

# Sex-Typed Social Development in *Lemur catta*

Stephanie L. Meredith

Department of Biological Sciences, University of Southern California, Los Angeles, CA, USA;  
Department of Sociology and Anthropology, University of La Verne, La Verne, CA, USA

---

### Keywords

Development · Infant · Ring-tailed lemur · Young · Madagascar · Social development · Social relationships · Sex differences · Juvenile · Subadult

---

### Abstract

Strong chemical control of strepsirrhine mating behaviour when compared to haplorhines might suggest that strepsirrhine behavioural development, generally, is under stronger somatic control. A comparative lack of reported behavioural sex differences in immature strepsirrhines would seem to support this hypothesis, but the recent discovery of sex differences in juvenile foraging behaviour in *Lemur catta* suggests that this difference might be an artefact of undersampling in strepsirrhines. Here, I document in wild *L. catta* the temporal development of a wider repertoire of social behaviours than have been studied in captivity over a longer developmental duration than has been studied in the wild to identify which behaviours might be and which cannot be linked to puberty. Sex differences in proximity and agonism did not appear before 2 years, consistent with previous reports and suggestions that they are linked to somatic or social changes at puberty. Immature females exhibited adult female-typical interest in infants; immature males demonstrated elements of adult male scent-marking behaviour, and immature males demonstrated marked attraction to adult males – sex differences that cannot be dependent on gonadal maturation. Immature *L. catta* exhibited some sex differences common in immature haplorhines, which are thought to be strategic choices by immatures to increase their later reproductive success.

© 2018 S. Karger AG, Basel

### Introduction

In haplorhine primates, sex-typed behaviour results from a complex interaction between an individual's body and environment [Wallen, 1996]. For juveniles, prenatal hormones shape the development of sex-typed vocalizations (*Macaca mulatta* [Tomaszycki et al., 2005]), mounting (*M. fuscata* [Eaton et al., 1986]), play (*M. mu-*

*latta* [Goy et al., 1988]), interest in infants (*M. mulatta* [Tomaszycki et al., 2001]) and grooming of mothers (*M. mulatta* [Goy et al., 1988]). For adults, they shape the development of landmark navigation (*M. mulatta* [Herman and Wallen, 2007]) and sexual behaviour (*M. mulatta* [Eisler et al., 1993]). In some species, neonatal hormones shape the development of sex-typed juvenile patterns of proximity to mothers (*M. mulatta* [Wallen et al., 1995]) and adult sexual behaviour (*Saguinus fuscicollis* [Epple et al., 1990]; *Callithrix jacchus* [Dixon, 1993]). In others, postpubertal gonadal hormones drive adults' interest in infants (*Macaca nemestrina* [Maestriperi and Zehr, 1998]) and sex-typed sexual behaviour (e.g., *M. mulatta* [Wallen et al., 1995]).

Variation in the early social environment shapes the development of sex-typed juvenile mounting behaviour (*M. mulatta* [Goy and Wallen, 1979]) and play (*M. mulatta* [Wallen, 1996]). In both *M. mulatta* [Harlow, 1965] and *Pan troglodytes* [Fritz et al., 1992], the early social environment influences the development of adult sexual behaviour. Extreme variation in social experience has even been shown to overwhelm hormonal effects on the development of these behaviours [Thornton et al., 2009].

Compared to haplorhines, strepsirrhine mating behaviour is more strongly under chemical than cognitive control [Petter-Rousseaux and Buettner-Janusch, 1964; Evans and Goy, 1968; Van Horn, 1975; Pereira, 1991; Cavigelli and Pereira, 2000; Alport, 2004]. This difference might be taken to suggest that sex-typed behaviour, in general, will depend more heavily on somatic and less heavily on social factors in strepsirrhines than haplorhines. An apparent relative lack of sex differences in social behaviour in immature strepsirrhines would seem to support this position (*Galago senegalensis* [Nash, 2003]; *Eulemur fulvus* [Barthold et al., 2009]). In *Lemur catta*, sex-typed spacing patterns [Jolly, 1966; Taylor and Sussman, 1985; Pereira and Weiss, 1991; Pereira, 1993], female dominance over males [Pereira, 1993; Sauther, 1993; Sauther and Sussman, 1993] and female-typical rates of agonism [Pereira, 1993] apparently develop upon sexual maturation, and, except for male scent-marking behaviours, “no sex difference has yet been discovered in the growth or social behaviour of prepubertal” individuals [Pereira, 1993, p. 291]. An apparent delay of behavioural sex differentiation until sexual maturation in these strepsirrhines contrasts with patterns of sex-typed development in many haplorhine primates, in which behavioural sex differentiation commonly occurs prepubertally [reviewed in Meredith, 2013]. This could imply that behavioural sex differentiation in strepsirrhines depends more heavily on either the activational or the late organizational effects of gonadal hormones [Phoenix et al., 1959; Schulz et al., 2009] than it does in haplorhines.

A recent study of dietary development in wild *L. catta* has discovered juvenile sex differences in feeding and foraging behaviour that parallel dietary sex differences of adults [O'Mara and Hickey, 2014]. This suggests that previous developmental studies of strepsirrhines may have failed to find prepubertal sex differences in social behaviour due to small sample sizes [Klopfer, 1974; Hosey and Jacques, 1994; Nash, 2003], because it was not their primary focus [Klopfer and Klopfer, 1970; Klopfer, 1972, 1974; Klopfer and Boskoff, 1979; Barthold et al., 2009], because sampling was limited to infants, who are most likely to be behaviourally similar [Gould, 1990], or because they focused on the development of only certain types of adult sex-typed behaviour (olfactory behaviour [Palagi et al., 2002]; agonism [Pereira, 1993]). Furthermore, the apparent synchronicity of sexual maturation and the development of sex differences in some behaviours that has been documented in captivity [Pereira, 1993] could be a coincidental artefact of accelerated sexual maturation in captive settings.

In both captivity and the wild, *L. catta* wean between 4 and 6 months of age [Sauther, 1991; Pereira, 1993], but sexual maturation usually occurs by 1.5 years of age in captivity [Sussman, 1991; Pereira, 1993] and not until 2.5 years of age in the wild [Sauther, 1991; Koyama et al., 2001; Gould et al., 2003]. As a result, behavioural sex differences that happen to develop at or around 1.5 years of age will coincide with sexual maturation in captivity even though they would substantially precede it in the wild. Behavioural sex differences that actually depend on sexual maturation for their development should appear later in the wild than they appear in captivity.

This study will document the developmental timing of sex differences in social behaviour prior to 2 years of age in a mixed longitudinal sample of immatures (infants and juveniles) from 2 birth cohorts of a wild population at Beza Mahafaly Special Reserve to distinguish behavioural sex differences that may be mediated by gonadal maturation from those that must be attributed to prepubertal causes. This study replicates and extends the work of previous studies of behavioural sex differentiation in *L. catta* by investigating the development of a wider repertoire of behaviours than has been studied in captive work [Pereira, 1993; Palagi et al., 2002] and by investigating a longer duration of the developmental period than has previously been examined by studies of social development in the wild [Gould, 1990]. Patterns of inter- and intra-sexual affiliation have been shown to vary across populations in adult *L. catta* [Gabriel et al., 2014]. Therefore, even though adult behavioural sex differences are not the focus of this study, I first identified behavioural sex differences in adults of my study population that the immature sample from this population could be expected to develop.

## Methods

### *Behaviours Tested*

I defined behaviours using the comprehensive published ethogram of *L. catta* by Pereira and Kappeler [1997]. I selected behaviours to test for the presence of prepubertal sex differences (Table 1) that commonly differ by sex prepubertally in haplorhines, have been reported to differ by sex in adult *L. catta*, or have been reported to differ by sex in other studies of prepubertal *L. catta*. While detailed analyses of play in haplorhines indicate that males of many species engage in rougher play than females [reviewed in Meredith, 2013], across all age/sex groups, immatures played very little (percent time observed: young infants, 1.01%; old infants, 0.26%; young juveniles, 0.07%; young yearlings, 1.74%; old yearlings, 0.21%). Therefore, except for tail play (dragging the tail through the forearms in the context of social play – the behavioural component of adult male tail anointing, but without the capacity to imbue the tail with glandular secretions from the antibrachial glands), I categorized all types of social play simply as “social play.” I recorded tail play separately from other types of social play because it has been reported to be a male-typical behaviour in captivity [Pereira, 1993; Palagi et al., 2002]. Immatures exhibited aggressive and dominance behaviours at such low rates that they could not be analysed individually; therefore, I summed the behavioural events bite, charge, chase, cuff, feint to cuff, jump fight, lunge and supplant as “aggressive and dominance behaviours.” I did not observe any other aggressive or dominance behaviours in immatures. I do not consider anogenital marking here because I did not observe it in individuals younger than 24 months. I do not consider submissive behaviours here because they are often a reaction to aggressive or dominant behaviours on the part of others and, therefore, may indicate more about the nature of aggressive and dominance behaviour received by the focal subject than about the behavioural tendencies of the focal subject. Because the focus of this study was the development of social behaviours, specifically, I did not collect data on solitary behaviours (such as solitary play) and do not consider them here.

**Table 1.** Age categories and sample sizes including number of individuals sampled, total observation hours per age category, mean  $\pm$  SD observation hours per individual within each age category

| Age                           | Sex | <i>n</i> | Total hours | Hours/individual |
|-------------------------------|-----|----------|-------------|------------------|
| Young infant (0–2 months)     | F   | 14       | 109         | 7.3 $\pm$ 4.6    |
|                               | M   | 14       | 74          | 5.3 $\pm$ 3.0    |
| Old infant (3–5 months)       | F   | 5        | 46.5        | 9.3 $\pm$ 0.6    |
|                               | M   | 3        | 28          | 9.3 $\pm$ 1.0    |
| Young juvenile (6–11 months)  | F   | 4        | 71.5        | 17.9 $\pm$ 0.5   |
|                               | M   | 3        | 37.5        | 12.5 $\pm$ 4.6   |
| Young yearling (12–17 months) | F   | 4        | 86          | 21.5 $\pm$ 0.7   |
|                               | M   | 5        | 83.5        | 16.7 $\pm$ 8.3   |
| Old yearling (18–23 months)   | F   | 4        | 61.5        | 15.4 $\pm$ 6.3   |
|                               | M   | 4        | 73.5        | 18.4 $\pm$ 0.6   |
| Adult (>30 months)            | F   | 10       | 139         | 13.9 $\pm$ 13.9  |
|                               | M   | 8        | 169.5       | 21.2 $\pm$ 14.8  |

#### *Study Site, Subjects and Sampling*

I conducted this study in and around Parcel I of Beza Mahafaly Special Reserve in Southwest Madagascar (23°39'20" S, 44°37'43" E) from September 2008 to August 2009. Parcel I comprises riparian gallery forest that grades into xerophytic forest with increasing westward distance from the Sakamena River [Sussman and Ratsirarson, 2006]. Most individuals aged 2 years and older from 9 habituated social groups were individually marked with collars and unique tag numbers prior to the onset of data collection. At the study's onset, I marked a subset of uncollared adults, yearlings and newborn infants so that I could individually identify them. I did so by squirting them with Nyanzol D (Greenville Colorants, Jersey City, NJ, USA), a permanent, black, non-toxic dye [Honest and MacDonald, 2003], from a distance of 1–5 m using a 10-ml syringe fitted with an 18-gauge hypodermic needle. I dyed individuals when they were facing away from me to protect their eyes, and I followed them closely to distract them from grooming until the dye had dried or they lost interest in it. I marked as few individuals as was necessary to individually identify all unmarked group members. The random nature of dye application made it easy to distinguish dyed individuals, and visible marks lasted for approximately 3 months. Long before the dye faded, I was able to identify individuals by face and did not repeat marking for the remainder of the study.

I collected behavioural data on a mixed-longitudinal sample of newborns (2008 birth cohort,  $n = 28$ , 366.5 h), yearlings (2007 birth cohort,  $n = 9$ , 304.5 h) and adults (>30 months old,  $n = 18$ , 308.5 h) from 6 habituated groups of *L. catta* that had both yearling and infant members. *L. catta* breeds strictly seasonally [Pereira, 1991; Sauther, 1991], resulting in discrete age cohorts that are easily distinguished prior to the age of 3 [Jones, 1983]. The 2008 birth cohort was observed from 0 to 10 months of age; the 2007 birth cohort was observed from 12 to 23 months of age. At Beza, females often mate and conceive at 2.5 years (30 months) old [Sauther, 1991], and males of the same age appear to be sexually mature based on their exhibition of adult secondary sexual characteristics and sexual behaviours [Sauther, 1991]; therefore, the immature sample from 0 to 23 months captured the majority of the prepubertal period.

I divided the developmental period into 5 stages (see Table 1 for definitions and sampling). Infant stages “young infant” and “old infant” correspond well with the major infant developmental landmarks of locomotor independence (approx. 14 weeks) and complete weaning (approx. 24 weeks) [Gould, 1990; O'Mara and Hickey, 2012]. I divided the long juvenile period of 6–24 months into 3 stages. “Young juveniles” were weaned individuals from the 2008 age cohort. I divided the second year of life (the 2007 cohort) into 2 stages (young yearling and old yearling) to avoid obscuring patterns of behavioural sex differentiation that might appear between 1.5 and 2

years, when sex differences in agonism and proximity appear in captivity [Pereira, 1993]. The 2008 cohort suffered substantial mortality at early ages, which constrained my sampling of the young juvenile age category, but 7 of the 9 yearlings from the 2007 cohort were present for the entire year of study. All adult female subjects were without infants when they contributed to the sample. When adult females were the social partner of an immature, I classified them from the perspective of the immature as either “mother” or “non-maternal adult female.” Non-maternal adult female social partners were not necessarily without infants but were simply not the mother of the focal individual. I did not analyse social interactions for all possible combinations of age-sex classes because infants and yearlings were distributed across groups such that not all individuals had access to social partners of all age-sex classes.

I collected data during 30-min focal animal follows [Altmann, 1974] between dawn and dusk. I recorded all social interactions with the focal individual continuously in JWatcher v1.0 [Blumstein and Daniel, 2007] on a Raon micro-PC. I recorded the identities and proximity of the nearest neighbour to the focal individual and all individuals within 3 m of the focal individual using instantaneous sampling at 3-min intervals. I used a randomized sampling order stratified by time of day to ensure that individuals were sampled as evenly as possible across active and resting periods. All data collection and marking procedures were approved by the Arizona State University Institutional Animal Care and Use Committee (#08–990R AL), the Madagascar Ministry of the Environment, Forests and Tourism, and the Madagascar National Association for the Management of Protected Areas and adhered to the American Society of Primatologists Principles for the Ethical Treatment of Primates.

### *Statistical Analysis*

I summarized behavioural events and bouts as counts per focal observation and behavioural states as the proportion of instantaneous samples per focal observation or proportion of total time per focal observation. This produced a mixed-longitudinal data set of non-normally distributed data with unbalanced sample sizes. I used generalized linear mixed models (which are most appropriate for analysing such data [Bolker et al., 2009]) to test the importance of age and sex on the exhibition (in adults) and development (in immatures) of specific behaviours using a model comparison approach [Johnson and Omland, 2004]. Using *lme4* [Bates et al., 2015] and *glmmADMB* [Fournier et al., 2012] in R 3.40 [R Core Team, 2017], I modelled count data with a Poisson or negative binomial error structure with a log link, the latter is appropriate for overdispersed count data with a high proportion of sampling zeros [Gardner et al., 1995]. I modelled proportional data using a binomial error structure with a logit link [Warton and Hui, 2011]. I included individual identity as a random factor to appropriately account for repeated sampling of individuals [Singer and Willett, 2003]. To control for known effects of ecological and reproductive seasonality on adult social behaviour [Gould, 1997; Sauter, 1993; Nakamichi and Koyama, 2000; Drea and Scordato, 2008; Gabriel et al., 2014], I included season as a random factor [Singer and Willett, 2003] in analyses of adults. To account for variation in the number and types of social partners to whom focal subjects had access, I included number of group members or number of group member type (e.g., number of adult males) as exposure variables when appropriate [Reitan and Nielsen, 2016]. I selected best fit models using Akaike’s information criterion for small samples [Burnham and Anderson, 2002] and evaluated the significance of sex on the dependent variable using a likelihood ratio test of nested models including and excluding the fixed effect of sex or the fixed effect of a stage by sex interaction [Lewis et al., 2011]. I used  $\alpha = 0.05$  for all tests of significance. All likelihood ratio tests presented here were tests of the effect of sex, except when the best fit model included a significant stage  $\times$  sex interaction term, which is noted.

## **Results**

### *Adult Sex Differences*

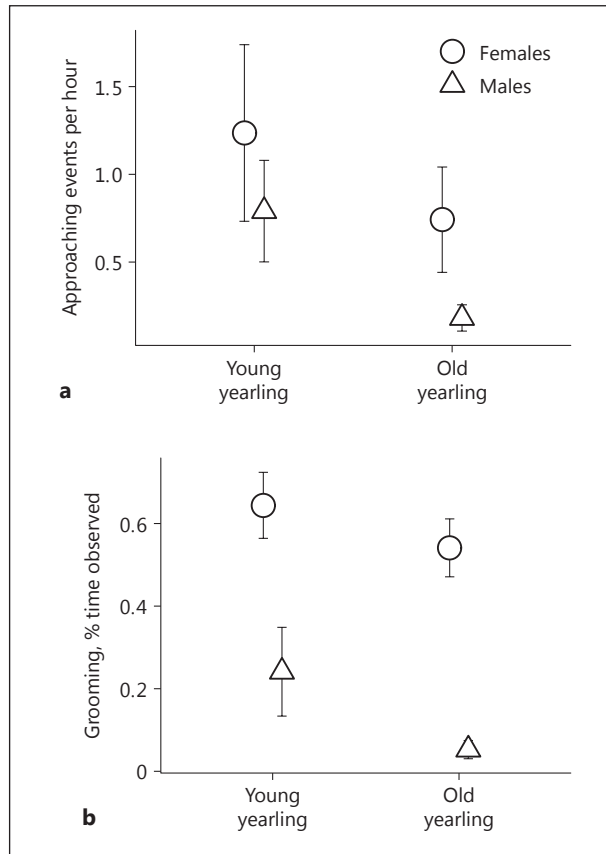
Compared to males, adult females were more gregarious by several measures (statistical results presented in Table 2). Adult females approached others significantly more often than adult males did, were significantly more often in contact with,

**Table 2.** Fitted generalized linear mixed model means and standard deviations, degrees of freedom, likelihood ratio statistics for likelihood ratio tests of nested models with and without fixed effect of sex in adult *Lemur catta*

|  | Female      | Male        | df | $\chi^2$ | <i>p</i> |
|--|-------------|-------------|----|----------|----------|
| General proximity measures                 |             |             |    |          |          |
| Approaches to others per hour              | 2.656±1.512 | 1.458±0.996 | 1  | 8.74     | **       |
| Percent time in contact with another       | 0.127±0.068 | 0.080±0.033 | 1  | 5.26     | *        |
| Percent time in reach of another           | 0.160±0.096 | 0.094±0.052 | 1  | 8.91     | **       |
| Percent time within 3 m of another         | 0.715±0.059 | 0.602±0.090 | 1  | 7.45     | **       |
| Percent group members in contact           | 0.010±0.006 | 0.005±0.002 | 1  | 8.22     | **       |
| Percent group members in reach             | 0.016±0.021 | 0.007±0.005 | 1  | 10.24    | ***      |
| Percent group members within 3 m           | 0.180±0.065 | 0.135±0.050 | 1  | 2.12     | ns       |
| General overt social behaviour             |             |             |    |          |          |
| Percent time grooming others               | 0.022±0.012 | 0.015±0.010 | 1  | 1.95     | ns       |
| Percent time in social play                | 0.001±0.004 | 0.001±0.003 | 1  | 0.37     | ns       |
| Aggression/dominance per hour              | 1.258±0.386 | 0.440±0.227 | 1  | 9.27     | **       |
| Olfactory communication                    |             |             |    |          |          |
| Brachial and antebrachial marking          | 0.000±0.000 | 9.059±5.358 | 1  | 34.42    | ***      |
| Affiliation toward adult females           |             |             |    |          |          |
| Approaches per hour                        | 1.309±0.821 | 0.545±0.436 | 1  | 10.70    | ***      |
| As nearest neighbour                       | 0.395±0.069 | 0.329±0.087 | 1  | 5.21     | *        |
| In contact with                            | 0.079±0.053 | 0.042±0.026 | 1  | 6.56     | **       |
| Grooming                                   | 0.011±0.007 | 0.006±0.004 | 1  | 0.31     | ns       |
| Affiliation toward infants/young juveniles |             |             |    |          |          |
| Approaches per hour                        | 0.495±0.613 | 0.070±0.113 | 1  | 9.13     | **       |
| As nearest neighbour                       | 0.078±0.036 | 0.040±0.024 | 1  | 5.20     | *        |
| In contact with                            | 0.023±0.017 | 0.001±0.001 | 1  | 19.73    | ***      |
| Grooming                                   | 0.006±0.008 | 0.001±0.001 | 1  | 2.56     | ns       |
| Affiliation toward yearlings               |             |             |    |          |          |
| Approaches per hour                        | 0.319±0.097 | 0.245±0.103 | 1  | 1.96     | ns       |
| As nearest neighbour                       | 0.144±0.033 | 0.134±0.038 | 1  | 2.36     | ns       |
| In contact with                            | 0.023±0.030 | 0.009±0.007 | 1  | 4.43     | *        |
| Grooming                                   | 0.002±0.003 | 0.002±0.002 | 1  | 1.27     | ns       |
| Affiliation toward adult males             |             |             |    |          |          |
| Approaches per hour                        | 0.595±0.213 | 0.506±0.181 | 1  | 0.00     | ns       |
| As nearest neighbour                       | 0.243±0.067 | 0.256±0.084 | 1  | 1.87     | ns       |
| In contact with                            | 0.025±0.008 | 0.027±0.018 | 1  | 0.90     | ns       |
| Grooming                                   | 0.003±0.002 | 0.006±0.006 | 1  | 0.10     | ns       |

Individual identity and season were included in all models as random factors. Behaviours that differ significantly by sex are marked: \*  $p \leq 0.05$ , \*\*  $p \leq 0.01$ , \*\*\*  $p \leq 0.001$ . Behaviours that do not statistically significantly differ by sex are marked “ns.”

**Fig. 1.** *Lemur catta* yearling fitted model means and standard deviations for approaching (a) and time spent grooming (b) infants and young juveniles. Yearling females approached and groomed their juniors significantly more than yearling males did, exhibiting the interest in infants/juveniles that is characteristic of adult females.



within reach of and within 3 m of another individual, and had a higher proportion of group members in contact and within reach of them. This did not lead to higher rates of overtly affiliative interaction, as there were no sex differences in time spent grooming others or in social play (Table 2).

Adult females affiliated more with each other and with infants/young juveniles than adult males did. Compared to adult males, adult females approached other adult females and infants/young juveniles significantly more often, more often had them as nearest neighbours and were significantly more often in contact with them (Table 2). Adult females were also significantly more often in contact with yearlings than adult males were but did not approach them or have them as nearest neighbours at higher rates (Table 2). These differences in proximity did not lead to higher rates of overtly affiliative interaction, as there were no sex differences in the time spent grooming adult females, infants/young juveniles or yearlings (Table 2).

Adult females exhibited significantly more aggressive and dominance behaviour than adult males did, while adult males exhibited significantly more brachial and antebrachial marking behaviour than adult females did. Brachial and antebrachial marking is not completely absent in females [pers. observation] but is exceedingly rare.

**Table 3.** Fitted generalized linear mixed model degrees of freedom and likelihood ratio statistics for likelihood ratio tests of nested models with and without fixed effect of sex in immature *Lemur catta*

|   | df | $\chi^2$ | <i>p</i> |             |
|---|----|----------|----------|-------------|
| <b>General proximity measures</b>                 |    |          |          |             |
| Approaches to others (per hour)                   | 1  | 0.460    | ns       |             |
| Percent time in contact with another              | 1  | 0.136    | ns       |             |
| Percent time in reach of another                  | 1  | 1.052    | ns       |             |
| Percent time within 3 m of another                | 1  | 2.255    | ns       |             |
| Percent group members in contact                  | 1  | 0.260    | ns       |             |
| Percent group members in reach                    | 1  | 0.760    | ns       |             |
| Percent group members within 3 m                  | 1  | 0.600    | ns       |             |
| <b>General overt social behaviour</b>             |    |          |          |             |
| Percent time grooming others                      | 1  | 0.000    | ns       |             |
| Percent time in social play                       | 1  | 0.149    | ns       |             |
| Aggression/dominance (per hour)                   | 1  | 1.042    | ns       |             |
| <b>Olfactory communication</b>                    |    |          |          |             |
| Brachial and antebrachial marking                 | 1  | 19.524   | ***      |             |
| Tail play (bouts)                                 | 1  | 12.866   | ***      |             |
| <b>Affiliation toward mother</b>                  |    |          |          |             |
| Approaches (per hour)                             | 1  | 3.440    | ns       |             |
| As nearest neighbour                              | 1  | 2.495    | ns       |             |
| In contact with                                   | 1  | 1.099    | ns       |             |
| Grooming  | 1  | 2.358    | ns       |             |
| Percent time on the nipple                        | 1  | 1.550    | ns       |             |
| <b>Affiliation toward adult females</b>           |    |          |          |             |
| Approaches (per hour)                             | 1  | 2.260    | ns       |             |
| As nearest neighbour                              | 1  | 0.860    | ns       |             |
| In contact with                                   | 1  | 1.607    | ns       |             |
| Grooming  | 1  | 2.600    | ns       |             |
| <b>Affiliation toward infants/young juveniles</b> |    |          |          |             |
| Approaches (per hour)                             | 1  | 4.030    | *        | sex × stage |
| As nearest neighbour                              | 1  | 1.000    | ns       |             |
| In contact with                                   | 1  | 3.420    | ns       |             |
| Grooming  | 1  | 221.500  | ***      | sex × stage |
| <b>Affiliation toward yearlings</b>               |    |          |          |             |
| Approaches (per hour)                             | 1  | 1.250    | ns       |             |
| As nearest neighbour                              | 1  | 1.113    | ns       |             |
| In contact with                                   | 1  | 0.006    | ns       |             |
| Grooming  | 1  | 2.739    | ns       |             |
| <b>Affiliation toward adult males</b>             |    |          |          |             |
| Approaches (per hour)                             | 1  | 9.320    | **       |             |
| As nearest neighbour                              | 1  | 5.308    | *        |             |
| In contact with                                   | 1  | 4.091    | *        |             |
| Grooming  | 1  | 0.201    | ns       |             |

Developmental stage was included as a fixed effect in all models where its effect was significant. Individual identity was included in all models as a random factor. Behaviours that differ significantly by sex are marked: \*  $p \leq 0.05$ , \*\*  $p \leq 0.01$ , \*\*\*  $p \leq 0.001$ . Behaviours that do not statistically significantly differ by sex are marked “ns.” Models for which the significant effect is an interaction between developmental stage and sex are denoted “sex × stage.”



### *Immature Sex Differences*

Naturally, there were significant stage effects on the development of nearly all behaviours examined across the first 2 years of life. However, because the subject of this study is the development of sex differences in behaviour, stage effects are not presented here except when discussed qualitatively to contextualize the development of behavioural sex differences.

Unlike adults, immatures in this sample did not differ by sex in any general measure of proximity or overt sociability or in any measure of interaction with non-maternal adult females (Table 3). They also did not differ by sex in any measure of proximity to or social behaviour directed toward their mothers (Table 3). Like adults, yearling females directed more affiliative social behaviour toward infants/young juveniles than yearling males did, but not in the same measures. Yearling females approached and groomed infants/young juveniles significantly more often than their male age mates, especially as older yearlings (Fig. 1), but did not more often have them as nearest neighbours or spend more time in contact with them (Table 3). Unlike adults, immatures did not differ by sex in any measure of social behaviour directed to yearlings (i.e., each other) (Table 3).

Unlike adults, immatures did not differ by sex with respect to displaying aggressive or dominance behaviour (Table 3), which they did much less often than adults. Like adults, immatures differed by sex in how often they exhibited brachial and antebrachial marking – only males exhibited this behaviour, although males exhibited it infrequently, and only as older infants and yearlings (Fig. 2). Additionally, immature males engaged in significantly more tail play than immature females did, but this was only marked in young yearlings – tail play was negligible in both sexes at other ages (Fig. 2).

Unlike adults, immatures differed by sex in their social interactions with adult males. Immature males approached (Fig. 3) and had adult males as nearest neighbours significantly more often than immature females did (Fig. 4), which resulted in immature males spending significantly more time in contact with adult males compared to immature females (Fig. 4).

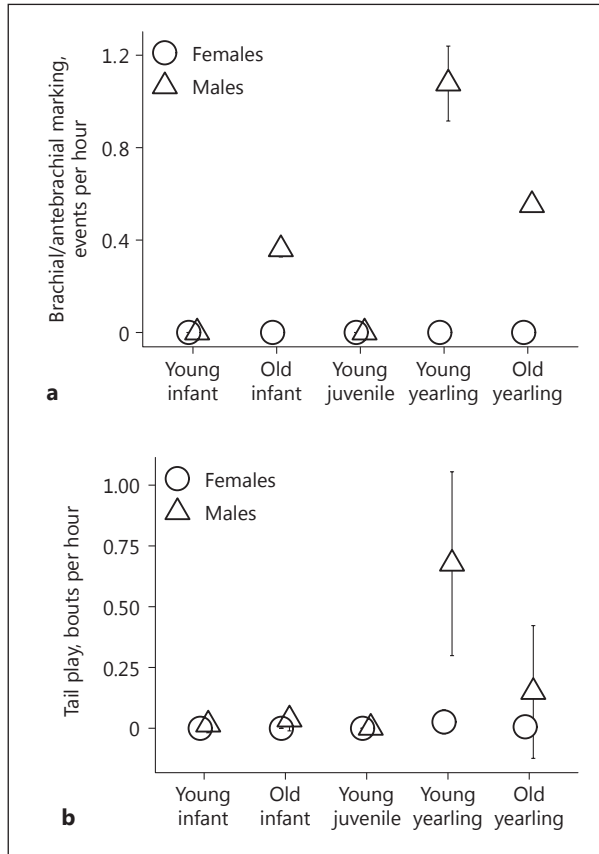
## **Discussion**

### *Development of Adult Behavioural Sex Differences Absent before Puberty*

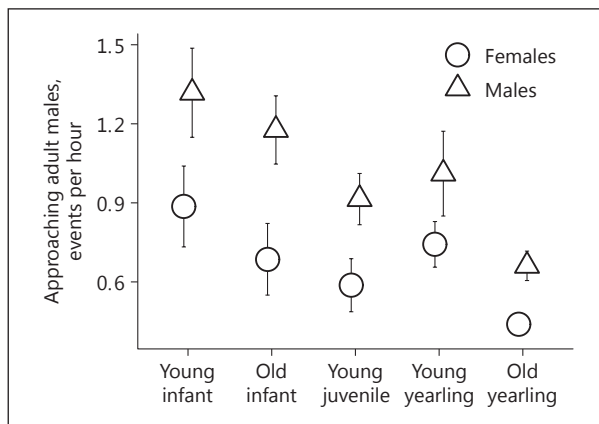
All adult behavioural sex differences found in this study were consistent with previous reports [Jolly, 1966, 1972; Budnitz and Dainis, 1975; Mertl-Millhollen, 1988; Kappeler, 1990a, b; Jolly et al., 1993; Sauther, 1993; Sauther and Sussman, 1993; Nakamichi and Koyama, 1997; Sauther et al., 1999; Gould, 1996; Nakamichi and Koyama, 2000; Gould, 2006; Erhart and Overdorff, 2008]. Also consistent with previous reports, sex differences in general proximity patterns [Gould, 1990; Pereira, 1993; Sauther and Sussman, 1993], affiliation with adult females and aggression/dominance were not exhibited by immatures.

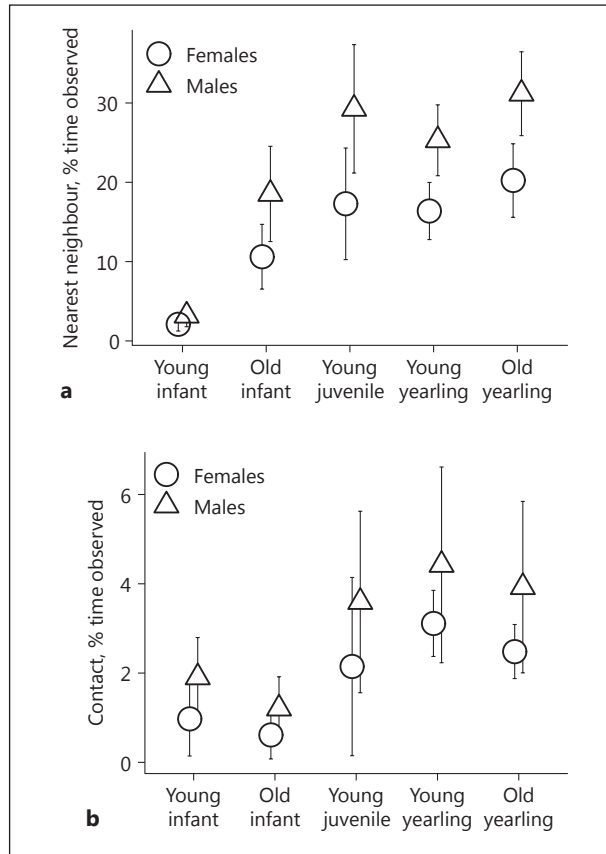
General patterns of adult sex-typical proximity must result from significant decreases in either male motivation or ability to maintain proximity to others sometime after the age of 2 years, possibly not until emigration. In this study, young infants invested the most effort into approaching and maintaining proximity to others, which gradually decreased to adult female levels in older yearlings of both sexes. Other stud-

**Fig. 2.** *Lemur catta* immature fitted model means and standard deviations for kinesthetic elements of adult male scent-marking behaviour (**a**, **b**). Immature males engaged in scent-marking-related behaviours significantly more often than immature females did, indicating that some scent-marking behaviour does not depend on gonadal maturation, at least when expressed by immatures. The similarity in the stage-related expression of brachial/antebrachial marking (**a**) and tail play (**b**) behaviours may indicate a common underlying proximate cause.



**Fig. 3.** *Lemur catta* immature fitted model means and standard deviations for approaching adult males. Immature males approached adult males significantly more often than immature females did, possibly indicating interest in developing relationships with adult males that are likely to have future utility.





**Fig. 4.** *Lemur catta* immature fitted model means and standard deviations for measures of proximity to adult males: time with an adult male as the nearest neighbour (**a**) and time in contact with adult males (**b**). Immature males were more often in proximity to adult males than immature females were, potentially allowing them to develop relationships with and/or learn behaviour from adult males that may have future utility.

ies from this population report that natal males maintain a close association with the central core of the group even at later ages [Sauther and Sussman, 1993].

*L. catta* are strongly female-philopatric [Sussman, 1992; Sauther and Sussman, 1993], making adult females far more likely to have access to matrilineal kin than adult males [Taylor and Sussman, 1985; Nakamichi and Koyama, 1997], which may explain adult sex differences in affiliation with adult females. This confounds direct comparisons of adult and immature males, who still live with their matrilineal kin. Nonetheless, adult sex differences in affiliation with adult females, specifically, do not arise after the age of 2. They may derive from a decrease in overall male gregariousness at postpubertal ages, or because males lose matrilineal kin as social partners upon emigration, or a combination thereof.

Because immature aggression was rare and undifferentiated by sex (in contrast to Gould [1990]), the development of adult sex-typed patterns of aggression and dominance would depend on substantial increases in these behaviours in females after the age of 2. This is consistent with previous descriptions of dramatic increases of female agonism toward adult males in sexually maturing females at 2.5 years of age in this population [Sauther and Sussman, 1993].

This study has produced further support for the hypothesis that puberty plays a role in the development of male-typical patterns of proximity to others and female-typical agonistic behaviour and dominance over males by documenting a temporal lag between the development of these sex differences in the wild compared to captivity. Captive subjects start to develop adult patterns of proximity, agonism and female dominance around the age of 16 months, approximately coincident with females' first mating seasons [Pereira, 1993]. In my sample, none of these adult behavioural sex differences developed prior to the age of 2, and at least female dominance and female-typical rates of agonism have been documented to develop coincident with sexual maturation in the wild, where females typically have their first mating season at 2.5 years of age [Sauther, 1993; Sauther and Sussman, 1993]. Pubertal causes of the development of these adult sex differences could act via changes in behavioural motivation driven by gonadal hormones of maturing individuals, or via behavioural responses to changes in social interactions directed at maturing individuals (such as when adult males begin to harass sexually maturing females [Sauther and Sussman, 1993]) or both.

#### *Development of Prepubertal Behavioural Sex Differences*

Adult female-typical interest in infants/young juveniles appears to be fully present in yearlings (Fig. 1) but is not expressed in fully adult ways. This is probably because yearling males maintain relatively close proximity to their mothers, placing them in proximity to infants/young juveniles by default, and preventing yearling females' interest in infants/young juveniles from translating into higher rates of contact or nearest neighbour status with them.

Adult male-typical scent-marking behaviour was also partially developed prior to the age of 2, consistent with previous descriptions from captivity [Pereira, 1993; Palagi et al., 2002] and the wild [Jolly, 1966]. Immatures also demonstrated prepubertal sex differences in attraction to adult males not seen in adults. Young infants of both sexes approached adult males frequently, but immature males approached adult males more than immature females and more than adults throughout the first 2 years of life. Immature males achieved relatively high rates of proximity to adult males at early ages and maintained them throughout the prepubertal period. Immature males had adult males as nearest neighbours near or above adult rates beginning as early as old infancy (3–5 months), whereas immature females never achieved adult rates of having adult males as nearest neighbours. Immature males were also in contact with adult males at higher rates than immature females throughout development, sometimes at or above adult rates of contact with adult males. All of these patterns indicate that immature males were particularly attracted to adult males.

These behavioural sex differences developed well before either the genital development or anogenital marking behaviour that signal the onset of puberty [Pereira, 1991, 1993, 1995], indicating that they do not depend on pubertal gonadal hormones for their appearance and maintenance and must have some other proximate cause, such as prenatal or neonatal hormone exposure or early socialization. Interestingly, the age-related patterns of immature male brachial/antebrachial marking and tail play were concordant, suggesting that these 2 behaviours share the same proximate motivation.

#### *Potential Fitness Benefits of Immature Social Sex Differences*

Immature *L. catta* in this sample demonstrated some prepubertal behavioural sex differences common in haplorhines that are usually attributed to immatures' mo-

tivations to engage in behaviours likely to increase their fitness as adults. Immature females in many haplorhine species demonstrate more interest in infants than their male age mates [reviewed in Meredith, 2015], which probably represents either an attempt to “learn to mother” [Lancaster, 1971; Meredith, 2015] or is a by-product of selection for adult female infant care behaviour [Silk, 1999; Meredith, 2015]. It is also common for immature males to seek out proximity to and interaction with males that may provide future benefits, such as forming alliances to increase survivorship during dispersal (e.g., *Alouatta seniculus* [Crockett and Pope, 1993]), learning to negotiate relationships with males that will eventually facilitate their success in adult male competition (e.g., *P. troglodytes* [Lonsdorf et al., 2014]), motor training for later adult contest competition (e.g., *Gorilla gorilla* [Maestriperi and Ross, 2004]) and/or learning male-typical foraging techniques (e.g., *Cebus nigrinus* [Agostini and Visalberghi, 2005]). In *L. catta*, immature males eventually emigrate from their natal groups, often with 1 or 2 other males [Sussman, 1992; Gould, 1997, 2006]. Interactions with adult males may provide immature males with learning opportunities about male-male interaction that will help them establish themselves in a male group hierarchy after immigration and may help them build “friendships” that could be beneficial during emigration or for thermoregulatory huddling when males are not able to maintain proximity to their mothers or other adult females [Gabriel et al., 2014]. In these ways, immature *L. catta* seem to engage in the same kinds of adaptive social strategies common in haplorhines.

## Acknowledgements

Many thanks go to Michelle Sauter, Frank Cuzzo and Leanne Nash for logistical support and mentorship. Special thanks go to Jacky Antho, the Beza Ecological Monitoring team, Andry Randrianandrasana and the staff of Beza Mahafaly Special Reserve for their logistical support and friendship during data collection. Several reviewers deserve credit for substantially improving this manuscript. Data collection for this project was funded by the Leakey Foundation, Sigma Xi, the ASU School of Human Evolution and Social Change, and the ASU Graduate and Professional Student Association. This study complied with all US and Malagasy animal care regulations and laws.

## Disclosure Statement

I have no conflicts of interest to report.

## References

- Agostini I, Visalberghi E (2005). Social influences on the acquisition of sex-typical foraging patterns by juveniles in a group of wild tufted capuchin monkeys (*Cebus nigrinus*). *American Journal of Primatology* 65: 335–351.
- Alport LJ (2004). Comparative analysis of the role of olfaction and the neocortex in primate intrasexual competition. *The Anatomical Record Part A: Discoveries in Molecular, Cellular and Evolutionary Biology* 281A: 1182–1189.
- Altmann J (1974). Observational study of behavior: sampling methods. *Behaviour* 49: 227–266.
- Barthold J, Fitchel C, Kappeler P (2009). What is it going to be? Pattern and potential function of natal coat change in sexually dichromatic red-fronted lemurs (*Eulemur fulvus rufus*). *American Journal of Physical Anthropology* 138: 1–10.

- Bates D, Maechler M, Bolker B, Walker S (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–48.
- Blumstein DT, Daniel JC (2007). *Quantifying Behavior the JWatcher Way*. Sunderland, Sinauer Associates.
- Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution* 24: 127–135.
- Budnitz N, Dainis K (1975). *Lemur catta*: ecology and behavior. In *Lemur Biology* (Tattersall I, Sussman RW, eds.), pp 219–236. New York, Plenum Press.
- Burnham K, Anderson D (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd ed. New York, Springer.
- Cavigelli SA, Pereira ME (2000). Mating season aggression and fecal testosterone levels in male ring-tailed lemurs (*Lemur catta*). *Hormones and Behavior* 37: 246–255.
- Crockett CM, Pope TR (1993). Consequences of sex differences in dispersal for juvenile red howler monkeys. In *Juvenile Primates: Life History, Development, and Behavior* (Pereira MA, Fairbanks LA, eds.), pp 104–118. Chicago, University of Chicago Press.
- Dixon AF (1993). Sexual and aggressive behaviour of adult male marmosets (*Callithrix jacchus*) castrated neonatally, prepubertally, or in adulthood. *Physiology and Behavior* 54: 301–307.
- Drea CM, Scordato ES (2008). Olfactory communication in the ringtailed lemur (*Lemur catta*): form and function of multimodal signals. In *Chemical Signals in Vertebrates 11* (Hurst J, Beynon RJ, Roberts SC, Wyatt T, eds.), pp 91–102. New York, Springer.
- Eaton GG, Johnson DF, Glick BB, Worlein JM (1986). Japanese macaque (*Macaca fuscata*) social development: sex differences in juvenile behavior. *Primates* 27: 141–150.
- Eisler JA, Tannenbaum PL, Mann DR, Wallen K (1993). Neonatal testicular suppression with a GnRH antagonist in rhesus monkeys: effects on adult endocrine function and behavior. *Hormones and Behavior* 27: 551–567.
- Epple G, Alveario MC, Belcher AM (1990). Copulatory behavior of adult tamarins (*Saguinus fuscicollis*) castrated as neonates or juveniles: effect of testosterone treatment. *Hormones and Behavior* 24: 470–483.
- Erhart EM, Overdorff DJ (2008). Rates of agonism by diurnal lemuroids: implications for female social relationships. *International Journal of Primatology* 29: 1227–1247.
- Evans CS, Goy RW (1968). Social behaviour and reproductive cycles in captive ring-tailed lemurs (*Lemur catta*). *Journal of Zoology* 156: 181–197.
- Fournier DA, Skaug HJ, Ancheta J, Ianelli J, Magnusson A, Maunder M, Nielsen A, Sibert J (2012). AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software* 27: 233–249.
- Fritz J, Nash LT, Howell SM (1992). Effects of temporary restricted social housing on later reproductive behavior in adolescent chimpanzees. *Lab Animal* 21: 21–25.
- Gabriel DN, Gould L, Kelley EA (2014). Seasonal patterns of male affiliation in ring-tailed lemurs (*Lemur catta*) in diverse habitats across southern Madagascar. *Behaviour* 151: 935–961.
- Gardner W, Mulvey EP, Shaw EC (1995). Regression analyses of counts and rates: Poisson, overdispersed Poisson, and negative binomial models. *Psychological Bulletin* 118: 392–404.
- Gould L (1990). The social development of free-ranging infant *Lemur catta* at Berenty Reserve, Madagascar. *International Journal of Primatology* 11: 297–318.
- Gould L (1996). Vigilance behavior during the birth and lactation season in naturally occurring ring-tailed lemurs (*Lemur catta*) at the Beza-Mahafaly Reserve, Madagascar. *International Journal of Primatology* 17: 331–347.
- Gould L (1997). Intermale affiliative behavior in ringtailed lemurs (*Lemur catta*) at the Beza-Mahafaly Reserve, Madagascar. *Primates* 38: 15–30.
- Gould L (2006). Male sociality and integration during the dispersal process in *Lemur catta*: a case study. In *Ringtailed Lemur Biology* (Jolly A, Koyama N, Rasamimanana HR, Sussman RW, eds.), pp 296–310. New York, Springer.
- Gould L, Sussman RW, Sauther ML (2003). Demographic and life-history patterns in a population of ring-tailed lemurs (*Lemur catta*) at Beza Mahafaly Reserve, Madagascar: a 15-year perspective. *American Journal of Physical Anthropology* 120: 182–194.
- Goy RW, Wallen K (1979). Experiential variables influencing play, foot-clasp mounting and adult sexual competence in male rhesus monkeys. *Psychoneuroendocrinology* 4: 1–12.
- Goy RW, Bercovitch FB, McBrair MC (1988). Behavioral masculinization is independent of genital masculinization in prenatally androgenized female rhesus macaques. *Hormones and Behavior* 22: 552–571.
- Harlow HF (1965). Sexual behavior in the rhesus monkey. In *Sex and Behavior* (Beach FA, ed.), pp 234–265. New York, Wiley.

- Herman RA, Wallen K (2007). Cognitive performance in rhesus monkeys varies by sex and prenatal androgen exposure. *Hormones and Behavior* 51: 496–507.
- Honess PE, MacDonald DW (2003). Marking and radio-tracking primates. In *Field and Laboratory Methods in Primatology: A Practical Guide* (Setchell JM, Curtis DJ, eds.), pp 158–173. Cambridge, Cambridge University Press.
- Hosey GR, Jacques M (1994). Interactions between infant ring-tailed lemurs (*Lemur catta*) and their parents and older siblings. In *Current Primatology* (Roeder JJ, Thierry B, Anderson JR, Herrenschildt N, eds.), vol 2: Social Development and Learning, pp 315–319. Strasbourg, University Louis Pasteur.
- Johnson JB, Omland KS (2004). Model selection in ecology and evolution. *Trends in Ecology and Evolution* 19: 101–108.
- Jolly A (1966). *Lemur Behavior: A Madagascar Field Study*. Chicago, University of Chicago Press.
- Jolly A (1972). Troop continuity and troop spacing in *Propithecus verreauxi* and *Lemur catta* at Berenty (Madagascar). *Folia Primatologica* 17: 335–362.
- Jolly A, Rasamimanana HR, Kinnaird MF, O'Brien TG, Crowley HM, Harcourt CS, Gardner S, Davidson J (1993). Territoriality in *Lemur catta* groups during the birth season at Berenty, Madagascar. In *Lemur Social Systems and Their Ecological Basis* (Kappeler PM, Ganzhorn JU, eds.), pp 85–109. New York, Plenum Press.
- Jones KC (1983). Inter-troop transfer of *Lemur catta* males at Berenty, Madagascar. *Folia Primatologica* 40: 145–160.
- Kappeler PM (1990a). Female dominance in *Lemur catta*: more than just female feeding priority? *Folia Primatologica* 55: 92–95.
- Kappeler PM (1990b). Social status and scent-marking behaviour in *Lemur catta*. *Animal Behaviour* 40: 774–776.
- Klopfer PH (1972). Patterns of maternal care in lemurs. II. Effects of group size and early separation. *Zeitschrift für Tierpsychologie* 30: 277–296.
- Klopfer PH (1974). Mother-young relations in lemurs. In *Prosimian Biology* (Martin RD, Doyle GA, Walker AC, eds.), pp 273–292. London, Duckworth.
- Klopfer PH, Boskoff KJ (1979). Maternal behavior in prosimians. In *The Study of Prosimian Behavior* (Doyle GA, Martin RD, eds.), pp 123–156. New York, Academic Press.
- Klopfer PH, Klopfer MS (1970). Patterns of maternal care in lemurs. I. Normative description. *Zeitschrift für Tierpsychologie* 27: 984–996.
- Koyama N, Nakamichi M, Oda R, Miyamoto N, Ichino S, Takahata Y (2001). A ten-year summary of reproductive parameters for ring-tailed lemurs at Berenty, Madagascar. *Primates* 42: 1–14.
- Lancaster J (1971). Play-mothering: the relations between juvenile females and young infants among free-ranging vervet monkeys (*Cercopithecus aethiops*). *Folia Primatologica* 15: 161–182.
- Lewis F, Butler A, Gilbert L (2011). A unified approach to model selection using the likelihood ratio test. *Methods in Ecology and Evolution* 2: 155–162.
- Lonsdorf EV, Anderson KE, Stanton MA, Shender M, Heintz MR, Goodall J, Murray CM (2014). Boys will be boys: sex differences in wild infant chimpanzee social interactions. *Animal Behaviour* 88: 79–83.
- Maestripieri D, Ross SR (2004). Sex differences in play among western lowland gorilla (*Gorilla gorilla gorilla*) infants: implications for adult behavior and social structure. *American Journal of Physical Anthropology* 123: 52–61.
- Maestripieri D, Zehr JL (1998). Maternal responsiveness increases during pregnancy and after estrogen treatment in macaques. *Hormones and Behavior* 34: 223–230.
- Meredith SL (2013). Identifying proximate and ultimate causation in the development of primate sex-typed social behavior. In *Building Babies: Primate Development in Proximate and Ultimate Perspective* (Clancy KBH, Hinde K, Rutherford JN, eds.), pp 411–433. New York, Springer.
- Meredith SL (2015). Anchoring the clade: primate-wide comparative analysis supports the relationship between juvenile interest in infants and adult patterns of infant care. *Folia Primatologica* 86: 117–123.
- Mertl-Millhollen AS (1988). Olfactory demarcation of territorial but not home range boundaries by *Lemur catta*. *Folia Primatologica* 50: 175–187.
- Nakamichi M, Koyama N (1997). Social relationships among ring-tailed lemurs (*Lemur catta*) in two free-ranging troops at Berenty Reserve, Madagascar. *International Journal of Primatology* 18: 73–93.
- Nakamichi M, Koyama N (2000). Intra-troop affiliative relationships of females with newborn infants in wild ring-tailed lemurs (*Lemur catta*). *American Journal of Primatology* 50: 187–203.
- Nash LT (2003). Sex differences in the behavior and the social interactions of immature *Galago senegalensis braccatus*. *Folia Primatologica* 74: 285–300.
- O'Mara MT, Hickey CM (2012). Social influences on the development of ringtailed lemur feeding ecology. *Animal Behaviour* 84: 1547–1555.
- O'Mara MT, Hickey CM (2014). The development of sex differences in ring-tailed lemur feeding ecology. *Behavioral Ecology and Sociobiology* 68: 1273–1286.
- Palagi E, Gregorace A, Tarli SMB (2002). Development of olfactory behavior in captive ring-tailed lemurs (*Lemur catta*). *International Journal of Primatology* 23: 587–599.

- Pereira ME (1991). Asynchrony within estrous synchrony among ringtailed lemurs (Primates: Lemuridae). *Physiology and Behavior* 49: 47–52.
- Pereira ME (1993). Agonistic interaction, dominance relation, and ontogenetic trajectories in ringtailed lemurs. In *Juvenile Primates: Life History, Development, and Behavior* (Pereira ME, Fairbanks LA, eds.), pp 285–305. New York, Oxford University Press.
- Pereira ME (1995). Development and social dominance among group-living primates. *American Journal of Primatology* 37: 143–175.
- Pereira ME, Kappeler PM (1997). Divergent systems of agonistic behaviour in lemurid primates. *Behaviour* 134: 225–274.
- Pereira ME, Weiss ML (1991). Female mate choice, male migration, and the threat of infanticide in ringtailed lemurs. *Behavioral Ecology and Sociobiology* 28: 141–152.
- Petter-Rousseaux A, Buettner-Janusch J (1964). Reproductive physiology and behavior of the Lemuroidea. In *Evolutionary and Genetic Biology of Primates* (Buettner-Janusch J, ed.), pp 91–132. New York, Academic Press.
- Phoenix CH, Goy RW, Gerall AA, Young WC (1959). Organizing action of prenatally administered testosterone propionate on the tissues mediating mating behavior in the female guinea pig. *Endocrinology* 63: 369–382.
- R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Reitan T, Nielsen A (2016). Do not divide count data with count data. A story from pollination ecology with implications beyond. *PLoS ONE* 11: e0149129.
- Sauther ML (1991). Reproductive behavior of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. *American Journal of Physical Anthropology* 84: 463–477.
- Sauther ML (1993). Resource competition in wild populations of ring-tailed lemurs (*Lemur catta*): implications for female dominance. In *Lemur Social Systems and Their Ecological Basis* (Kappeler PM, Ganzhorn JU, eds.), pp 135–152. New York, Plenum Press.
- Sauther ML, Sussman RW (1993). A new interpretation of the social organization and mating system of the ringtailed lemur (*Lemur catta*). In *Lemur Social Systems and Their Ecological Basis* (Kappeler PM, Ganzhorn JU, eds.), pp 111–121. New York, Plenum Press.
- Sauther ML, Sussman RW, Gould L (1999). The socioecology of the ringtailed lemur: thirty-five years of research. *Evolutionary Anthropology: Issues, News, and Reviews* 8: 120–132.
- Schulz KM, Molenda-Figueira HA, Sisk CL (2009). Back to the future: the organizational-activational hypothesis adapted to puberty and adolescence. *Hormones and Behavior* 55: 597–604.
- Silk J (1999). Why are infants so attractive to others? The form and function of infant handling in bonnet macaques. *Animal Behaviour* 57: 1021–1032.
- Singer JD, Willett JB (2003). *Applied Longitudinal Data Analysis: Modeling Change and Event Occurrence*. New York, Oxford University Press.
- Sussman RW (1991). Demography and social organization of free-ranging *Lemur catta* in the Beza Mahafaly Reserve, Madagascar. *American Journal of Physical Anthropology* 84: 43–58.
- Sussman RW (1992). Male life histories and inter-group mobility among ring-tailed lemurs (*Lemur catta*). *International Journal of Primatology* 13: 395–413.
- Sussman RW, Ratsirarson J (2006). Beza Mahafaly Special Reserve: a research site in southwestern Madagascar. In *Ringtailed Lemur Biology* (Jolly A, Sussman RW, Koyama N, Rasamimanana H, eds.), pp 43–51. New York, Springer.
- Taylor L, Sussman RW (1985). A preliminary study of kinship and social organization in a semi-free-ranging group of *Lemur catta*. *International Journal of Primatology* 6: 601–614.
- Thornton J, Zehr JL, Loose MD (2009). Effects of prenatal androgens on rhesus monkeys: a model system to explore the organizational hypothesis in primates. *Hormones and Behavior* 55: 633–645.
- Tomaszycki ML, Davis JE, Gouzoules H, Wallen K (2001). Sex differences in infant rhesus macaque separation-rejection vocalizations and effects of prenatal androgens. *Hormones and Behavior* 39: 267–276.
- Tomaszycki ML, Gouzoules H, Wallen K (2005). Sex differences in juvenile rhesus macaque (*Macaca mulatta*) agonistic screams: life history differences and effects of prenatal androgens. *Developmental Psychobiology* 47: 318–327.
- Van Horn RN (1975). Primate breeding season: photoperiodic regulation in captive *Lemur catta*. *Folia Primatologica* 24: 203–220.
- Wallen K (1996). Nature needs nurture: the interaction of hormonal and social influences on the development of behavioral sex differences in rhesus monkeys. *Hormones and Behavior* 30: 364–378.
- Wallen K, Maestriperi D, Mann DR (1995). Effects of neonatal testicular suppression with a GnRH antagonist on social behavior in group-living juvenile rhesus monkeys. *Hormones and Behavior* 29: 322–337.
- Warton DI, Hui FKC (2011). The arcsine is asinine: the analysis of proportions in ecology. *Ecology* 92: 3–10.