau, 2008; Silk et al., 2010; Clutton-Brock and Huchard, 2013].

In most primates, adult males dominate adult females in dyadic interactions, though female dominance is observed in some species [Hemelrijk et al., 2008]. However, dominance has been defined in various ways; most studies investigating dominance used rates of affiliative and agonistic interactions such as aggression and grooming [Pochron et al., 2003; Foltz, 2009; Port et al., 2009; Ramanamisata et al., 2014]. Studying dominance could be extended to consider feeding priority and other interactions [Radespiel and Zimmerman, 2001; Ramanamisata et al., 2014]. In this respect, Lewis [2002, 2018] introduced the concept of “power,” encompassing “dominance” (force-based power) and “leverage” (power with respect to a resource that cannot be taken by force such as fertilisable eggs and services). These discussions may explain why evolutionary models seeking to explain the origin of female dominance (in combination with male-female monomorphism and other behavioural characteristics [Kappeler and Schäßler, 2008]) in lemurs are debated. Many have inferred that female dominance is an adaptation to unusually high reproductive costs, or to resource scarcity and unpredictability [Wright, 1999; Dunham, 2008]. Others [White et al., 2007] suggested that some aspects of female dominance, particularly priority access to resources, could result from male deference, a non-aggressive strategy for increasing reproductive success through cultivating female choice.

Like most lemurs [Wright, 1999; Dunham, 2008; Hemelrijk et al., 2008], the genus *Propithecus* is documented to be female-dominant. This trait has been reported in *P. edwardsi* [Hemingway, 1999; Pochron et al., 2003; Foltz, 2009], *P. coronatus* [Ramanamisata et al., 2014; Razanaparany et al., 2014], *P. verreauxi* [Norscia and Palagi, 2015] and *P. diadema* [Irwin, 2006]. Past investigations on *P. diadema* mostly focused on feeding ecology, health and sensitivity to forest fragmentation [Powzyk and Mowry, 2003; Irwin, 2006]; studies to date suggest female dominance but most narrowly focused on agonism and did not explore non-aggressive manifestations of dominance, such as grooming, group leadership and feeding priority.

In this paper, we assess social relationships in diademed sifakas (*P. diadema*) using dominance scores during the lean season, explore the extent to which female power is evident in agonistic (aggression and displacement during feeding) and non-agonistic behaviours (grooming, leadership), and test whether female power affected feeding outcomes. Our objectives were to: (1) rank individuals in each group using normalised David's scores (NormDS) and (2) compare aggression, displacement, leadership, grooming duration and diet characteristics among age-sex classes. Breeding females were expected to: (a) be aggressively dominant to groupmates, (b) be groomed more and groom others less, (c) lead group movements (presumably allowing them to choose destinations and benefit from feeding priority), (d) elicit higher rates of displacements, allowing monopolisation of foods and (e) spend more time feeding, with more time on fruits (which are preferred to leaves) and less time on mistletoe, a less preferred fallback food [Irwin et al., 2015].

## Materials and Methods

### *Study Subjects and Area*

This study took place in Mahatsinjo (19°40.94' S, 47°45.46' E, 1,590 m) in the western half of Tsinjoarivo-Ambalaomby forest [Irwin, 2008a]. Mahatsinjo contains hill and ridgetop forest fragments, which are disturbed by anthropogenic extraction and non-anthropogenic edge effects, surrounded by settlements and cultivated land.

Observations were conducted on three habituated groups of *P. diadema* (FRAG2, FRAG4 and FRAG5), each containing one breeding male and female. FRAG2 and FRAG5 had 3 group members (FRAG2: adult female, adult male and 6-year-old natal male; FRAG5: adult female, immigrant adult male, 4-year-old natal male) while FRAG4 had 7: adult male and female plus 5 offspring (6-year-old male, 3-year-old female, 2-year-old female, 1-year-old male and male newborn). Individuals were collared, allowing individual recognition.

Three of these natal individuals were past the age of first reproduction ( $\geq 4$  years old) seen in *P. diadema* and the related *P. edwardsi* [Wright, 1995; Irwin, unpubl. data] and should be considered as adults physically. In FRAG2 and FRAG4, the natal adult males were group mates with both parents; in FRAG5 the natal adult male lived with his mother and a recently immigrated male. All three lacked the developed chest gland characteristic of breeders (suggesting they are physiologically immature). Thus, for analysis we considered "breeding adults," "non-breeding natal adults" and immatures ( $\leq 3$  years) separately; some analyses lumped the first two categories as "adults."

### *Behavioural Data Collection*

Data were collected by the authors and local assistants using focal animal sampling [Altmann, 1974] from June to August 2014 (dry season [Irwin, 2006]), focusing on adults and immatures (2–3 years old). We applied two protocols: for the first, we collected instantaneous and continuous data. General activity data were collected using instantaneous sampling (5-min interval), with records classified as feeding, travel, resting and social (and social records subclassified as grooming, vocalisation, play, scent-marking and aggression). We simultaneously recorded social interactions continuously (grooming, playing, vocalisation, scent-marking, aggression and displacement). Aggression included physical contact such as biting and hitting, but not displacements without contact. "Displacement" was defined as individual A (initiator) approaching an eating individual B within 3 m, so that B stopped eating, retreated and ceded its feeding spot (individual plant). For each observation, we noted start and stop times, direction (initiator/receiver) and type (grooming: unidirectional/mutual; aggression: e.g. slap, hit, bite...). Finally, for all feeding bouts we recorded start and stop time, food species and item(s) (bud, flower, leaves). For inferring dominance, we included both displace-

**Table 1.** Animals within the *Propithecus diadema* study groups at Tsinjoarivo and sample size of focal animal days for the two data protocols; FRAG4 had a newborn infant that was excluded from data collection

Individual	Demographic class	Number of days activity budget, displacements, feeding and aggression	Number of days movement
FRAG2: RAD1	Adult F, breeding	3	3
FRAG2: BR1	Adult 6-year-old M, non-breeding	3	3
FRAG2: TR	Adult M, breeding	3	3
FRAG4: RAD2	Adult F, breeding	3	3
FRAG4: BG	Adult M, breeding	3	3
FRAG4: BR2	Adult 6-year-old M, non-breeding	4	4
FRAG4: RG	3-year-old F	3	3
FRAG4: PB	2-year-old F	3	3
FRAG4: JUV	1-year-old M	0	0
FRAG5: RAD3	Adult F, breeding	4	4
FRAG5: BP	Adult M, breeding	3	3
FRAG5: PO	Adult 4-year-old M, non-breeding	3	3
Total		35	35
Total breeding females		10	10
Total breeding males		9	9
Total non-breeding (natal) adults (4 years and older)		10	10
Total immatures		6	6

ments and aggressions; we considered that an aggressor “wins” when the victim retreats without displaying aggression, with or without calls (for aggression), or retreats without aggressing the initiator (for displacement). This data set totalled 35 focal-animal days and 324.6 h (Table 1).

The second protocol focused on movements. When the focal animal moved  $\geq 15$  m without pausing in a directed manner, we initiated a specific data collection protocol. If no individual had moved before the focal animal within  $45^\circ$  of the same direction, the focal animal was coded as “initiating” the movement; otherwise, we coded the focal animal as a “follower” when at least one other animal was in front and moving in the same direction or was stationary but in front of the vertical plane perpendicular to the focal animal’s direction of movement. Initiatorship was further divided into “independent movement” (no followers) and “leadership” ( $\geq 50\%$  of the group members, excluding newborns, followed in the focal animal’s direction within 3 min). For analyses, we only considered movements where all animals were visible. This data set totalled 35 days (Table 1); for the first part of the study, the two protocols were performed on separate days, but after July 7, they were performed simultaneously by S.M.R. and one assistant.

#### Data Analyses

To establish dominance ranks within groups, we calculated David’s score (DS) and NormDS [David, 1987; de Vries, 1998]; these indices measure both individuals’ ranks and the steepness of the hierarchies [Hemelrijk et al., 2005; de Vries et al., 2006] (Table 2). Then, we used NormDS values based on  $P_{ij}$  to measure steepness of hierarchies, allowing a comparison between

**Table 2.** Group composition and matrix of proportions of wins ( $P_{ij}$ ) of aggressions and displacements and the values for  $w$ ,  $w_2$ ,  $l$  and  $l_2$  used to calculate David's score (DS) and the normalised DS (NormDS) for each study group

Group FRAG2	RAD1	BR1	TR			DS	NormDS	Rank	Sex	Age
RAD1	–	1.00	1.00			3.00	2.00	1	F	AD
BR1	0.00	–	0.80			–0.60	0.80	2	M	6
TR	0.00	0.20	–			–2.40	0.20	3	M	AD
Group FRAG4	BG	RAD2	BR2	RG	PB	DS	NormDS	Rank	Sex	Age
BG	–	0.25	1.00	0.00	1.00	4.33	2.87	1	M	AD
RAD2	0.75	–	0.50	0.00	1.00	3.83	2.77	2	F	AD
BR2	0.00	0.50	–	1.00	0.71	0.57	2.11	3	M	6
RG	0.00	0.00	0.00	–	0.67	–3.17	1.37	4	F	3
PB	0.00	0.00	0.29	0.33	–	–5.57	0.89	5	F	2
Group FRAG5	RAD3	BP	PO			DS	NormDS	Rank	Sex	Age
RAD3	–	1.00	1.00			3.00	2.00	1	F	AD
BP	0.00	–	1.00			0.00	1.00	2	M	AD
PO	0.00	0.00	–			–3.00	0.00	3	M	4

DS, individual David's score values; NormDS, normalised David's score values; F, female; M, male; AD, adult.  $DS = [w + w^2 - l - l^2]$ ;  $NormDS = [DS + N(N - 1)/2]/N$ , where  $N$  is the group size.

the study groups [de Vries et al., 2006]. We included all animals followed as focal animals (i.e. we excluded FRAG4's juvenile). Thus, our hierarchies include multiple age-sex classes considered together.

Differences in frequency or duration of behaviours between age-sex groups were compared using Mann-Whitney U tests (at least some comparisons for each analysis had non-normal data; normality was tested using Shapiro tests). Frequencies of movement types (the largest data set) were tested using ANOVA (after log transformation to improve normality) and Tukey post hoc tests. The rates of intersexual and intrasexual displacements, and within-group movement counts, were compared with two-tailed binomial tests. Statistical analyses were performed in R [R Core Team, 2018], and significance was set at  $p < 0.05$ .

## Results

### *Activity Budget*

The study species spent most time resting (55.5%) and feeding (35.7%). Overall, only 0.03% of time was spent in agonism and 3.49% in other social interactions (grooming: 2.70%, play: 0.05%, vocalisations: 0.23%, scent-marking: 0.51%), for a total of 3.52% in all social activity. Of that total, 2.75% was spent in “affiliative” social behaviours (grooming and play). Time spent in affiliative social behaviours was higher in breeders (3.19%) and non-breeding natal adults (3.93%) than in immatures (2.08%).

### *Dominance Hierarchy*

Animals were ranked (Table 2) based on DS and NormDS values, reflecting proportions of wins during dyadic aggressions and displacements. Rank orders given by DS and NormDS values were identical. In FRAG2 and FRAG5, breeding females were dominant; in FRAG2 second rank was occupied by the eldest male offspring while in FRAG4 second rank was occupied by the immigrant breeding male. FRAG4 showed a different pattern: the two breeders occupied the top two positions, with the breeding female dominant to the male in dyadic interactions, but overall the male was top-ranking due to a higher proportion of wins over non-breeders. Thus, this group exhibits “female dominance” if strictly defined as “female dominance over breeding male(s),” but the female appears more deferential to her offspring than the male. FRAG5 showed the steepest hierarchy, suggesting a more despotic social structure (Table 2).

### *Frequency of Aggression*

Within 324.6 observation hours, we observed 21 acts of aggression (0.065 events/h). Among them, 52.4% (11/21) were intersexual interactions, and the remaining 47.6% (10/21) were male-male; no female-female aggression was observed. Most (61.9%, 13/21) aggressions were initiated by males, but the frequency of aggressions initiated by females and males did not statistically differ, either overall (binomial test,  $p = 0.4$ ) or in terms of frequency per hour (Mann-Whitney U test,  $W = 15$ ,  $p = 1$ ,  $n = 11$  individuals). Females received 28.6% (6/21) of aggressions while males received 71.4% (binomial test:  $p = 0.08$ ), and the frequency per hour did not differ (Mann-Whitney U test:  $W = 7.5$ ,  $p = 0.19$ ).

Considering aggressions among adults, 46.7% (7/15) were initiated by males, all being directed towards other males, while 53.3% were initiated by adult (breeding) females. Two of the 7 male-male aggressions were an adult natal male aggressing towards a breeding male (FRAG2), while 5 were the opposite (FRAG5); females were aggressive towards breeding males ( $n = 5$ ) and natal adult males ( $n = 3$ ). The frequency of aggressions initiated by females and males did not statistically differ, either overall (binomial test,  $p = 0.5$ ) or in frequency per hour (females: 0.029; males: 0.028; Mann-Whitney U test:  $W = 11$ ,  $p = 0.7$ ,  $n = 9$  individuals). Females did not receive aggression; all 15 aggressions were directed towards males. Overall, the number of aggressions received by males was higher (binomial test:  $p = 0.00015$ ), though males and females statistically received aggressions at the same rate (females: 0 events/h; males: 0.045 events/h; Mann-Whitney U test:  $W = 1.5$ ,  $p = 0.06$ ,  $n = 9$  individuals).

There were only 5 aggressions among breeding adults during the entire period of study; all were initiated by females (0.055 events/h) and directed towards males (binomial test:  $p = 0.06$ ). Further statistical testing was not attempted due to the low sample size.

### *Grooming*

Grooming was infrequent; mean total grooming per day was 1,045 s (17 min 25 s), of which grooming given (197 s/day) and grooming received (190 s/day) totalled less than 4 min each. Overall, the age-sex classes were largely uniform in time spent grooming and in each type (Table 3). Mann-Whitney U tests detected a lower daily duration of “received-only” grooming in non-breeders compared to breeders

**Table 3.** Mean cumulative daily grooming durations in *Propithecus diadema* of different age-sex classes at Tsinjoarivo (seconds per day  $\pm$  SD)

	All animals ( <i>n</i> = 35 days)	Breeding adults ( <i>n</i> = 19 days)	Breeding females ( <i>n</i> = 10 days)	Breeding males ( <i>n</i> = 9 days)	Non-breeding adults ( <i>n</i> = 10 days)	Immatures ( <i>n</i> = 6 days)
Daily duration, “give only”	197 $\pm$ 242	183 $\pm$ 273	145 $\pm$ 283	225 $\pm$ 273	189 $\pm$ 147	256 $\pm$ 290
Daily duration, “receive only”	190 $\pm$ 222	218 $\pm$ 158	236 $\pm$ 157	197 $\pm$ 165	63 $\pm$ 89	313 $\pm$ 421
Daily duration, “mutual”	658 $\pm$ 465	584 $\pm$ 389	595 $\pm$ 334	571 $\pm$ 462	995 $\pm$ 474	332 $\pm$ 383
Daily duration, all grooming <sup>1</sup>	1,045 $\pm$ 563	984 $\pm$ 539	976 $\pm$ 458	993 $\pm$ 646	1,247 $\pm$ 579	901 $\pm$ 619

<sup>1</sup>All grooming values may differ from sums of the three preceding values due to rounding.

**Table 4.** Frequency of group movements (mean  $\pm$  SD) led, followed and independent movements per day in different contexts in *Propithecus diadema* at Tsinjoarivo

	All animals ( <i>n</i> = 35 days)	Breeding adults ( <i>n</i> = 19 days)	Breeding females ( <i>n</i> = 10 days)	Breeding males ( <i>n</i> = 9 days)	Non-breeding adults ( <i>n</i> = 10 days)	Immatures ( <i>n</i> = 6 days)
Frequency of group movements led per day	3.71 $\pm$ 3.47	4.79 $\pm$ 4.25	6.80 $\pm$ 4.18	2.56 $\pm$ 3.21	2.50 $\pm$ 1.72	2.33 $\pm$ 1.37
Frequency of group movements followed per day	9.09 $\pm$ 5.89	7.37 $\pm$ 4.65	5.20 $\pm$ 2.35	9.78 $\pm$ 5.47	13.70 $\pm$ 6.93	6.83 $\pm$ 3.43
Frequency of independent movements per day	2.17 $\pm$ 1.96	2.11 $\pm$ 2.02	2.20 $\pm$ 1.62	2.00 $\pm$ 2.50	2.70 $\pm$ 2.31	1.50 $\pm$ 0.84

( $W = 216$ ,  $p = 0.03$ ), but no difference in mutual, give-only or total grooming. Similarly, there were no significant differences between breeding males and breeding females, or between adults and immatures.

### Group Movement

We observed 581 movements (including individual movements); for 524 all group members were visible. The mean daily number of movements for an individual was  $16.60 \pm 6.98$  SD. On average, a breeding female led her group 6.80 times/day while breeding males did so only 2.56 times/day (Table 4); breeding females led 68 of the 91 movements led by breeding adults (74.7%). The four age-sex classes differed in daily frequencies (ANOVA,  $F = 4.86$ ,  $p = 0.007$ ), and Tukey tests revealed significant differences: breeding females' frequencies were higher than those of breeding males ( $p = 0.008$ ) and non-breeding adults ( $p = 0.003$ ). The difference among male and female breeders was significant within each group (FRAG2: females led 16/23 leadership movements, binomial test:  $p = 0.047$ , expected proportion 50%; FRAG4: 12/12,  $p < 0.001$ , expected proportion 50%; FRAG5: 40/56,  $p = 0.02$ , expected proportion 57.1%).

Opposite trends were seen in “follow” movements: breeding females followed group mates 5.20 times/day compared with 9.78 for breeding males; breeding males followed in 88 of the 140 movements for which a focal breeding adult followed group mates (62.9%). The four age-sex classes differed in daily frequencies (ANOVA,  $F = 4.91$ ,  $p = 0.007$ ), and Tukey tests revealed one significant difference: breeding females’ frequencies were lower than those of non-breeding adults ( $p = 0.004$ ). However, a difference among male and female breeders was found within two groups (FRAG2: males accounted for 24/44 follows, binomial test:  $p = 0.3$ , expected proportion 50%; FRAG4: 39/57,  $p = 0.004$ , expected proportion 50%; FRAG5: 25/39,  $p = 0.006$ , expected proportion 42.9%).

“Individual” movements were rare (<3 per day); no significant differences were detected among age-sex classes (ANOVA,  $F = 0.8$ ,  $p = 0.5$ ).

#### *Feeding Priority: Displacements*

During feeding, 53 displacements were recorded; 73.6% (39/53) were intersexual while 26.4% were intrasexual. Among intrasexual displacements, male-male interactions (71.4% or 10/14) were represented in higher proportion. In intersexual interactions, females caused a male to retreat in 79.5% of cases (31/39; binomial test,  $p < 0.001$ ). Of the 53 displacements, 42 were among adults; 76.2% (32/42) of these were intersexual while 23.8% were intrasexual. Intrasexual displacements were only male-male since each study group contains only one adult female. In intersexual interactions, females displaced a male in 90.6% (29/32) of cases (binomial test,  $p < 0.001$ ). This pattern also held for interactions between breeders: 90% (18/20) were displacements of males by females (binomial test,  $p < 0.001$ ).

The frequency of being displaced in breeding males (1.56/day) was higher than that of breeding females (0.00/day), while breeding females provoked displacement from a food site (0.89/day) more frequently than breeding males did (0.67/day).

#### *Daily Feeding Outcomes*

Across all individuals, an average of  $11,999 \pm 2,537$  s was spent feeding, of which 53% were devoted to the mistletoe *Bakerella clavata*, and 9% were dedicated to fruits. Breeding males and females did not differ significantly in feeding time (males:  $11,800 \pm 2,498$  s/day; females:  $12,033 \pm 2,806$  s/day), time spent eating *B. clavata* (males:  $6,082 \pm 1,988$  s/day; females:  $6,522 \pm 2,201$  s/day) or time spent eating fruits (males:  $1,265 \pm 745$  s/day; females:  $1,272 \pm 700$  s/day) (Mann-Whitney U test,  $p > 0.05$  for all tests). Likewise, there were no significant differences between breeders and non-breeders in feeding time (breeders:  $11,922 \pm 2,593$  s/day; non-breeders:  $12,090 \pm 2,550$  s/day), time spent eating *B. clavata* (breeders:  $6,314 \pm 2,057$  s/day; non-breeders:  $6,324 \pm 2,373$  s/day) and time spent eating fruits (breeders:  $1,269 \pm 701$  s/day; non-breeders:  $907 \pm 675$  s/day) (Mann-Whitney U test,  $p > 0.05$  for all tests).

## **Discussion**

#### *Dominance Relationships and Agonism*

Though female dominance is found in most lemurs [Wright, 1999; Hemelrijk et al., 2008], dominance style varies widely from egalitarian to despotic; for example, *Propithecus verreauxi* hierarchies are weak compared to *Lemur catta* [Kappeler, 1990; Norscia and Palagi, 2015], *Varecia rubra* or *Varecia variegata* [Raps and White,



1995]. Here, breeding females of *P. diadema* were agonistically dominant over breeding males, but the male occupied the top rank in FRAG4 due to his greater dominance over non-breeders. The second rank position was held either by the eldest male offspring (FRAG2), the female herself (FRAG4) or the dominant female's breeding partner (BP in FRAG5). Admittedly, these rankings are based on few aggressive interactions, but they mirror the findings of a year-long study [Irwin, 2006] which counted 255 aggressions among breeding adults and confirmed female dominance among breeding adults in four groups (all breeding females occupied top position). It therefore appears that *P. diadema* groups vary in dominance structure, with males varying in dominance over non-breeders, and that kinship may affect the hierarchy. The eldest adult male in FRAG2 seemed to cede the second rank and express tolerance towards his offspring, but the steep hierarchy in FRAG5 suggests a more despotic situation, perhaps because BP (adult male) was an immigrant who arrived in November 2011 and was unrelated to PO (4-year-old male). Similar variation was reported in *P. coronatus*, dominated by an alpha reproductive female, but whose dominance model is non-linear and difficult to characterise after the dominant female [Razanapary et al., 2014]. It thus appears that variation within and among populations may be an important part of understanding female dominance in lemurs more generally.

As with many lemurs [Erhart and Overdorff, 2008], agonism was rare in this study (0.065 events/h); half of the aggressions were intersexual interactions (11/21), the rest being male-male interactions. This rate was half that observed in *P. diadema* at Tsinjoarivo during a year-long study in 2003: 803 acts of aggression in 6,456 focal animal hours (0.124 events/h) [Irwin, 2006]. In that study, groups in the less disturbed forest had higher rates (0.13–0.23), while groups at Mahatsinjo were similar to our results (FRAG1: 0.079, FRAG2: 0.048). Further, our rate for breeding adults (0.055) was similar to the 2003 rate for FRAG breeders (0.064). Interestingly, there was no apparent seasonal variation in aggression rates [Irwin, 2006], meaning that our results, though restricted to the lean season, may still be fairly representative.

#### *Grooming, Leadership and Displacements*

In addition to hygienic functions, grooming serves tension-reducing and social functions [Leinfelder et al., 2001]; thus, grooming a dominant female could be a male strategy to receive less aggression from her, as seen in *Eulemur rufifrons* [Port et al., 2009]. Alternatively, grooming could represent a service given in exchange for grooming in return or other services, following the biological market theory [Noë and Hammerstein, 1995; Port et al., 2009]. In *P. verreauxi*, males giving more grooming receive more copulations [Norscia et al., 2009], while in *P. edwardsi* [Foltz, 2009], *P. verreauxi* [Lewis, 2010] and *Eulemur coronatus* [Marolf et al., 2007], females tend to give less and receive more grooming. In contrast, we detected no meaningful differences in grooming profiles between breeding males and females. This reflects the reciprocal character of grooming seen in other primates [e.g. Ventura et al., 2006], but it raises the question of what benefits female *P. diadema* derive from grooming subordinates.

We found that group leadership in *P. diadema* was influenced by sex: breeding females led more movements than breeding males, and followed less often, similar to previous findings in *Haplemur alaotrensis* [Waeber and Hemelrijk, 2003], *Eulemur rufifrons* [Erhart and Overdorff, 1999] and *P. verreauxi* [Trillmich et al., 2004]. Multiple factors, both social and environmental, are thought to drive the success of group movement in lemurs [Pyritz et al. 2011]: in *E. rufifrons*, a male's decision to join a collective

movement depends on his favourite partner (i.e., he is “following his friend”) [Jacobs et al., 2011], while for *H. alaotrensis*, the likelihood for a male to lead varied with the terrain [Waeber and Hemelrijk, 2003]. In *P. edwardsi*, female leadership is still ambiguous; although the species displayed female initiatorhip, Foltz [2009] found that females and males were equally likely to be followed, while Erhart and Overdorff [1999] stated that female *P. edwardsi* were more likely to be followed. Our results suggest that choices regarding movements and feeding sites belong primarily to breeders, suggesting that non-breeders may rely on older groupmates’ knowledge of food distribution. However, we also found that adult non-breeders had unexpectedly high following rates. This suggests that breeders may choose to follow younger offspring, while older offspring must more actively follow group mates or risk being left alone. Initiating and directing group movement to feeding sites could benefit higher-ranked females because this strategy tends to promote her first access to the resource [Foltz, 2009; Erhart and Overdorff, 1999]. For instance, when female *V. variegata* directed more group movements and arrived first at food sites, they had increased food intakes [Overdorff et al., 2005].

We found that *P. diadema* females provoked displacement more frequently than males, and that retreats by breeding males were more frequent than retreats by breeding females; this means that females can have improved feeding outcomes even in the absence of direct aggression. *L. catta* [White et al., 2007] and *Propithecus edwardsi* [Pochron et al., 2003] displayed the same behaviour. Even *Pan paniscus*, whose males are agonistically dominant, exhibit female feeding priority [White and Wood, 2007]. This asymmetry, which could result from female power, male deference or both, may help females overcome their high reproductive costs [Young et al., 1990]. Male deference may be more likely here, especially since some males in this study were more dominant over immatures than were breeding females. Males’ deference may help ensure their own reproductive success because it increases access to fertile females in the next breeding season while also promoting the survival of their offspring by helping females overcome the costs of gestation and lactation [Pochron et al., 2003; White et al., 2007]. However, it is also worth noting that displacements were exceedingly rare, suggesting that subordinates tend to avoid conflict, perhaps using subtler cues, or avoiding preferred food patches.

#### *Consequences of Social Dominance*

Dominance relationships influence feeding in social species [Janson, 1990; White et al., 2007], and the presence of a dominant can cause reduced food intakes in subordinates [Saito, 1996]. Female dominance, male deference and/or female leadership were expected to affect feeding or food intake of *P. diadema*, but no such evidence was found in this study. The *P. diadema* diet in the disturbed forests of Mahatsinjo consists mainly of *B. clavata*, present abundantly throughout the year [Irwin, 2008b] although non-mistletoe fruits are their preferred food when available. Feeding competition seems reduced, as the animals have come to rely on this mistletoe, a less preferred but more abundant food. These results, coupled with the overall less aggressive nature of lemurs, suggests that lemur foods may be less contestable than those of other primates, either due to spatial characteristics like small patch size or plant secondary metabolites that limit intakes [Marsh et al., 2006]. However, further study is needed concerning subtler aspects of diet, nutritional value of foods, nutritional intakes and social patterns such as order of access at food sites and monopolisation of resources. It is possible that female leadership does cause nutritional differences in ways that we were unable to detect.

### Conclusions and Future Directions

Agonistic dominance of the breeding female over group mates (aggressions and displacements included) was confirmed in two of three *P. diadema* groups, but breeding females dominated breeding males in all groups; we found low rates of both aggression and affiliative behaviours. Female power was not manifested in grooming duration and frequency of aggressions, suggesting these groups probably experienced more relaxed dominance hierarchies during this study, reflecting infrequent overt competition. This reinforces the fact that studies examining female power in lemurs should take a multi-faceted approach and not rely on a single measure. We also found that sex influenced spatial dynamics, with females tending to lead movements, and males routinely retreating from feeding locations. We cannot distinguish whether females' feeding priority is caused by female dominance or male deference (or both), but the fact that the male in FRAG4 occupied a higher rank than the female suggests the latter. Though we expected that the observed asymmetries would result in better feeding outcomes for females, this was not the case, suggesting relaxed feeding competition, or possible competition for resources other than food.

Our ability to draw generalisations is constrained by our low sample size (particularly the aggressive interactions and the DS based on them), and the restriction of our sampling to the lean season. Additional sampling should explore the rainy (and mating) season, and groups with more than two breeding adults (these exist elsewhere in the population). A more detailed study of feeding outcomes would be required to better understand the consequences of female dominance in *P. diadema* and its evolutionary origin. Although feeding outcomes may not differ between females and males, females might be using richer patches (both in terms of abundance and the nutritional quality of food items). Finally, we must also consider the possibility that female dominance may be expressed in feeding outcomes only in times of extreme food scarcity, when it is most needed to ensure survival and successful reproduction.

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### Statement of Ethics

All research methods reported in this paper adhered to the legal requirements of Malagasy authorities and to the American Society of Primatologists' Principles for the Ethical Treatment of Primates and were approved by Madagascar's Ministry of Environment and Forests (Permit 116/14/MEF/SG/DGF/DCB.SAP/SCB) and Northern Illinois University IACUC (LA12-0011).

## Disclosure Statement

The authors have no conflicts of interest to declare.

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## Author Contributions

S.M.R. designed the study and collected field data with research assistants. M.T.I. assisted in study design and field logistics. Both authors conducted data analysis and manuscript writing.

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