RESEARCH ARTICLE

Food availability and male deference in the female-dominant ring-tailed lemur, *Lemur catta*

Joyce A. Parga[1] | Emma Thurau[2,3]

[1]Department of Anthropology, California State University—Los Angeles, Los Angeles, California, USA

[2]Department of Anthropology, City University of New York, New York, New York, USA

[3]New York Consortium of Evolutionary Primatology (NYCEP), New York, New York, USA

Correspondence

Joyce A. Parga, Department of Anthropology, California State University—Los Angeles, 5151 State University Dr., Los Angeles, CA 90032, USA.
Email: Jparga2@calstatela.edu

Abstract

Female dominance, a trait common to some Malagasy lemurs, has been viewed as an adaptation that decreases intersexual feeding competition. A hypothesized relationship exists between male "deference" (male submission in the absence of female aggression) and food availability. Sauther (1993) suggested that male ring-tailed lemurs at the Duke Lemur Center (Pereira et al., 1990) show more deference to females than do males in the wild owing to food abundance in captivity. To reexamine the link between food availability and male deference, we studied agonism and foraging in two nonwild ring-tailed lemur (*Lemur catta*) populations: the Los Angeles Zoo and St. Catherines Island (SCI). On SCI, we collected data under two feeding conditions: Low Provisions (low food availability) and High Provisions (high food availability). As expected, male deference measures at our study sites were more similar to measures of deference from other studies of *L. catta* in captivity than in the wild. Additionally, the change at SCI from low to high food availability was associated with increased male deference to females. Interestingly, male proximity to females during foraging at this location did not notably change between the low to high food availability conditions, suggesting that males were food competitors of females just as often under both feeding conditions. The increase in male deference under conditions of high food availability on SCI was due to males withdrawing more rapidly from female approaches during agonistic interactions. Hence, where food is more abundant, male *L. catta* are more likely to show submission to females, which appears to be a self-serving means of avoiding female aggression. Lemur males who are well-fed appear less apt to risk female aggression to obtain resources than more nutritionally stressed males. Our results support the view of female dominance in lemurs as an adaptive evolutionary response to conditions of resource limitation.

KEYWORDS

agonism, feeding competition, female dominance, food availability, ring-tailed lemur

1 | INTRODUCTION

Female dominance over males, whereby all adult females consistently "win" in agonistic interactions against males, is a trait shown by some of the Malagasy lemurs (Richard, 1987), including some species of bamboo lemurs, *Hapalemur* spp. (Digby & Mclean Stevens, 2007; Eppley et al., 2017; Waeber & Hemelrijk, 2003), black lemurs, *Eulemur macaco* (Bayart & Simmen, 2005; Digby & Mclean Stevens, 2007), mouse lemurs, *Microcebus* spp. (Hohenbrink et al., 2016; Radespiel & Zimmermann, 2001), sifaka, *Propithecus* spp. (Kubzdela et al., 1992; Pochron et al., 2003), and the ring-tailed lemur, *Lemur catta* (Jolly, 1966, 1984; Sauther et al., 1999). Ultimate explanations for female dominance have included such ideas as male "chivalry" or male submission as a form of reproductive investment in females and their offspring (Hrdy, 1981; Jolly, 1984). Two factors have predominated among the hypotheses offered to explain the evolution of female dominance in lemurs: female reproductive stress and male–female feeding competition (Dunham, 2008; Gould, Sauther, et al., 2011; Jolly, 1984; Richard & Nicoll, 1987; Sauther, 1993, 1998; Sussman, 1999; Young et al., 1990). Female dominance over males is generally regarded as one evolutionary solution to the reproductive challenges faced by females in a highly seasonal habitat with scarce and unpredictable resources (Wright, 1999) where males are competitors for food (Sauther, 1993). Given the prominent role that intersexual resource competition is thought to play in the evolution of female dominance, it is important to understand the conditions that determine female agonistic superiority in lemurs, especially as it applies to food availability.

In this study, we focus on female-to-male agonism in the ring-tailed lemur (*L. catta*), a strepsirhine that lives in multimale, multifemale groups (Gould, 2006; Jolly, 1966; Jolly et al., 2006; Kappeler, 1993; Pereira et al., 1990; Sauther et al., 1999; Sussman, 1991, 1992). We reevaluate the relationship between food availability and male submissive behavior, which are two variables that seem to show a positive relationship in *L. catta*. The evidence for this relationship comes from a comparison of captive and wild data (Sauther, 1993). Among wild *L. catta*, female–male agonism most often takes the form of female aggression (e.g., bites, cuffs, lunges) to males. Sauther (1993) found that only 37% of agonistic wins by females over males lacked female aggression in *L. catta* from Bezà Mahafaly, Madagascar. In contrast, among *L. catta* at the Duke Lemur Center, the majority (75%) of female–male agonistic interactions consisted of spontaneous shows of male submission, including male withdraws from approaches by females who showed no aggressive behavior (Pereira et al., 1990). Sauther (1993) suggested that this difference between wild and captive *L. catta* in the frequency with which females used aggression in intersexual competition was due to food abundance in captivity making males more likely to show submission to females.

Artificially high resource abundance due to provisioning has been shown to have profound and varied effects on primate behavior (Asquith, 1989; Hill, 1999; Sugiyama & Ohsawa, 1982). One common finding is that provisioned primates spend less time foraging on wild

foods. For example, wild bearded capuchin monkeys, *Cebus libidinosus*, in the Parque Nacional de Brasília having access to human foods from park visitors showed decreased time spent foraging on wild foods compared to capuchins in comparable habitats without access to human foods (Sabbatini et al., 2008). Distributing provisions can also increase aggression among individuals if food is provided in a clumped manner, as was observed among mouse lemurs, *Microcebus lehilahytsara*, at the Zurich Zoo, where several individuals were provided with fruit at two feeding stations, prompting feeding competition even though food amount was unlimited (Jürges et al., 2013).

Although provisioning can be associated with increased aggression in *L. catta* (Cavigelli et al., 2003), much of the aggression in *L. catta* groups generally occurs between females competing for food (Sauther, 1993). Our study's focus instead was the phenomenon of increased male submission to females that has been reported to occur under provisioned conditions in captivity (Pereira et al., 1990) in comparison to nonprovisioned wild *L. catta* (Sauther, 1993). The proximate mechanism controlling male deferential behavior to females in a female-dominant species such as this (Jolly, 1966; Sauther et al., 1999) may be a male's cost–benefit analysis based upon his nutritional status. Males may be more willing to risk female aggression as part of feeding competition where there is a greater benefit to obtaining food—namely, where food is scarce. Male lemurs in the wild may simply be more willing to risk female aggression to obtain resources owing to being in a more nutritionally stressed state than males in captivity.

Our study's aim was to revisit the hypothesized link between high food availability and increased male submission to females in *L. catta* (Sauther, 1993). We studied two populations of this species: a zoo population entirely dependent on artificial food, and a free-ranging provisioned population maintained on an island in the United States having access to naturally growing foods. We predicted that these two *L. catta* populations would more closely resemble *L. catta* at the Duke Lemur Center (Pereira et al., 1990) in that the majority of female-to-male agonistic interactions would lack female aggression. Moreover, because one of our research sites underwent a feeding protocol change mid-way through the study that increased the amount of provisioned food available, we were able to measure female–male agonism under two different feeding conditions at that site: Low Provisions (low food availability) and High Provisions (high food availability). We predicted that male submission to females would be more common under High Provisions than Low Provisions, as measured by the proportion of female–male agonism lacking female aggression.

2 | METHODS

2.1 | Ethics statement

All research described in this paper adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-

Human Primates and adhered to the legal requirements of the United States. Permission for each study was given by the Los Angeles Zoo and St. Catherines Island Foundation, respectively. Data collection at the latter location was approved by the Institutional Animal Care and Use Committee of the University of Texas-Austin (#3061703) and followed the American Society of Primatologists Code of Best Practices for Field Primatology.

2.2 | Study locations

This study focused on *L. catta* maintained at two locations (Table 1). The first study population was a captive group of *L. catta* at the Los Angeles Zoo (LAZ) in Los Angeles, California, USA. This group was studied by E. T. between August 2016 and March 2017. The group consisted of three related adult females (a mother and her two daughters), and one unrelated adult male. All animals were between 7 and 20 years of age. No animal was on contraception or pregnant during the course of the study. Once per day, the group was fed primate chow and fresh vegetables and was provided with browse (branches with leaves that the lemurs would consume). The primate chow was scattered on the ground throughout the enclosure, and the vegetables were provided in four bowls on standing trays. This mode of food distribution remained the same throughout the months of data collection at the LAZ. Only provisioned food was consumed by lemurs at the LAZ, because no natural vegetation grew in the lemurs' enclosure. At the LAZ, the lemurs were not housed with any other animal species.

The second study population was a provisioned *L. catta* colony (Keith-Lucas et al., 1999; Parga & Lessnau, 2005) maintained on St. Catherines Island (SCI), Georgia, USA (Thomas et al., 1978). Similar to the lemurs at the LAZ, the lemurs on SCI were not on any form of contraception during the study period. Neither was any female on SCI pregnant, because data collection for this study occurred before the breeding period in each year. This lemur colony free-ranges in a habitat consisting largely of mixed oak, pine, and palmetto forest (Keith-Lucas et al., 1999). During the course of this study, the lemurs were provisioned once daily with primate chow and fresh fruits (e.g., grapes, banana, or apple slices) and vegetables (e.g., kale, sweet potato, carrot slices). The SCI lemurs also foraged extensively on wild vegetation, which included such items as fruits, leaves, and seeds (Dierenfeld & McCann, 1999; Keith-Lucas et al., 1999; Parga, unpublished data). Data on feeding and agonism were gathered on SCI across three consecutive years (2000–2002) by J. A. P. as part of a larger study on lemur social and reproductive behavior (Parga, 2003, 2006). The data presented here were gathered during September–October, in the weeks preceding the first cycle of the mating season of each year, which typically begins in late October on SCI (Parga & Lessnau, 2005). Only data collected in the weeks before mating were used in these analyses, as agonism rates can be extremely high during mating periods, being largely centered around sexual activity (Parga, 2006). Two lemur groups on SCI were studied in each year: Group 1 and Group 3 in 2000–2001, and Group 2 and

TABLE 1 Data on group composition, foraging, and intersexual agonism for lemurs in this study

Location	Year	Group name	Group composition: Total # (M:F)[a]	Sampling time (h)	Number of female-to-male agonistic interactions	% Time spent foraging in activity budget	% Foraging time spent on natural foods	Male deference (% of agonistic wins by females w/out female aggression)—All contexts	Male Deference (% of agonistic wins by females w/out female aggression)—Foraging contexts only
LAZ	2016-17	-	4 (1M:3F)	92	62	7	0	70	Unknown[b]
SCI	2000 (Low Provisions)	Group 1	10 (5M:5F)	27	128	12	69	58	62
		Group 3	16 (7M:9F)	23	103	15	60	51	64
	2001 (Low Provisions)	Group 1	12 (5M:7F)	24	150	26	69	61	71
		Group 3	12 (6M:6F)	63	335	11	58	60	69
	2002 (High Provisions)	Group 2	13 (5M:8F)	21	108	14	39	69	68
		Group 3	12 (4M:8F)	23	93	13	11	74	80

Abbreviations: LAZ, Los Angeles Zoo; SCI, St. Catherines Island.

[a]Group composition, which includes all animals >1 year of age, differed from year to year on SCI due to births, deaths, male dispersal (Parga & Lessnau, 2008), and one fission event in Group 3 in which three adult females were ejected from the group in the spring of 2001.

[b]Context of agonistic interactions was not recorded during all occurrences sampling at the LAZ.

Group 3 in 2002. Although the original intent was to focus on the same study groups in all years, a management decision unrelated to the research resulted in the relocation of Group 1 to a captive location off the island in 2002, between the second and third years of this study. As such, only Group 3 was able to be followed across all 3 years of the study. Each study group on SCI contained between 5–9 females and 5–7 males between 1 and 14 years of age (Table 1).

Although the overall amount of food provided to each lemur group on SCI remained the same throughout the study (90 g of HMS Primate Diet chow and 100 g of fruit and vegetables per lemur, per day), the protocol for provisioning changed between the second and third years of the study. The first 2 years of the study (2000–2001) on SCI are considered the Low Provisions condition in this paper. At that time, the lemurs' provisioned foods were distributed by placing one to two food bowls containing chow and fruits/vegetables in each group's shelter site (a structure that the lemurs could freely enter and exit) and scattering the remaining food (chow and fruits/vegetables) on the ground in a technique known as "broadcasting." Due to the unique nature of SCI, which is a site replete with endemic wildlife (Thomas et al., 1978), the ground-scattered provisions were rapidly consumed by species such as white-tailed deer (*Odocoileus virginianus*) and raccoons (*Procyon lotor*). These animals frequently fed on the lemurs' food following the distribution of provisions, with the deer often feeding at the same time as the lemurs. As a result, the most highly preferred foods of the lemurs—the fruit and vegetable portion of the provisioned diet—were typically only available for 30 min or less each day during the Low Provisions period (Parga, personal observation).

The third year of the study (2002) ushered in a new feeding protocol on SCI and is termed the High Provisions condition in this paper, as it marked a greater abundance of provisioned food for the lemurs. In the new method of distributing provisions, instead of the majority of food being ground-scattered as was previously done, one to two food bowls were still placed inside each lemur group's shelter site, but the majority of food was now provided in feeding platforms located within several meters of each lemur group's shelter site. Per shelter site, four to six feeding platforms were installed. Each feeding platform supported a single bowl of provisions and was placed on a vertical wooden post measuring approximately 1.25 m above the ground. Each platform had enough space for more than one lemur to sit, and the typical pattern was for a platform to be occupied by one to three individuals, usually one to two adult females and their subadult offspring (Parga, personal observation). As during the Low Provisions period, both chow and fruits/vegetables were provided together in the food bowls. The feeding platforms greatly increased the overall amount of food available to the lemurs by eliminating interspecific competition with other animals on SCI (Parga, personal observation). Cylindrical PVC piping around the wooden post of each platform kept raccoons from climbing the posts to access the provisioned food. Chow as well as fruits (one of the most preferred foods of the lemurs) were commonly still available in the feeding platforms several hours following the distribution of food during the High Provisions period (Parga, personal observation).

2.3 | Data collection

At the LAZ, unique physical differences were used to identify each lemur. On SCI, individuals were identified using uniquely colored radio collars or cat collars fitted on each lemur by the animal husbandry staff. To collect data, a behavioral ethogram was used at both locations that was based upon those developed by Gould (1994), Jolly (1966), Pereira and Kappeler (1997), and Taylor (1986) for *L. catta*. At both study sites, the category of "foraging" included both the consumption of food (feeding) and searching for food (foraging). Hereafter, in this paper, the term foraging will be used to refer to both the consumption of, and searching for, food.

At both study sites, data were collected during daytime hours (between 07:00 and 19:00) alternating between focal animal sampling and "all occurrences" sampling (Altmann, 1974) for agonism (behaviors defined as agonism can be found in Section 2.4). At the LAZ, both sampling types were 15 min in duration. On SCI, each sampling type was 20 min in duration during 2000–2001 and shortened to 15 min in duration in 2002. An equal number of focal samples were collected on each individual per study group (and per study year on SCI). Ad lib notes were also collected at all times to record additional pertinent information at each site.

All occurrences sampling for agonism at both locations was carried out by watching the entire group for the duration of sampling and recording all agonistic interactions, noting the identity of the actor and recipient, and outcome of the interaction. On SCI, the context of each agonistic interaction was recorded (foraging, grooming, resting, traveling) and the food type (provisioned or naturally growing) was noted.

Focal sampling was performed slightly differently at each site. At the LAZ, point (instantaneous) sampling (Altmann, 1974; Martin & Bateson, 2007) was used to record the general behavior of and distance between the focal animal and all other individuals in meters once per minute. On SCI, continuous-time focal animal sampling was used, with the observer recording the start and stop time of all activities by the focal animal in seconds, making note of all agonism involving the focal individual. On SCI, the identity of the focal individual's single nearest neighbor was recorded in seconds for the duration of the focal sample, along with a distance category for that individual, as follows: 1 (touching), 2 (≤1 m, but not touching), 3 (>1 m ≤ 3 m), 4 (>3 m ≤ 5 m), 5 (>5 m).

During focal sampling and all occurrences sampling for agonism on SCI, an additional measure was recorded in cases in which a subordinate individual retreated from a more dominant individual: "latency to withdraw," which is defined here as the time that elapsed (in seconds) before a subordinate individual withdrew after first looking in the direction of an approaching dominant individual.

2.4 | Data analysis

At both sites, focal sampling was used to gather data on time spent foraging relative to other activities (and time spent foraging on

provisioned vs. natural foods on SCI). Our proximity/nearest neighbor data also derived from focal samples. At the LAZ, data on agonism originated from all occurrences sampling, as the point/instantaneous sampling conducted on focal animals at this location were primarily used to record foraging data. Data on female–male agonism on SCI came from both focal sampling and all occurrences sampling. The sampling regimes at the two sites were comparable for this analysis because the main variables of interest for this study were the relative proportion of female-to-male agonism that lacked female aggression and the relative time individuals spent foraging.

Following the example of Sauther (1993), we made a distinction between female and male agonism involving female aggression versus nonaggressive female–male agonism (e.g., approach–withdraw interactions). Female aggression toward males included bite, chase, cuff, nose poke, and lunge (Gould, 1994; Jolly, 1966; Pereira & Kappeler, 1997; Taylor, 1986). Nonaggressive agonism in this study included all instances of (1) approach–withdraw interactions between females and males (including displacements, wherein a dominant individual takes the physical space vacated by a subordinate) and (2) spontaneous submissive vocalizations (e.g., "yip": Bolt, 2021; Jolly, 1966; Macedonia, 1993) made by males to females. Because some female approaches led to affiliative behavior with males (i.e., were followed by grooming between individuals), only those approaches that elicited a submissive response (submissive vocalizations and/or withdraws) from the individual being approached were scored as agonistic interactions. We consider male "deference" as agonistic interactions in which males showed submission to females in the absence of female aggression (Kappeler, 1993). We calculated male deference as the percentage of female agonistic wins over males that occurred without the use of female aggression.

Although data collected at one of our study sites (LAZ) spanned a longer period of time (from late summer through spring) than at our second site (SCI) where data were collected in the fall months of each year, we still found it useful to compare the data collected at the two locations. We expected that because animals at the LAZ were fed an identical diet year-round and had no access to natural vegetation, any changes in behavior that would normally be associated with seasonal changes in feeding ecology in wild or free-ranging animals would be absent. Additionally, though females at the LAZ were allowed to reproductively cycle, the fact that the study females did not conceive probably minimized seasonal hormonal effects on intersexual agonistic behavior, aiding a comparison of data collected at each site.

We analyzed our data using nonparametric statistics. We compared our group-level data on male deference and foraging (the proportion of foraging time spent exploiting naturally growing foods) with similar data from other published *L. catta* studies using a Spearman rank correlation test. The test made use of data from one wild study conducted in Bezà Mahafaly, Madagascar (Sauther, 1993), one study at the Duke Lemur Center (Pereira et al., 1990), and included seven data points from our two study sites combined (one data point from the LAZ, and six data points from SCI representing each study group in each year of the project). All other analyses were limited to data sets collected from one of the two populations

observed as part of this study. All means are reported with standard deviations (SD). Data were analyzed using STATISTICA, v13.5.0.17 (TIBCO Software Inc.), with alpha set at $p < 0.05$.

3 | RESULTS

Each *L. catta* group that we studied spent <30% of their activity budget foraging, from a low of 7% at the LAZ to a mean of $15 \pm 5.5\%$ (range: 11%–26%) on SCI (Table 1). Although the overall time groups spent foraging as part of their activity budget on SCI was similar when comparing the Low Provisions and High Provisions periods, the proportion of time spent foraging on naturally growing foods on SCI was lower during the period of High Provisions compared to the previous two Low Provisions years (Table 1). The lemur groups on SCI spent a mean of $64 \pm 5.8\%$ (range: 58%–69%) of foraging time on natural foods during the Low Provisions years, but only $25 \pm 19.8\%$ (range: 11%–39%) of foraging time on natural foods during the High Provisions period (Table 1).

Although the introduction of feeding platforms on SCI (marking the High Provisions period) might have been expected to greatly increase intragroup competition due to increased food clumping, female-to-male agonism rates within the groups on SCI (calculated from the number of intersexual agonistic interactions and sampling time per group in Table 1) remained largely consistent, and even slightly decreased, after food platforms were installed. In the Low Provisions period, a mean of 5.2 ± 0.8 agonistic interactions/hr (range: 4.5–6.4) occurred between females and males in the study groups, and these values remained similar in the High Provisions period, at a mean of 4.6 ± 0.8 agonistic interactions/hr (range: 4.0–5.1). Given that overall male-female agonism rates in the groups were not markedly different before or after feeding platform installation on SCI, we calculated male deference levels at our two study locations, and we investigated whether the shift from Low to High Provisions on SCI affected male deference.

At the LAZ, male deference (the proportion of female–male agonism comprised of male submission in the absence of female aggression) was 70% across all contexts (Table 1). On SCI, male deference levels in each group were similarly high. Calculated across all contexts on SCI using data on all female–male agonism occurring within each group, male deference ranged between 51% and 61% during the Low Provisions period, rising to 69%–74% during the High Provisions period (Table 1). Considering female–male agonism in the groups only during foraging contexts, male deference increased from 62% to 71% during the Low Provisions period to 68%–80% during the High Provisions period.

Specifically considering data from SCI Group 3, the only group for which both before-and-after feeding platform data were available, male deference (measured across all contexts) increased in this group from 51% to 60% during Low Provisions to 74% in the High Provisions period. For foraging contexts specifically, the increase in male deference in this group was similarly notable, increasing from 64% to 69% during Low Provisions to a high of 80% during the High Provisions period (Table 1).
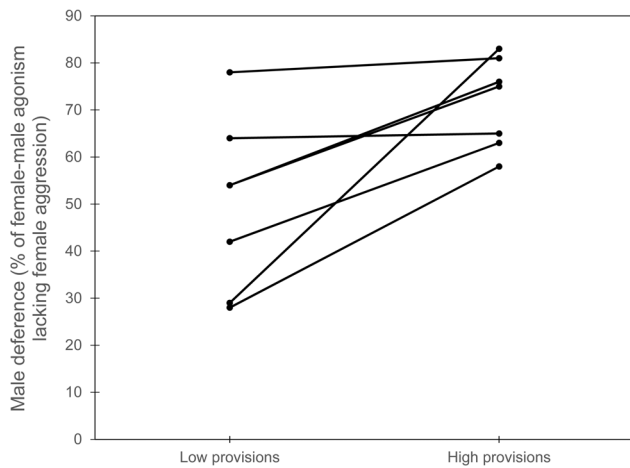
FIGURE 1 Each line represents the change in individual males' mean deference values on St. Catherines Island for those males who were present in the study groups under both feeding conditions. Every male showed an increase in deference from the Low Provisions (low food availability) to High Provisions (high food availability) condition (Wilcoxon: $N = 7$, $Z = 2.37$, $p < 0.018$).

Following these group-level analyses, we quantified deference per male to see whether the apparent increase in male deference from Low to High Provisions on SCI would still hold for individual males. We included data from all males who were present in the SCI study groups during both Low and High Provisions periods ($N = 7$). Five of these males belonged to a different study group before versus after the change in feeding condition. Individual mean measures of male deference encompassed a broad range of values, especially during the Low Provisions period, but the consistent pattern observed was one in which male deference was higher during the High Provisions period (Figure 1). Every male exhibited a deference increase (some more drastic than others) when moving from the Low to High Provisions period, a trend which was statistically significant (Wilcoxon matched-pairs test: $N = 7$, $Z = 2.37$, $p < 0.018$).

Returning to group-level measures, we compared our male deference data from LAZ and SCI with that from other published *L. catta* studies and found a significant inverse correlation between male deference and the proportion of total foraging time spent exploiting naturally growing (as opposed to provisioned) foods (Spearman rank: $r_S = -0.79$, $N = 9$, $p < 0.012$; Figure 2) despite the differences in habitat conditions from site to site.

One obvious question was whether males were acting as food competitors to females, as measured by nearest neighbor patterns and proximity between individuals during foraging. At the LAZ, the maximum distance any animal could be from another was 3 m due to the enclosure size. At this location, the single group male was infrequently in close proximity to foraging females. The male was 1 m away or less from foraging females in 12% (15 of 122) of instances of female foraging.

We also analyzed nearest neighbor patterns on SCI, investigating whether the increase in male deference when moving from Low Provisions to High Provisions was reflected in males acting less
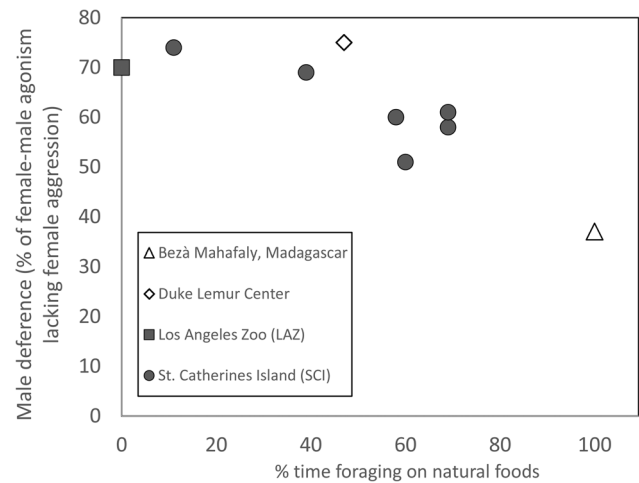
FIGURE 2 Across *Lemur catta* study sites, there is a significant inverse correlation between the amount of deference shown by males to females and the proportion of total time foraging spent on naturally occurring foods at each location (Spearman rank: $r_S = -0.79$, $N = 9$, $p < 0.012$). Data from LAZ and SCI are in Table 1. Data from Bezà Mahafaly are from Sauther (1993). Data on agonism from the Duke Lemur Center are from Pereira et al. (1990) and data on feeding at the same site are from Ganzhorn (1986). LAZ, Los Angeles Zoo; SCI, St. Catherines Island.

frequently as food competitors of females under the latter condition. To address this question, we analyzed nearest neighbor data for Group 3, the only SCI group for which we have data from both the Low Provisions and High Provisions periods. Group 3 males did not show notable changes in the frequency with which they were nearest neighbors of foraging females under both feeding conditions, especially when taking into consideration the number of males per study year (Table 1). Males in Group 3 were nearest neighbors to foraging females 29% and 36% of the time, respectively, during each year of the Low Provisions period and 21% of the time in the High Provisions period (Table 2). Although the percentage of time males were nearest neighbors to foraging females seems to be decreasing slightly over time, dividing by the number of males residing in the group in each study year shows that the frequency with which males were found to be the nearest neighbors of foraging females was a consistent function of the number of males in a group in a given year (Table 2). Because Group 3 males were not less likely to be nearest neighbors to foraging females in the High Provisions versus Low Provisions period, we then asked whether males were found at greater distances from foraging females during the High Provisions period relative to the Low Provisions period. We found no major differences in males' mean distance rank to foraging females under the two feeding conditions. In fact, the value for males' mean distance to foraging females during the High Provisions period fell in between the two corresponding values for the Low Provisions years (Table 2). Males' mean distance to foraging females remained fairly consistent from year to year, with males maintaining a mean distance of between 1 and 3 m away from foraging females regardless of feeding condition (Table 2).

TABLE 2 Nearest neighbor (NN) and latency to withdraw data for SCI Group 3 before and after installation of feeding platforms, which shifted feeding conditions from Low to High Provisions

Year	% Time males were NN to females in foraging contexts	% Time males were NN to females in foraging contexts/# males in group	Mean distance rank (±SD) of NN males in foraging contexts[a]	Mean male latency to withdraw (±SD) in foraging contexts (seconds)	Mean male latency to withdraw (±SD) in all contexts (seconds)
2000 (Low Provisions)	36	5.1	3.1 (±0.8)	1.22 (±1.02)	1.37 (±0.7)
2001 (Low Provisions)	29	4.8	2.4 (±0.8)	0.98 (±0.81)	0.95 (±0.64)
2002 (High Provisions)	21	5.3	2.9 (±0.4)	0.55 (±0.21)	0.53 (±0.19)

[a]Distance rank categories for NN: 1, touching; 2, ≤1 m but not touching; 3, >1 m ≤ 3 m; 4, >3 m ≤ 5 m; 5, >5 m

A final set of analyses concerned the latency with which males withdrew upon first looking in the direction of an approaching female during agonistic interactions. We first considered data from SCI Group 3 for this analysis, as it allowed for a comparison of male behavior before and after the change in feeding condition within the same group. Due to dispersal events, male membership changed between the study years and only three males belonged to this group under both feeding conditions. We analyzed male withdraws from female approaches that occurred during foraging contexts, and separately, across all contexts, expecting that males might more rapidly withdraw during the High Provisions period. As expected, during the High Provisions period, Group 3 males withdrew more rapidly from female approaches than they did during the Low Provisions period, though interestingly the difference only reached statistical significance for male withdraws occurring across all contexts (Mann–Whitney, one-tailed: $N_1 = 13$, $N_2 = 4$, $U = 7.0$, $p = 0.036$; Figure 3), not during foraging contexts alone (Mann–Whitney, one-tailed: $N_1 = 13$, $N_2 = 4$, $U = 15.5$, $p = 0.26$).

Because the above analysis was limited to males belonging to Group 3, we broadened the analysis to see whether the same trend would be found if we used data from all males for whom we had data from before and after the feeding condition changed, regardless of whether or not they belonged to a different group under the two conditions. Seven males were studied both before and after the feeding condition changed on SCI. For all but one male, the expected relationship held, with males making more rapid withdraws from female approaches during the High Provisions as opposed to the Low Provisions period (Wilcoxon matched-pairs test: $Z = 2.2$, $p < 0.028$; Figure 4).

To put the male deference behavior documented here in some context, it is important to note that in some of the male withdraws from females at our study sites, males were observed to carry food away with them while withdrawing. For example, on SCI in Group 3 during foraging contexts, ad lib notes describe three different instances involving two different males in which the males manually carried away portable pieces of provisioned food with them when they withdrew from approaching females. The single male studied at the LAZ was also observed to occasionally carry food away with him upon a female's approach.

4 | DISCUSSION

The captive lemurs in our study at the LAZ and on SCI generally spent less of their activity budget foraging than wild lemurs (e.g., Berenty: 37%: Howarth et al., 1986; >20%: Rasamimanana et al., 2006; 15%–46%: Ellwanger & Gould, 2011; Gould, Power, et al., 2011; Bezà Mahafaly: 22%–26%: Sauther, 1992; 37%–54%: LaFleur & Gould, 2009), with the exception of *L. catta* at Cap Sainte-Marie, who spent a very small amount of their activity budget foraging, 9%–13% (Kelley, 2011). The short time spent foraging by lemurs at our study sites was unsurprising, because both populations were provided with high quality provisioned food daily. At one of our
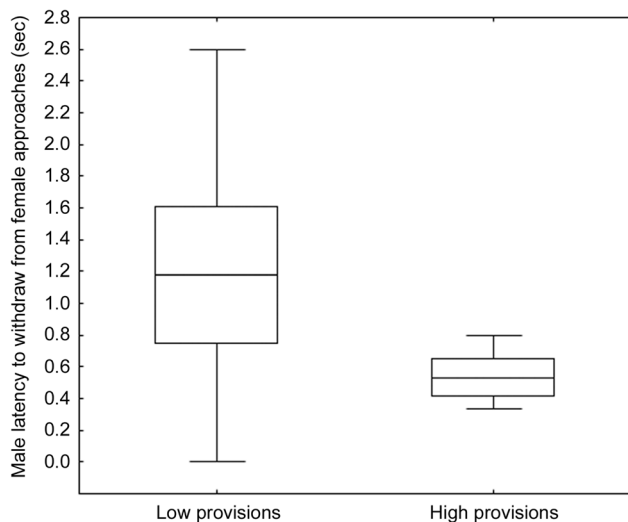
FIGURE 3 For males in St. Catherines Island Group 3, across all agonistic contexts, mean latency to withdraw following a female's approach was significantly shorter during the High Provisions (high food availability) period than during the Low Provisions (low food availability) period (Mann–Whitney: $N_1 = 13$, $N_2 = 4$, $U = 7.0$, $p = 0.036$). Whiskers represent maximum and minimum values, horizontal lines represent means, and boxes represent the interquartile range (25%–75%).
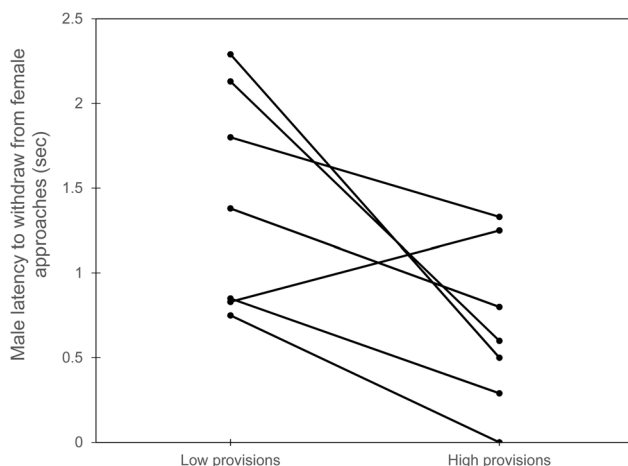
FIGURE 4 For males on St. Catherines Island who were present under both feeding conditions (regardless of study group), the mean latency to withdraw from female approaches across all agonistic contexts was shorter during the High Provisions period than the Low Provisions period for all but a single male. The overall trend of more rapid male withdraws from female approaches under conditions of greater food availability (High Provisions) reached statistical significance (Wilcoxon: $N = 7$, $Z = 2.2$, $p < 0.028$).

study sites, SCI, a change in the distribution of provisioned food between the second and third years of the study allowed us to document lemur behavior under two feeding conditions: Low Provisions and High Provisions. During Low Provisions, foods provided to the lemurs were ground-scattered daily and were rapidly

consumed and depleted by other animals on SCI (e.g., white-tailed deer, *O. virginianus*, and raccoons, *P. lotor*). The third year of the study ushered in a period of high food availability, when provisioned foods were presented to the lemurs in feeding platforms, drastically decreasing the amount of interspecies feeding competition between the lemurs and other animals on SCI. During this High Provisions period, the SCI lemurs spent overall less time foraging on naturally growing foods than in the previous two Low Provisions study years. Moreover, although the provisioned food was distributed in a more clumped fashion by being placed onto feeding platforms during the High Provisions period, female-male agonism rates in the groups were not notably different before as opposed to after the feeding condition changed on SCI.

As expected, our measures at the LAZ and on SCI of male deference (the proportion of female-male agonism lacking female aggression) more closely resembled the male deference shown among captive *L. catta* at the Duke Lemur Center (Pereira et al., 1990) than that shown among wild *L. catta* from Bezà Mahafaly, Madagascar (Sauther, 1993). Moreover, within the same group and study year on SCI, male deference levels during foraging were similar to male deference measured across all contexts. When comparing male deference levels for the single group on SCI (Group 3) for which we have data from before and after the platform installation and food availability increase, the High Provisions period resulted in an increase in male deference to a high of 80% in foraging contexts, which is the highest measure of male deference yet recorded at any *L. catta* study site. Analyzing male deference at the level of individual males revealed a broad range of values from male to male, but the same pattern of increased male deference being shown to females under conditions of greater food abundance (High Provisions) held for every male for whom data were available under both feeding conditions.

Interestingly, when comparing our results on foraging and male deference to similar published data from other *L. catta* locations, both captive (Ganzhorn, 1986; Pereira et al., 1990) and wild (Sauther, 1993), a consistent trend was observed: male deference positively correlated with the proportion of foraging time that was allocated to the consumption of nonnatural (provisioned) foods. For provisioned nonwild locations in which foraging on naturally growing foods is possible (e.g., Duke Lemur Center, SCI), a greater reliance on naturally growing foods likely signals that less provisioned food is available. Under such conditions (decreased food abundance), it appears that males are less apt to be deferential to females. We admit that our across-site comparison of data on foraging and male deference in lemurs is less than ideal owing to the vastly different ecological conditions at each site and the data in each study being collected at different times of the year. Sauther's (1993) data from Madagascar were collected year-round, whereas Pereira et al. (1990) collected data at Duke from the summer throughout the fall mating season, and data on SCI were collected in the weeks leading up to the fall mating season. Data collection at the LAZ began in the summer and continued throughout the fall mating season and winter into the spring in what would have been the birth/lactation period if any of the females had become pregnant. The data on foraging among the

L. catta at Duke were also taken from Ganzhorn (1986), in a study which was conducted 5 years before the data collection period of Pereira et al. (1990) on male deference at the same location. Nonetheless, we include the comparison here to point out the surprisingly consistent inverse relationship between decreased time spent foraging on natural food items and increased male deference to females. As suggested by Sauther (1993), it appears that male *L. catta* across different locations are more likely to exhibit deference (submission to females without female aggression) where food is more abundant and males are less nutritionally stressed.

However, it should not be assumed based on our results that male *L. catta* are showing "gallant deference" or "chivalry" to females (Hrdy, 1981; Jolly, 1984) by relinquishing food to them as an investment in the female or her future offspring. Pollock (1979) suggested that in the pair-bonded and female dominant indri, a male's "food sacrifice" to the female may be a form of investment in the female and her current or future offspring. This hypothesis is unlikely to apply to *L. catta* for a couple of reasons. First, unlike in the pair-living and assumed-to-be-monogamous indri where paternity certainty is believed to be high (Pollock, 1979), paternity for male *L. catta* is highly uncertain because females mate with multiple males (Gould, 1994; Jolly, 1966; Koyama, 1988; Sauther, 1991) and their offspring can be sired by more than one male across a few years' period (Parga et al., 2016) or even as part of the same birth event (Parga & Nansen, 2019). Male *L. catta* have also been found to act as food competitors for females in the wild (Sauther, 1993) and in our study. We found that males on SCI were posing as food competitors in Group 3 approximately 29%–36% of the time during the Low Provisions period and 21% of the time during the High Provisions period. Therefore, males on SCI acted as food competitors even after more food was available due to food platform installation. Moreover, due to the free-ranging nature of the site, males on SCI could easily have chosen to be further away from foraging females, but they were often found within just a couple of meters of foraging females under both feeding conditions. It was notable that at the LAZ, where food was exceptionally plentiful, the male was in close proximity to females (within 1 m) in just 12% of female foraging instances. The LAZ male's lack of frequent close proximity to foraging females was especially remarkable given the small size of the enclosure and was probably due to the lesser need by the male to engage in direct feeding competition with his female group-mates due to high food abundance in this captive location. Still, we observed males at both sites carrying pieces of provisioned food away with them while fleeing from the approach of a female. Wild male lemurs in Madagascar have similarly been observed to transport portable food, such as *Tamarindus indica* fruit, away in their mouths rather than relinquish the food to females (Sauther, 1993). Therefore, at least under some circumstances, *L. catta* males can act as food competitors to females, even where there is food provisioning. Consequently, we do not interpret male deferential behavior to females in *L. catta* as a form of investment in females or their future offspring.

One of the most telling male behaviors that shifted with the increase in food availability to the High Provisions condition on SCI was the rapidity with which males departed from female approaches in agonistic interactions. Males on SCI in Group 3 withdrew more rapidly from female approaches under conditions of greater food availability (High Provisions), but statistical significance was only reached when such male withdraws were measured across all contexts, not when male withdraws were measured in foraging contexts alone—which suggests that males were less apt to leave food sources than they were to depart from females in other contexts (e.g., resting, traveling). Repeating the analysis of male withdraws from female approaches at the individual level for all males (not just those in Group 3) on whom data were gathered both before and after platform installation showed much the same result. With one exception, males on SCI withdrew from female approaches faster during the High Provisions period, when food was more abundant. We surmise that the more rapid male withdraws that took place under conditions of food abundance on SCI were a self-serving way by which males avoided female aggression such as cuffs, lunges, or bites. Indeed, Sauther (1993, p. 145) points out that among wild *L. catta*, female retribution for a "slow responding" or "lingering" male at food sites could be quick and violent and might involve such aggression as chasing or biting the male.

On a proximate level, a male's "motivation" (Lewis, 2002) to engage in feeding competition with a female (from whom he might receive aggression) likely depends upon his nutritional state. Males who are more nutritionally stressed may decide based on a cost–benefit analysis to risk female aggression to obtain food only when food is more limited. Although none of the lemurs in our study can be considered very "nutritionally stressed" due to being artificially fed, the lemurs on SCI spent more time (and effort) foraging on naturally growing foods during the Low Provisions period. Hence, during the Low Provisions period, males had less access to high-quality food and may have consequently been less inclined to show deference in the form of rapid retreats from female approaches. Therefore, the proximate driver controlling male submissive behavior to females among *L. catta* (regardless of study location, captive, or wild) may be male nutritional condition.

On an ultimate level, our findings support the idea that female dominance in lemurs evolved in an environment of food scarcity and that female dominance is a behavioral solution to the problem that males pose to females as competitors for food (Wright, 1999). Indeed, among wild nonprovisioned *L. catta* in Madagascar where food stress is high, the majority of female–male agonism involves female aggression (Sauther, 1993). Of course, female dominance and female reproductive stress are by no means exclusive to Malagasy lemurs among the primates (Lewis, 2018). However, considering our findings in the context of other *L. catta* research on intersexual agonism (Pereira et al., 1990; Sauther, 1993) suggests that female aggression to males (and male submissive behavior) are highly dependent on food availability in this species.

One admitted weakness of our study is that the transition from the Low to High Provisions period on SCI was marked by a change in both the distribution of food (from scattering to more clumped platform feeding) and an increase in the amount of food available (due to decreased competition with other animal species on SCI who could not

easily access the lemurs' food in the platforms). Although it is impossible to separate the effects of these two changes that occurred concurrently, we suggest that the food increase rather than the food's spatial distribution was responsible for the increased male deference. First, increased clumping of food for *L. catta* does not seem to be associated with increased male deference. Taking LAZ as a case study, primate chow was scattered throughout the enclosure (opposite of clumping), and vegetables were offered in enough bowls for every animal to have its own bowl. Yet in this environment where contest competition over food was exceedingly low, male deference was extremely high (70%, Table 1). Consequently, we attribute the high male deference at the LAZ to food abundance. Second, if food distribution was thought to be responsible for the increase in male deference behavior on SCI from Low to High Provisions, one would assume that the mechanism would be related to distance between animals when feeding. However, nearest neighbor patterns on SCI between males and foraging females showed no major differences from Low to High Provisions (Table 2). Instead, one variable showing a marked change after the switch to platform feeding on SCI was the amount of time the lemurs spent foraging on naturally occurring foods, which decreased because the amount of available high-quality provisioned food increased. Moreover, our data from SCI are only one representative example in which there was an inverse relationship between male deference to females and the proportion of foraging time allocated to exploiting naturally growing foods. Because the same pattern (a high percentage of foraging time spent on provisioned food corresponding to high levels of male deference) was found among *L. catta* at more than one location, including the LAZ (this study), and the Duke Lemur Center (Pereira et al., 1990), we suggest that food amount, not the change in food distribution, was likely the driving force behind the increased male deference behavior we observed on SCI in the High Provisions condition.

5 | CONCLUSIONS

Previous discussions of female dominance in lemurs have highlighted the roles of seasonality, unpredictability of habitat, and high reproductive costs to females (Hrdy, 1981; Jolly, 1984; Sauther, 1993; Wright, 1999; Young et al., 1990). Early ideas about male dominance in lemurs also included the possibility that males might be acting "chivalrous" to females as a form of reproductive investment in the female and/or her offspring (Hrdy, 1981; Jolly, 1984). Our study along with other research on *L. catta* (Sauther et al., 1999) has found no evidence to support the suggestion of male chivalry or investment. Neither wild males nor males on SCI appear to be selflessly relinquishing food to females. Instead, males appear to be competing with females for food (Sauther, 1993; this study). When male deference increased on SCI under conditions of greater food availability, the male deference took the form of more rapid retreats from female approaches—thereby functioning as a self-serving way for males to avoid female aggression.

Our results have implications for intersexual agonistic relationships in this and other primate species. First, for *L. catta* groups that

experience very high levels of food availability, as in captivity or where provisioning has been carried out in the wild (e.g., Berenty, Madagascar: Jolly et al., 2002; Koyama et al., 2001), our data suggest that food abundance may change the nature of female–male agonism such that intrasexual agonism consists less of female aggression and more of spontaneous male submission. This relationship between greater food availability and increased male submissive behavior may also be found beyond *L. catta* in other female dominant lemurs (Richard, 1987) or even in other female dominant primates. For example, in squirrel monkeys (*Saimiri* spp.), females can be aggressive to males (Boinski et al., 2002). It is telling that in at least one squirrel monkey species, *Saimiri sciureus*, females were able to displace males from food sources throughout the year with the exception of the mating season, when males experience especially high energetic demands (Mitchell, 1990). Knowing how food conditions can influence female aggression and male submission is critical to a complete understanding of female dominance and intersexual relationships, and we look forward to future studies investigating how various environmental factors can affect male–female relationships in this and other species.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Joyce A. Parga http://orcid.org/0000-0003-2605-6398
Emma Thurau http://orcid.org/0000-0001-9554-2010

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