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# Communal nesting, kinship, and maternal success in a social primate

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**Abstract** Communal nesting, where several mothers regularly pool and cooperatively rear offspring, is unusual in mammals. This type of crèching behavior is especially rare among primates, with the notable exceptions of humans, some nocturnal strepsirrhines, and—as we show in this study—black-and-white ruffed lemurs (*Varecia variegata*). Here, we combine data on nesting behavior, genetic relatedness, and infant survivorship to describe variation in ruffed lemur infant care and to examine the potential benefits of ruffed lemur communal breeding. Reproductive events were rare, and females produced litters (synchronously) only once in 6 years of observation. We show that not all mothers participate in communal crèches, but those that did had greater maternal success; communal breeders spent more time feeding and their offspring were more likely to survive. Although cooperating mothers were often related, females also cooperated with non-kin, and those who shared infant care responsibilities had greater maternal success than mothers who did not participate. If there is indeed a causal link between maternal cooperation and reproductive success, this unusual behavior, like that of human communal rearing, may have evolved via some combination of kin selection and mutualism.

**Keywords** Reproductive success · Communal breeding · Crèching behavior · Lemurs · Allomaternal care

## Introduction

The costs and benefits of cooperative breeding have been well studied, particularly in systems where one or few individuals monopolize reproduction and receive help from non-breeding adult conspecifics (Stacey and Koenig 1990; Emlen 1991; Solomon and French 1997; Clutton-Brock 2002; Browning et al. 2012). However, in some cooperatively breeding societies, including humans (e.g., Hrdy 1999, 2009; Sear and Mace 2008; Hill and Hurtado 2009; Meehan et al. 2013), reproduction is not monopolized (reviewed in Johnstone 2000); rather, several females breed and together share in maternal care (i.e., communal breeding, e.g., Hayes 2000; reviewed in Gilchrist 2007). In some cases, synchronously breeding females crèche litters in communal nests or dens (e.g., Hayes 2000; White and Cameron 2009; Riehl 2010, 2012) and cooperatively provide grooming, guarding, predator protection, and/or energy transfer (e.g., provisioning, allomaternal nursing) to each other's young (reviewed in Stacey and Koenig 1990; Gittleman 1985; König 1997). The risks of leaving dependent offspring with potentially negligent allomothers are high (Gittleman 1985), and investing resources in allomaternal "babysitting" likely poses additional opportunity costs. These costs could be mitigated if communal nesting partners are kin (Hamilton 1964; Maynard Smith 1964; Clutton-Brock 2002) and/or if participating mothers increase their direct fitness through increased foraging time and enhanced survival of offspring. Assessing

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the evolutionary factors that promote such communal care is challenging, especially among mammals, where crèching is rare (e.g., Lee 1987; Packer et al. 1990; Eberle and Kappeler 2006; Hrdy 2006; Tecot et al. 2012, 2013). Moreover, understanding the scenario in which such communal rearing might evolve requires not only identifying the relationships among mothers, but also comparing the fitness payoffs for mothers who do and do not participate in communal care.

Here, we combine behavioral and genetic data to quantify and compare maternal success for females who do and do not participate in communal nest use (i.e., those who do and do not crèche infants) in a wild primate population. This is the first systematic study to quantify the potential benefits of this unique communal breeding system in wild black-and-white ruffed lemurs (*Varecia variegata*), a large-bodied, diurnal primate. Ruffed lemurs are highly gregarious, 3–4 kg Malagasy strepsirrhines (Baden et al. 2008) that form social communities, the members of which cooperatively defend jointly used territories that are characterized by high fission–fusion dynamics (Morland 1991; Vasey 2006; Baden 2011). Community membership is generally stable, and community size varies from 18 to 30 individuals (Vasey 2003). Social relationships among community members are egalitarian (weak or no within-sex dominance hierarchies occur; reviewed in Erhart and Overdorff 2008); however, within a community, individuals vary in their patterns of association and range use (Morland 1991; Vasey 2006; Baden 2011).

Like a majority of primates, ruffed lemurs have relatively slow life histories and, as with most Malagasy strepsirrhines, are strict seasonal breeders (Bogart et al. 1977a, b; Boskoff 1977a; Rasmussen 1985; Morland 1993), only coming into vaginal estrus for 24–72 h each year (Foerg 1982). Ruffed lemurs are the only diurnal primates known to bear litters of altricial offspring during these seasonal reproductive events (Foerg 1982; Rasmussen 1985). Because infants cannot cling at birth, litters are parked in nests and tree tangles until capable of independent travel (Morland 1990; Vasey 2007; Baden 2011), and it is during this time that evidence of communal breeding has been reported, including use of communal nests (crèches) and cooperative infant care (e.g., babysitting, allonursing) (Morland 1990; Vasey 2007; Baden 2011). It has also been suggested that ruffed lemurs exhibit "boom-bust" reproduction (sensu Rubenstein 1982), producing litters of young only during periods of resource abundance (Ratsimbazafy 2002), a rare reproductive strategy, even among mammals. Thus, if communal nesting (crèche use) confers fitness-related benefits, then communal breeding in this species may prove particularly important to ensuring infant survival during these rare reproductive events.

While communal nests in ruffed lemurs have been previously documented (Pereira et al. 1987; Morland 1990; Vasey 2007; Baden 2011), it remains unclear whether and to what extent mothers vary in their tendency to crèche offspring and how they might benefit from crèche-use. Here, we compare patterns of communal nesting across eight parous females over six consecutive years to examine potential relationships between crèche use and maternal activity budget and infant survival. Specifically, we quantify feeding and foraging times for mothers who do and do not crèche offspring (communal versus single nesters), and we compare maternal strategies in terms of infant survival. Moreover, we examine patterns of spatial proximity, association and kinship, and ask: Do mothers show a bias for specific communal nesting partners? If so, does this bias for certain partners relate to their spatial, social, and/or genetic relationships? And finally, is communal nesting among related mothers more successful than among unrelated mothers? If communal nesting occurs equally among kin and non-kin, the synergistic benefits gained from communal breeding may exceed the immediate costs and risks of cooperation, thus suggesting that kin selection has a limited role in the evolution of communal breeding (Clutton-Brock 2009; Riehl 2010), as is the case for other forms of cooperation (such as among male chimpanzees; Langergraber et al. 2007).

## Methods

### Study site and subjects

Data were collected from one wild, habituated ruffed lemur community ($n=22$ adults; see below regarding limits on sample size) in Ranomafana National Park (Mangevo 21°22′60″S, 47°28′0″E), Madagascar (Wright 1992; Wright et al. 2012) over a 6-year period (2005–2010). Prior to the onset of behavioral sampling, all members of the focal community were captured following established protocols (Glander 1993). Captured individuals were given subcutaneous AVID® microchips and fitted with unique collar-tag combinations to enable individual identification during behavioral observations. Biological samples (10 mg/kg blood and 4×2 mm tissue biopsies) were collected and stored for subsequent genetic analyses following Louis et al. (2005). Data presented here were collected from a subset of eight adult females studied during 17 consecutive months of observation (August 2007–December 2008; $n=2{,}730$ observation hours). Research protocols were in compliance with and permission was granted by Stony Brook University IACUC #2005-20081449, Yale University IACUC #2010-11378, and Madagascar's National Parks (ANGAP/MNP).

### Data collection

Two independent observers each selected a subject at random for all-day behavioral observations of focal individuals (Altmann 1974). Observations were rotated among individuals daily and sampling was distributed evenly among subjects

(Table 1). During each observational bout, we used instantaneous sampling at 5-min intervals to record behavioral states (feeding, foraging, resting, traveling, social, other), diet (plant species and part eaten, stage of ripeness), and subgroup size, composition (identity and age/sex class of individuals in a subgroup), and cohesion (the distance between each subgroup member and the focal subject). A subgroup was defined as all individuals within 25 m of one another who exhibited behavioral coordination (e.g., feeding, resting, traveling together). From these 5-min focal samples, we could calculate individual activity budgets based on the proportion of time an individual engaged in particular activities (e.g., the proportion of time spent feeding was calculated as the number of 5-min samples that involved feeding divided by the total number of 5-min samples), as well as the proportionate amount of time any two individuals were found in association (i.e., in the same subgroup).

Simultaneous GPS coordinates were collected at 10-min intervals from as close to the focal individual as possible to document individual range use and determine spatial proximity among females' home ranges. Ad libitum data were collected when a female was observed building nests, including start and stop times of nest building and details of nest construction. Nesting trees were flagged, mapped using GPS coordinates, and given unique IDs for future identification.

During the 10 weeks following parturition (mid-October to December 2008), observational protocols were supplemented with all-day nest observations ($n$=808 observation hours). Thereafter, infants were capable of independent travel and communal nesting ceased. To document nesting patterns, including communal nest use and nest composition, we used instantaneous nest scans conducted at 5-min intervals. At each sampling point, we recorded the nest ID and location, as well as the number and identity of litters in the nest. We measured initial litter size as the number of visible offspring counted in each female's natal nest. Living infants move around in the nest and are generally visible. This measure was used as a minimum estimate of litter size, as it did not include infants that may have been stillborn or that died prior to being counted. We monitored infant survival by counting the number of infants alive during each subsequent focal observation of the respective female. We also opportunistically monitored litter size changes for those females who were not the subjects of a given day's focal sampling.

Two of eight females included in this study used the periphery of the communal territory during most of the year but did not use the center of the territory, and were thus not the subjects of focal observations; however, in the 10 weeks following parturition, both females and their litters were contacted regularly and were often found associating and nesting their litters communally with focal individuals. We were unable to quantify activity budgets, diet, and nesting time (either total or communal) for these females; however,

**Table 1** Details of nest use, maternal nesting strategy and infant survival during the first 3 months post-parturition

| Female ID | Birth | Natal nest use [days] | Initial nest transfer | Exclusive maternal care [days] | First observed in communal nest | Strategy | Communal nesting [%] | Litter size at birth | Infant survival | | | Survival [%] | Genotype? | Focal? | Observation hours | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | Month 1 | Month 2[a] | Month 3 | | | | Total | Post-birth |
| rYellow | 14 Oct | 7 | 21 Oct | n/a | n/a | Single | 0.0 | 2 | 2 | 1 | 1 | 50 | Y | Y | 510 | 172 |
| rRed | 13 Oct | 22 | 4 Nov | 44 | 26 Nov | Single | 0.4 | 3 | 3 | 3 | 1 | 33 | Y | Y | 560 | 145 |
| rOrange | 20 Oct | 3 | 23 Oct | 44 | 3 Dec | Communal | 14.7 | 3 | 3 | 2 | 2 | 67 | N | Y | 560 | 144 |
| rBlue | 8 Oct | 21 | 29 Oct | 42 | 19 Nov | Communal | 19.4 | 2 | 2 | 2 | 2 | 100 | Y | Y | 510 | 180 |
| rGreen | 16 Oct | 16 | 1 Nov | 34 | 19 Nov | Communal | 22.8 | 3 | 3 | 3 | 3 | 100 | Y | Y | 590 | 167 |
| Pink-Yellow[b] | – | – | – | – | 2 Dec | Communal | – | 3 | 3 | 3 | 3 | 100 | Y | N | – | – |
| Yellow-Green[b] | – | – | – | – | 3 Dec | Communal | – | 3 | 3 | 3 | 3 | 100 | Y | N | – | – |
| Average | | 13.8 | | 41 | | | | 2.7 | 2.7 | 2.4 | 2.1 | 79 | | | 555 | 159 |

*Natal nest use* nest use (in days) prior to the first nest transfer, *Communal nesting [%]* percent time mother was observed communally nesting her infants, relative to total nesting time overall

[a] Onset of communal nesting (approximately 6 weeks post-parturition)

[b] Note: Females Pink-Yellow and Yellow-Green were not subject to with focal follows and thus birth dates and details of nest use are unknown. Females were, however, observed co-nesting with each other, as well as with focal mothers during the post-parturition period

regular observations of co-nesting associations between these two females allowed us to characterize them as communal nesters and to monitor changes in litter size during their communal nesting period. We calculated communal nesting and association indices for these females based on the time they nested or associated with focal subjects and thus represent minimum estimates of association.

## Nesting analyses

Prior to statistical comparisons, mothers were characterized as taking one of two “nesting strategies”: single nesters (i.e., solitary brooding) or communal nesters. Two females crèched their offspring less than 1 % of their total observed nesting time (single nesters), whereas the remaining five were regularly observed in communal nesting associations (communal nesters; Table 1). To characterize pairwise patterns of communal nesting among individuals further, we used a twice-weight association index (Cairns and Schwager 1987) to estimate the time two mothers nested their infants together relative to their total observed nesting time. Indices were calculated from data generated during instantaneous nest scans. This index, referred to from here forward as the communal nesting index (CNI), was calculated as CNI=$N_{A,B}/\sum(N_A,N_B,N_{A,B})$, where $N_{A,B}$ was the number of scans in which individuals A and B nested their infants together, $N_A$ was the number of scans individual A was observed nesting her infants in the absence of litter B, and $N_B$ was the number of scans individual B was observed nesting her infants in the absence of litter A. Possible indices ranged from 0 to 1.

## Factors related to choice of communal nesting partners

To describe the potential factors associated with female nesting patterns, we examined three possible variables: spatial proximity (*m*), patterns of long-term association (AI), and kinship (*r*).

The percent of the community home range used varies across females, as does the extent of ranging overlap (e.g., Vasey 2006; Baden 2011). We predicted that communal nesting would be associated with close spatial proximity among female home ranges. Individual range use also varies across seasons (Vasey 2006; Baden 2011), and we were most interested in understanding how immediate spatial proximity was related to nesting strategy (i.e., whether females nested with neighbors, regardless of social or kinship ties). We identified individual home ranges using GPS coordinates generated during post-parturition follows only. To conform to assumptions of statistical independence, samples from the same individual (up to 60 per follow) were subsampled to include only those data points that were separated by at least 1 h. We first removed 5 % of the points that were outliers to account for rare excursions outside of an individual’s range and then drew a minimum convex polygon around the remaining 95 % of ranging coordinates using the program Hawth’s Tools in ArcMap 9.3 (ESRI 2011). Spatial proximity was calculated as the pairwise distance (in meters) between home range centroids.

Because infant mishandling/infanticide risk is associated with unfamiliar individuals or social antagonists in many species (reviewed in van Schaik and Kappeler 1997), we predicted that communal nesting would occur more often among familiar individuals or close social associates. Because community members vary in their patterns of subgroup membership and social association (Morland 1991; Vasey 1997; Baden 2011), we again used a twice-weight index of association (Cairns and Schwager 1987), or AI, to estimate the proportion of time two females spent in association relative to their total observation time following previous studies of fission–fusion primates (e.g., Symington 1988; Ramos-Fernandez et al. 2009; Lehmann and Boesch 2009). To account for the influence of long-term patterns of association, AIs were generated from subgroup membership data collected during the full 17-month study period.

Finally, because communal babysitters can incur costs, individuals might be more willing to help close kin and thereby gain indirect fitness benefits (König 1997; Hayes 2000). Thus, we also estimated genetic pairwise relatedness (*r*) among females. Individuals were genotyped at a suite of 15 polymorphic microsatellite loci (Electronic Supplemental Material 1). Total genomic DNA was extracted from blood and tissue samples using standard nucleic acid extraction kits (QIAamp DNA Mini Kit; Qiagen). Extraction procedures followed the manufacturer’s protocols, with the following modification: prior to DNA isolation, tissue samples were allowed to soak at 25 °C in ASL lyses buffer for 24–48 h. PCR amplifications were carried out in a total volume of 25 μl consisting of 2 μl template, 12.5 μl Qiagen HotStar Taq Master Mix, and 10 μM of each primer. Amplification conditions were as follows: initial denaturation at 95 °C for 15 min; 35 cycles of 30 s at 94 °C, 40 s at 54 to 60 °C (see Louis et al. 2005), 1 min at 72 °C, and a final extension of 7 min at 72 °C. The 5′ end of the forward primer was fluorescently labeled, and amplification products were separated using capillary electrophoresis (ABI 3730xl Genetic Analyzer). Allele sizes were assessed relative to an internal size standard (ROX-500) using Gene Mapper software (Applied Biosystems), and final genotypes were scored based on multiple independent reactions (Taberlet et al. 1996). Panels yielded $PI_{sib}$ (Queller and Goodnight 1998) values of $2.7\times10^{-5}$, demonstrating the very low probability that two individuals would share the same multilocus genotype by chance.

Kinship or pairwise relatedness among individuals (*r*) was estimated following Queller and Goodnight (1989) using the program ML-RELATE (Kalinowski et al. 2006). Relatedness was based on allele frequencies derived from a larger population of 38 adult multilocus genotypes (Baden 2011). Mothers were generally considered close relatives if $r \geq 0.25$ (expected average dyadic relatedness of half-sibs) and likelihood ratios were significant ($p<0.05$) for half- and/or full-sib primary hypotheses. Statistical analyses compared average relatedness ($R$) among communal versus single nesters rather than dyadic scores, as fine-scale relatedness assessments, require large panels of numerous microsatellite loci (Blouin 2003; Csilléry et al. 2006; van Horn et al. 2008). Significant differences were evaluated by permutation analysis (Manly 1997; Lukas et al. 2005; Bradley et al. 2004).

Due to non-independence of dyadic data, all correlation tests described below were run using Mantel matrix and partial matrix correlation procedures. All three predictor variables ($m$, AI, $r$) were significantly correlated at $p<0.05$ ($n=21$ dyads). Therefore, partial Mantel tests were used to examine the relationships between the predictor variables and CNIs. The partial Mantel method uses a randomization approach to conduct pairwise comparisons between the elements of two distance matrices while holding a third distance matrix constant. For each dataset, all variables were transformed into $Z$ scores (Sokal and Rohlf 1995). Ten thousand randomizations were performed for each test to determine statistical significance. By using this method, the relationship between each independent variable and the predictor variable was evaluated twice, controlling for each of the two remaining variables in sequence. Alpha was set at 0.05 and adjusted using the Holm–Bonferroni method, a sequentially rejective multiple test procedure which controls for family wise error for all $k$ hypotheses at level alpha in the strong sense (Holm 1979). All tests were two tailed.

To generate standard graphical representations of association and relatedness networks (CNI, AI, $r$), matrix values were used to draw weighted association networks using NetDraw (Borgatti 2002). The definition of relative weight classes is given in the legend of Fig. 1. In these networks, colored nodes, representing individuals, were arranged according to spatial proximity ($m$) within the communal range. Wedges (or lines between nodes) represent relative association indices and/or estimates of pairwise relatedness and the weight of each line corresponds to the relative value of CNI, AI, or $r$.

### Activity budget, diet, and infant survival

To evaluate the possible benefits related to communal nesting, we compared activity budgets and infant survival across mothers. First, to test whether infant care imposed significant constraints on female behavior, we compared female activity budgets pre- and post-birth. Because females were their infants' sole care providers in the first month post-parturition, the months prior to and following birth were analyzed ($n=8$ weeks; 970 observation hours). Because variation in diet (i.e., food quality) can impact individual feeding time (e.g., Watts 1988; Harris et al. 2010), we also compared the proportion of ripe fruit included in the diet pre- and post-birth to ensure that changes in feeding time were unrelated to changes in dietary composition. To evaluate how maternal nesting strategy relates specifically to maternal energy intake, we then compared the proportion of time single versus communal nesters spent feeding during the period of communal nest use. We also investigated whether communal nesting was related to tradeoffs in infant care and feeding. Using weekly activity budgets derived from 5-min instantaneous scans, we ran bivariate correlations comparing communal nesting time with both female feeding time and the time a mother spent caring for infants at the nest. Finally, we pooled females into single versus communal nester categories and compared infant survival. In all cases, comparisons were made using nonparametric statistics. Because we made a priori predictions regarding the effects of infant care strategies on maternal activity budget and diet, as well as infant survival, we used directed tests (Rice and Gaines 1994) to assess these relationships. $P$ values are then indicated by $P_{\mathrm{dir}}$. In cases where directed tests were used, we allocated 0.04 of the overall alpha to a predicted tail and 0.01 to the tail contrary to prediction.

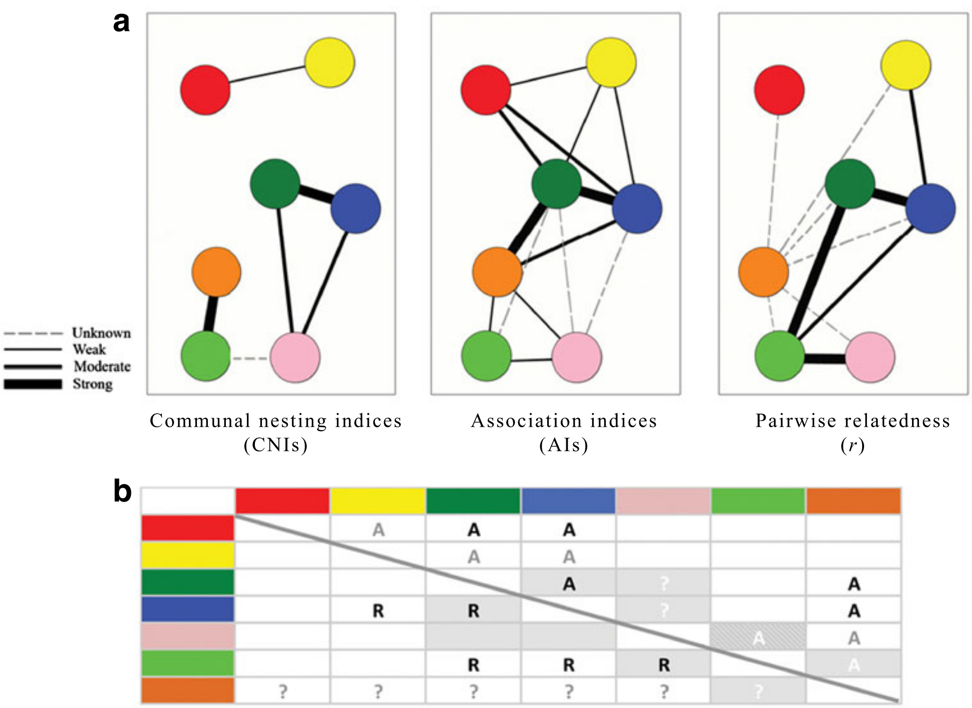
## Results

### Litter size and nesting strategy

Females reproduced only once 2008 during six consecutive years of observation. Throughout gestation, females were observed constructing an average of 7.8 nests ($n=5$; range, 3–15). Females constructed nests only within their own ranges and were the sole nest constructors (they were never observed participating in communal or coordinated nest construction nor were non-mothers observed to construct nests). Prior to parturition, nest construction ceased.

Births were highly synchronized over a 2-week period (Table 1; Baden 2011). Seven of eight females reproduced, each bearing litters of two or three altricial offspring (mean=2.7±0.45 SD, $n=7$ litters). This synchronous breeding, combined with a long and unpredictable interbirth interval, makes quantitative studies of reproductive behavior and breeding success in this species challenging. Our dataset of seven litters, though a relatively small sample, nonetheless represents reproductive output over 48 lemur-years.

Females selected among their previously constructed nests (3–15 nests, see above) to give birth, referred to here as their "natal nest." Females kept litters exclusively within their natal nests for an average of 13.8 days ($n=5$; range, 3–22 days; Table 1) and were the sole care providers during this time.



Communal nesting indices (CNIs)

Association indices (AIs)

Pairwise relatedness ($r$)

**Fig. 1** **a** Diagrams illustrating female communal nesting associations (communal nesting indices or CNI), social associations (association indices or AI), and pairwise relatedness ($r$). *Colored nodes* represent females and are arranged according to spatial location, i.e., individual home range centroids within the larger communal territory. *Solid lines* indicate dyadic relationships. *Dashed gray lines* indicate unresolved relationships/missing data. *Line weight* indicates the strength of relationships. In all cases, indices range from 0 to 1 (*0* indicates no relationship; *1* indicates 100 % association). For CNI and AI networks, a *heavy line weight* indicates that an index falls above the mean (calculated across females; CNI: mean=0.02, range=0–0.27; AI mean=0.04, range=0–0.09); *medium weight* indicates an index at or near the mean; *light weight* indicates an index below the mean. For pairwise relatedness, *heavy line weight* indicates pairwise relatedness of $r \geq 0.5$; *medium weight* indicates $r$ of 0.25 to 0.49. Dyads exhibiting $r \leq 0.25$ are considered unrelated. **b** Matrix indicating dyadic patterns of CNI, AI, and $r$. *Colors* correspond to female identities, as illustrated in Fig. 1a. *Gray shaded cells* represent communally nesting pairs. *Gray hashed cells* indicate communally nesting dyads that were regularly observed, but were not quantified. *A* (*black*, *top matrix*) denotes strong or moderate social associations. *A* (*gray*, *top matrix*) denotes weak social associations. *R* (*bottom matrix*) denotes related dyads ($r \geq 0.25$). *Question mark* denotes an unknown/unquantified relationship

Initial transfers from natal nests occurred at approximately 3 weeks of infant age. Nest transfers were, at first, infrequent (daily nest transfers between 0 and 3 weeks infant age: mean=0.6; range, 0–3; $n=5$), though transfers increased significantly through time (Spearman's rank test $r_s=0.909$, $P_{\mathrm{dir}}=0.001$). On average, females used 2.8 confirmed nests ($n=5$; range, 2–4) and 36.4 unconfirmed nests/parking locations ($n=5$; range, 24–47) during the infant parking period, of which a mean of 11.4 locations was used communally ($n=5$; range, 0–21). Nesting and parking locations were reused and were used in both single and communal nesting contexts. Communal nests typically comprised two litters. One communal nest was used regularly by four different females, though only two litters were ever observed together in the nest at one time. Only once were three litters observed together in a communal nest.

The extent of communal nesting varied among mothers (Table 1), as did their patterns of communal nesting associations (Fig. 1). Six of the seven reproductive females were observed to crèche offspring at least once. Of these, three females regularly crèched their litters (mean=18.9 %±3.32 SD; Table 1), whereas two females rarely or never communally nested (mean=0.2 %±0.14 SD; Table 1). Two females (Pink-Yellow and Yellow-Green) were not the subjects of focal sampling (see "Methods" section), but were frequently observed in co-nesting associations with focal mothers. Whether females communally nested their offspring was unrelated to when infants were born or their time in the natal nest (Table 1).

## Factors related to choice of communal nesting partners

Variance in litter size ($n_i$) was small ($\sigma=0.085$; range, 2–3 infants/litter) and was unrelated to whether females were single or communal nesters. Spatial association ($m$) was also unrelated to patterns of communal nesting among females (partial Mantel test: $r_{(\mathrm{CNI}-m)r}=-0.053$, $p=0.66$; $r_{(\mathrm{CNI}-m)\mathrm{AI}}=-0.103$, $p=0.77$). In contrast, both kinship ($r$) and long-term social relationships (AI) showed clear associations with crèching behavior: communal nesters (CN) shared significantly higher average pairwise relatedness ($R$) than the mean relatedness found among female–female dyads overall (mean $R_{\mathrm{CN}}=0.28\pm0.09$ SEM versus mean $R_{\mathrm{overall}}=0.13\pm0.02$ SEM, $p<0.001$), and both pairwise relatedness (partial Mantel test: $r_{(\mathrm{CNI}-r)\mathrm{m}}=0.692$, $p<0.001$; $r_{(\mathrm{CNI}-r)\mathrm{AI}}=0.409$, $p=0.010$) and association indices (partial Mantel test: $r_{(\mathrm{CNI-AI})m}=0.704$, $p<0.001$; $r_{(\mathrm{CNI-AI})r}=0.432$, $p=0.004$) were significantly positively correlated with the occurrence and frequency of communal nest use (Fig. 1a).

However, not all cooperative dyads were related and not all related dyads cooperated (Fig. 1b). Some females (Blue, Yellow-Green) crèched only with relatives, while others (Green, Pink-Yellow) crèched infants with both kin and non-kin (Fig. 1). Moreover, not all related dyads cooperated, and at least one single nester had a relative in close proximity, indicating that patterns of communal nesting are not strictly dependent on the availability of related co-nesters (Fig. 1b).

## Activity budget, diet, and infant survival

Females provided exclusive infant care until communal nesting commenced approximately 6 weeks post-parturition (mean=41 days post-parturition, $n=4$). In the time before communal nesting began, maternal activity budgets departed significantly from pre-parturition values (Friedman's two-way ANOVA by rank, $\chi^2=24.646$, $p=0.001$) and there was a trend toward decreased feeding time (Wilcoxon signed ranks, $Z=-2.023$, $P_{\mathrm{dir}}=0.054$, Fig. 2), a change that was not significantly correlated with changes in dietary composition (Spearman's rank test $r_s=0.1$, $p=0.87$). Feeding time did not differ among mothers as a function of litter size (Mann–Whitney $U=51.1$, $n_1=2$, $n_2=5$, $Z=-0.04$, $p=0.97$; Fig. 3); thus, females were equally burdened with infant care during this earliest period of infant development. With the onset of communal nesting, female activity budgets diverged again: communally nesting females spent less time at their nests (Mann–Whitney $U=61$, $n_1=2$, $n_2=5$, $Z=2.539$, $P_{\mathrm{dir}}=0.013$) and significantly more time feeding (Mann–Whitney $U=56$, $n_1=2$, $n_2=5$, $Z=2.049$, $P_{\mathrm{dir}}=0.050$) than did single nesting females (Fig. 3). Moreover, as crèche use increased among communal nesters, mothers spent increasingly less time at their nests (Spearman's rank test $r_s=-0.572$, $P_{\mathrm{dir}}=0.050$) and more time feeding and foraging (Spearman's rank test $r_s=0.792$, $P_{\mathrm{dir}}=0.004$).

Overall, infant survival was moderate (mean=79 %; Table 1). In the first 6 weeks post-parturition (i.e., exclusive maternal infant care), infant survival was high ($n=19$, 100 % survival). However, upon the onset of communal nest use, infant survival decreased. Infants belonging to single nesters suffered significantly greater mortality (mean=60 %, three of five infants, $n=2$ mothers) than infants belonging to communal nesters (mean=7 %; 1 of 14 infants, $n=5$ mothers; Mann–Whitney $U=0$, $n_1=2$, $n_2=5$, $Z=-2.137$, $P_{\mathrm{dir}}=0.041$, Fig. 4). There was also a significant positive relationship between the

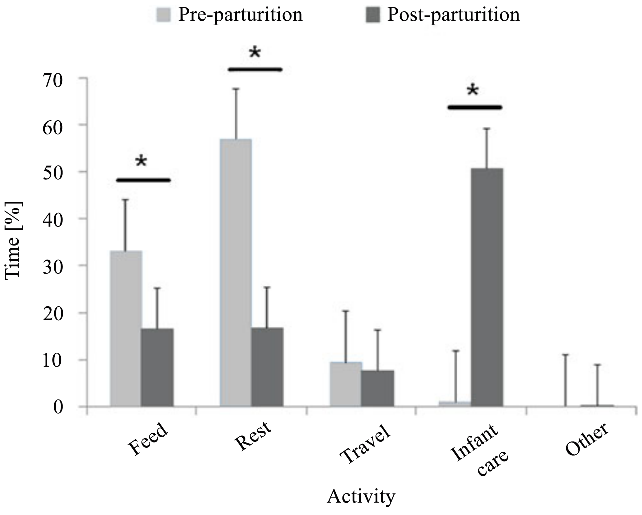


**Fig. 2** A comparison of maternal activity budgets pre- and post-parturition. Female activity budgets post-parturition differed significantly from pre-parturition patterns (Friedman's two-way ANOVA by rank, $\chi^2=24.646$, $p<0.001$). There was a trend toward decreased feeding and resting time (Wilcoxon signed ranks, $Z=-2.023$, $P_{\mathrm{dir}}=0.054$) and increased infant care (Wilcoxon signed ranks, $Z=2.023$, $P_{\mathrm{dir}}=0.054$). Travel and other/social did not differ. *$p=0.05$. *Error bars* calculated as standard error. See the "Methods" for more details on these comparisons

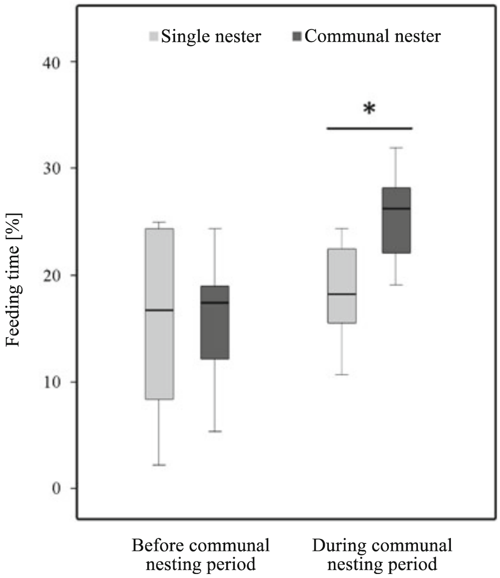


**Fig. 3** Average proportion of time females spent feeding prior to and during communal nesting. Prior to the onset of communal nest use, females did not differ significantly in their percentage of time spent feeding (Mann–Whitney $U=51.10$, $Z=-0.04$, $p=0.971$). However, during the communal nesting period, communal nesters (*dark boxes*) spent a significantly greater percentage of their time feeding than did single nesters (Mann–Whitney $U=56$, $Z=-2.049$, $P_{\mathrm{dir}}=0.050$). *Error bars* calculated as 95 % CIs

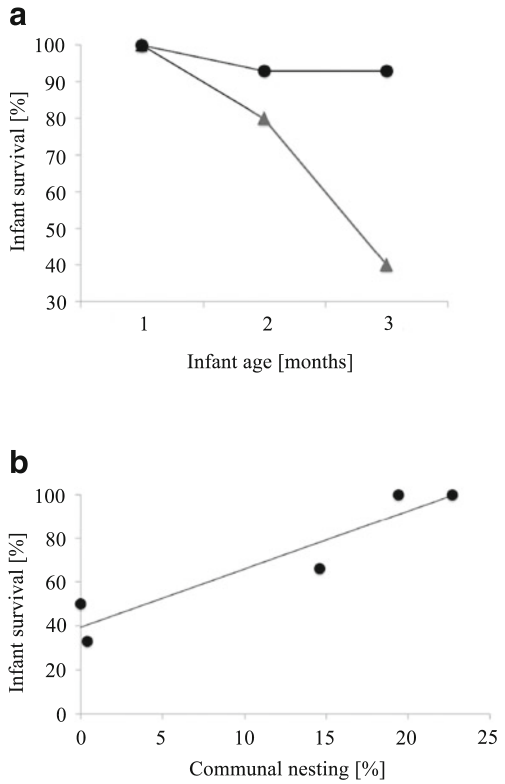


**Fig. 4** Nesting strategy and infant survival. **a** Infants belonging to communal nesters [*black circle*] experienced significantly higher survival than did those belonging to single nesters [*gray up-pointing triangle*] (Mann–Whitney $U$=0.00, $Z$=−2.137, $P_{\mathrm{dir}}$=0.041). **b** Infant survival is positively correlated with the intensity of communal nesting (Spearman's rank test $r_s$=0.872, $P_{\mathrm{dir}}$=0.033)

overall proportion of communal nest use and infant survival (Spearman's rank test $r_s$=0.872, $P_{\mathrm{dir}}$=0.033, Fig. 4), suggesting that the intensity of communal care might also contribute to a female's reproductive success. Notably, infant survival for communally nesting females who nested infants with unrelated mothers was equal to that of females who nested infants only with kin (Table 1).

## Discussion

Despite long-standing assumptions regarding the benefits of communal breeding (Gittleman 1985), few studies have compared maternal success of participants and nonparticipants in wild populations (reviewed in König 1997; Cockburn 1998). If our results are indicative of general patterns, this species demonstrates a remarkable and effective system of communal breeding in which (a) reproductive events are rare and synchronous; (b) cooperation appears facultative and is common among but not exclusive to kin; and (c) those females who participate gain fitness benefits in terms of maternal energetics and offspring survival.

Because of the rarity of reproductive events in ruffed lemurs, our sample size is necessarily small and our results should be viewed with that in mind. Our observations may simply reflect individual variation (e.g., in behavioral style or personal history) rather than a causal relationship between nesting cooperation and maternal success. Nonetheless, the difference in maternal success between females that cooperated (13/14 infants survive) and those that did not (2/5 survive) is striking. Even with our limited sample, this study represents a rare case in which the observed fitness differences (i.e., infant survival) between cooperative and non-cooperative individuals are notable. This suggests that shared care confers benefits that directly affect reproductive success (Gittleman 1985; Mitani and Watts 1997; Ross and MacLarnon 2000).

We found a positive association between the time a mother communally nested her offspring and the time she spent away from her nest feeding and foraging, a tradeoff that might ultimately translate into improved maternal energetics. These results are consistent with previous studies demonstrating that helpers relieve mothers from the burdens of infant care (Gittleman 1985; Mitani and Watts 1997; Creel and Creel 1991; but see Ebensperger et al. 2007) by allowing them to feed longer or at faster rates than when they are the sole care providers (e.g., Stanford 1992), thereby conferring energetic benefits that can directly affect their reproductive success (e.g., Ross and MacLarnon 2000; Lemon and Barth 1992; Fairbanks and McGuire 1995; Lewis and Kappeler 2005; Mann and Watson-Capps 2005). While previous reports suggest that allomaternal nursing also occurs in ruffed lemurs (Morland 1990; Vasey 2007; Pereira et al. 1987), given the height and structure of nests used by mothers during this study, allosuckling could not be confirmed. Future research might consider the use of high-tech camera systems (Eberle and Kappeler 2006) to assess whether and to what extent allomaternal suckling also acts to alleviate the energetic burden shared by communally nesting females. In any case, our observations suggest that communal breeding in ruffed lemurs is a strategy to help offset the comparatively high energetic costs of suckling litters (e.g., König et al. 1988; Prentice and Prentice 1988).

Given the benefits seemingly associated with communal nest use in ruffed lemurs, this leads to the question of why all females do not participate. Although our sample size is small, we recognize some potentially important trends. Communal nesting was unrelated to litter size and there were no obvious differences between nests that were used during single versus communal nesting (i.e., no indication that single nests were too small for multiple litters). Moreover, there was no evidence of active exclusion from communal nests. That is female nesting strategies appeared unrelated to dominance or female–female competition over access to resources. Individual variation in behavioral style or in long-term social relationships might contribute to differences in nesting behavior. Trying to disentangle reasons why female nesting strategies vary is part of our ongoing study of this population.

Further analyses aimed at understanding why females select particular nesting locations may help to uncover additional mechanisms driving the patterns observed here. Some nests might have been jointly used because of their proximity to high-quality resources or because of particular characteristics of the nest sites themselves—that is, perhaps females prefer the nests, not necessarily their communal nesting partners. Future work should also consider the role of ecological factors such as habitat complexity and topography as these are known to influence nest selection in other taxa (e.g., flying squirrels: Patterson 2012; falcons: Kassara et al. 2012; black-legged kittiwake: Bled et al. 2011).

Our results have potential implications for understanding the evolution of communal breeding, particularly if the patterns of individual participation documented here are confirmed with subsequent observations. We found a positive correlation between relatedness, proximity, and association, suggesting that female philopatry might give rise to networks of closely related, potentially cooperating females, as in other cooperative breeders (Painter et al. 2000; Kappeler et al. 2002; Scelza and Bird 2008). Yet, not all cooperative dyads were related and not all related dyads cooperated, as observed in humans (e.g., Ivey 2000) and callitrichines (e.g., Huck et al. 2004), but unlike cheirogaleids (e.g., Eberle and Kappeler 2006). Kinship may have facilitated the evolution of cooperative breeding in primates, but the mutual benefits may outweigh the costs of helping, irrespective of kinship. Our results contribute to a growing body of evidence suggesting that kin selection alone cannot explain the extensive cooperation observed in many animal taxa (Langergraber et al. 2007; Clutton-Brock 2009; Silk 2009; Riehl 2010; Lukas and Clutton-Brock 2012).

### Ruffed lemur communal breeding: adaptations to an island environment?

Several lemur traits are thought to have evolved as a means of coping with Madagascar's often harsh and unpredictable climate (Wright 1999; Dewar and Richard 2007). This includes both a "slowing down" (e.g., *Propithecus verreauxi*: Richard et al. 2002; *Lemur catta*: Gould et al. 2003) and a "speeding up" (e.g., *Cheirogaleus* spp.: Lahann and Dausmann 2011) of lemur life histories. Here, we consider still a third possible strategy for coping with Madagascar's unusual island environment. Ruffed lemurs, among the most frugivorous of the extant lemurids (Morland 1991; Balko 1998; Ratsimbazafy 2002; Britt 2000), appear to have combined both fast and slow life history traits to cope with resource unpredictability, creating a seemingly unique suite of reproductive characteristics among lemurs. For example, ruffed lemurs resemble cheirogaleids in that they reach reproductive maturity early (18–21 months, Boskoff 1977a; Foerg 1982) and upon doing so reproduce quickly. Ruffed lemurs have the shortest gestation lengths (Boskoff 1977b; Bogart et al. 1977a; Foerg 1982; Shideler and Lindburg 1982; Rasmussen 1985; Brockman et al. 1987), largest mean litter sizes (Rasmussen 1985), and richest milk (Tilden and Oftedal 1997) of any lemurid, making ruffed lemur pre- and postnatal investment an extreme, even among primates (Young et al. 1990; Tilden 1993). In contrast, they resemble the "slower" larger bodied indriids in that females reproduce until late ages (i.e., no obvious reproductive cessation, Wright et al. 2008) and have longer adult life expectancies than mammals of similar size, at least in captivity (Rowe 2012). In addition, females have the potential for "boom-bust" reproduction, bearing litters of young only during periods of resource abundance (Ratsimbazafy 2002).

In this study, females reproduced once in 6 years. Communal nesters experienced relatively higher infant survival than non-communal nesters, suggesting that cooperative infant care combined with boom-bust reproduction in ruffed lemurs allows females to "make up for lost time" by bearing litters even after several non-reproductive years. Our observations are in contrast to previous studies, where ruffed lemur females reproduced every 1 to 2 years (Table 2). These disparities across years may well be linked to environmental stochasticity and variation in resource availability, much like

**Table 2** Variation in ruffed lemur interbirth intervals across sites and study periods

| Species | Site | Observed births | IBI | Average litter size (*n*) | Study period | Reference |
|---|---|---|---|---|---|---|
| *V. rubra* | Masoala | 1993, 1994 | 1 | 2.1 (9) | 1993–1994 | Vasey (2007) |
| *V. variegata* | Nosy Mangabe | 1987, 1988 | 1[a] | 1.7 (7) | 1987–1988 | Morland (1991) |
| | Ranomafana National Park | | | | | |
| | Vatoharanana | 1993 | 2 | 2.0 (1) | 1992–1994 | Balko (1998) |
| | Valohoaka | 1993 | 2 | 2.5 (2) | 1992–1994 | Balko (1998) |
| | Mangevo | 2008 | ±3 | 2.7 (7) | 2005–2010 | Baden, this study |
| | Manombo | 2001 | 4 | 2.0 (1) | 1997–2001 | Ratsimbazafy (2002) |

[a] Not all females reproduced in consecutive years

*IBI* interbirth interval

those observed in cooperatively breeding birds (Jetz and Rubenstein 2011; Cockburn and Russel 2011). Though such a connection has yet to be empirically demonstrated in ruffed lemurs, recent studies have found significant associations between lemur reproduction and both cyclone landfall and climatic variability (Dunham et al. 2010).

Thus, obligate frugivory and environmental unpredictability might have driven this species toward an unusual solution, involving an extension of reproductive lifespan (a combination of speeding up age at first reproduction and delaying age at last reproduction), an increase in litter size, and facultative communal infant care to compensate for potential lags in reproduction during an individual's reproductive lifespan. Testing this scenario, however, awaits longitudinal studies.

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**Conflict of interest** The authors declare that they have no conflict of interest.

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