Reciprocity and rotating social advantage among females in egalitarian primate societies

Kaia J. Tombak [a, *], Eva C. Wikberg [b], Daniel I. Rubenstein [a], Colin A. Chapman [c, d, e, f]

[a] Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, U.S.A.
[b] Department of Anthropology, University of Texas, San Antonio, TX, U.S.A.
[c] Department of Anthropology, Center for the Advanced Study of Human Paleobiology, The George Washington University, Washington, DC, U.S.A.
[d] Department of Anthropology, McGill University, Montreal, QC, Canada
[e] School of Life Sciences, University of KwaZulu-Natal, Scottsville, Pietermaritzburg, South Africa
[f] Shaanxi Key Laboratory for Animal Conservation, Northwest University, Xi'an, China

ARTICLE INFO

Interfemale competition regimes in primate societies have been described as despotic or egalitarian based on female social behaviour. Hierarchies and nepotism are typical of despotic primates, where dominance rank and kinship are known to be strong drivers of who grooms whom and who fights with whom. However, a general theory for what structures female—female interactions in egalitarian societies remains underdeveloped. We present two nonmutually exclusive hypotheses that each propose a mechanism for levelling social advantages in a group by conferring social favour to all or most females over time: transitory states (age, residency status and reproductive state) bias social interactions and/or reciprocity governs social interactions. In this study, we (1) determined that a group of red colobus monkeys, *Procolobus rufomitratus tephrosceles*, in Kibale National Park, Uganda, are highly egalitarian; (2) tested our hypotheses for how egalitarianism may be maintained in this group; and (3) analysed findings across primate studies for support for either hypothesis. In red colobus, agonistic interactions were predicted by age — a transitory state — and transitory states and reciprocity predicted grooming interactions: avid groomers, older females and short-term resident females received more grooming. In addition, behavioural indicators of social status (aggression given and grooming received) were not associated with reproductive success in red colobus, as might be expected in an egalitarian group where variance in fitness should be low. Across primates, we found that transitory states commonly structure social interactions in egalitarian societies but not in despotic societies and that reciprocity is highly variable, especially among egalitarian societies. Rotating social advantage as females shift among transitory states and/or reciprocate grooming may lower interfemale skew in social benefits and potentially in lifetime reproductive success in egalitarian groups, setting them apart from despotic societies where dominance hierarchies and kinship maintain a more static and unequal distribution of social advantage.
© 2019 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

An egalitarian society is defined by Vehrencamp (1983) as one where benefits are evenly distributed or received in proportion to effort or risk taken. In contrast, a despotic society is one where the distribution of benefits is biased in favour of dominants. These 'benefits' are frequently taken to mean some measure of reproductive success. Among mammals, competition for mates and reproductive skew is typically high in males, putting them at the despotic end of the spectrum, while skew in female reproductive

success is more dependent on socioecological circumstances and more variable between species (Emlen & Oring, 1977).

Lifetime reproductive success is difficult to measure in animals with slow life histories like primates, and researchers have instead used female behaviour to describe primate societies as egalitarian or despotic. The same terms are occasionally used to describe male relationships as well (Pandit & van Schaik, 2003; van Schaik, Pandit, & Vogel, 2006) but here we use 'egalitarian' and 'despotic' in reference to female—female social relationships. Researchers have determined which competitive regime is at work in a particular primate population based on whether females form coalitions, express nepotism, have formal submission signals, exhibit linear hierarchies and tend to be philopatric, each of which is a trait linked

* Correspondence: Kaia J. Tombak, Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, U.S.A.
E-mail address: ktombak@princeton.edu (K. J. Tombak).

to despotism (Sterck, Watts, & van Schaik, 1997; reviewed in Koenig, 2002). Socioecological models posit that the competitive regime expressed by a population arises from the degree and type of resource competition within and between conspecific groups (Isbell, 1991; Janson & van Schaik, 1988; Koenig & Borries, 2006; Snaith & Chapman, 2007; Sterck et al., 1997; van Schaik, 1989; Wrangham, 1980). Despotic societies should generally form when resources are limited and monopolizable by dominants, while primates in egalitarian societies should feed on relatively abundant and evenly distributed resources (Janson & van Schaik, 1988; Lomnicki, 1988; Nicholson, 1954; Vehrencamp, 1983). An egalitarian competition regime should therefore be associated with less skew in resource acquisition between females, presumably reducing skew in their reproductive success.

A wealth of research on primate behaviour, particularly in despotic societies, has added complexity to the socioecological models. Sterck et al. (1997) suggested that primate societies vary along three axes: one between despotism and egalitarianism, another between individualism and nepotism (where kinship structures social interactions) and a third comprising degree of tolerance (indicated by metrics such as aggression intensity). However, as the authors pointed out, these three dimensions must covary because higher skew in female reproductive success (associated with greater despotism) encourages increasing fitness indirectly through nepotism and should also increase aggression intensity as females fight for higher stakes. Accordingly, in despotic and nepotistic societies where females rank close to maternal kin, kinship and dominance ranks typically structure within-group grooming and aggressive interactions (Seyfarth, 1976; Silk, 2002; Silk et al., 2010a; Thierry, 1990).

But what structures female social interactions in egalitarian primates? These societies are characterized by weak or undetectable dominance hierarchies and often by female dispersal, which reduces access to female kin. At the theoretical level, the reigning assumption has been that egalitarian societies are relatively unstructured, characterized by undifferentiated female relationships, individualism and tolerance (as per the three axes of social variation introduced by Sterck and colleagues; Sterck & Steenbeek, 1997; van Schaik, 1989). Empirical support for this has been found in studies capitalizing on the variation in despotism expressed in macaques and baboons. Where dominance hierarchies are weaker, aggression is of lower intensity and kinship has less influence on aggression (in terms of coalitionary support; Butovskaya, 1993) and affiliation (measured by grooming rates: Bergman & Beehner, 2003; or tendencies for postconflict reconciliation: Demaria & Thierry, 2001; Thierry, 2007).

Alternatively, rather than lacking structure, it is possible that social interactions in egalitarian societies are skewed by traits other than dominance and kinship. Intergroup variation within a population of white-thighed black-and-white colobus, Colobus vellerosus, provides some interesting clues. In groups with strongly expressed female dominance hierarchies, aggression networks were explained by dominance ranks, while in one group with a relatively weak hierarchy, maturational stage better predicted aggression (Wikberg, Ting, & Sicotte, 2014b). In groups where females had access to more than one female kin on average, grooming behaviour was structured by kinship except when the group contained recent female immigrants, in which case residency status had a stronger influence on grooming (Wikberg et al., 2014b; Wikberg, Ting, & Sicotte, 2014a). It is possible, therefore, that age and/or residency status drive social structure (sensu Crook, 1965) on the egalitarian side of the spectrum. Another possibility is that reciprocity structures egalitarian social interactions. Seyfarth

(1977) formulated a model with a focus on hierarchical societies, but its prediction of closer grooming reciprocity between female dyads of similar rank suggests that high grooming reciprocity may be prevalent in the absence of rank differences. Furthermore, biological markets theory views grooming as a commodity to be traded and predicts close matching in grooming effort between partners in an egalitarian setting (Barrett, Henzi, Weingrill, Lycett, & Hill, 1999; Barrett, Henzi, Weingrill, Lycett, & Hill, 2000; Barrett, Gaynor, Henzi, 2002; Noë & Hammerstein, 1995).

A theory for what should structure egalitarian societies has yet to be fully developed. Here we present two hypotheses to counter the null hypothesis that aggression and grooming interactions in egalitarian societies are relatively unstructured. Our first hypothesis posits that regularly shifting phenotypic and social states, such as age, residency status or reproductive state (hereafter 'transitory states'), structure social interactions. The white-thighed colobus studies point to age or residency status as candidate predictors, and reproductive state has been associated with grooming rates in many primates (Frank & Silk, 2009; Gumert, 2007; Henzi & Barrett, 2002; Muroyama, 1994; Seyfarth, 1976; Tiddi, Aureli, & Schino, 2010; Wei et al., 2013). If this hypothesis holds, there is opportunity for social advantage to rotate among females as they shift and cycle through transitory states. Our second hypothesis is that reciprocal relationships structure egalitarian societies. Reciprocity should even out social advantage within a group unless there are substantial differences between females in tendency to interact. Each hypothesis presents a mechanism by which bias in social advantage is reduced, potentially lowering skew in reproductive success (affiliative social bonds, and sometimes domination in agonistic interactions, have been linked to reproductive success in primate females; Fedigan, 1983; Janson, 1985; Pusey, Williams, & Goodall, 1997; Silk, 2007; Silk, Alberts, & Altmann, 2003; Silk et al., 2009, 2010b; but see Cheney, Seyfarth, & Fischer, 2006).

In this study, we focused on a population of red colobus, Procolobus rufomitratus tephrosceles, in Kibale National Park, Uganda, which is thought to be egalitarian based on female-biased dispersal patterns, low female aggression rates (Struhsaker, 1975, 2010) and low potential for contest competition for food (they feed on abundant, aseasonal and evenly distributed foods; Chapman & Chapman, 1999; Chapman, Chapman, Bjorndal, & Onderdonk, 2002). We had three principal objectives. (1) We investigated the strength of the red colobus female dominance hierarchy, the frequency of female coalitions and the frequency of formal submissive signals to verify that they are representative of an egalitarian society. Genetic data were not available for us to evaluate the degree of nepotism or estimate the degree of female philopatry. We predicted that they would be highly egalitarian, exhibiting a very weak or undetectable hierarchy and forming coalitions or using formal submission signals only rarely. (2) We tested the transitory states hypothesis and the reciprocity hypothesis on red colobus females by (a) determining whether the amount of aggression given or the amount of grooming received by a female (behavioural indicators of social status) were explained by dyadic reciprocity and/or by transitory states. We also accounted for the possibility that reciprocity can take the form of exchange across currencies, namely trading grooming for access to infants (Henzi & Barrett, 2002; Muroyama, 1994). We then (b) analysed the relative influence of these social status indicators (aggression given, grooming received) and transitory states (age, residency status) on female reproductive success. (3) Our final objective was to evaluate the generality of our findings through a comparison of the traits that bias grooming and aggression in egalitarian and despotic primates.

METHODS

Field Data Collection

We conducted a year-long intensive study on red colobus in Kibale National Park, near the foothills of the Ruwenzori Mountains, Uganda (795 km^2, 0°13′–0°41′N, 30°19′–30°32′E) (Chapman et al., 2017; Struhsaker, 1975). The group ranged in the moist, evergreen, mid-altitude (1500 m above sea level) forest of the Kanyawara area, near Makerere University Biological Field Station. Rainfall varies bimodally throughout the year, with an average of 1676 mm of total annual rainfall (1990–2016; Chapman & Chapman, n.d.).

We studied a large, multimale–multifemale group of habituated red colobus ('SC' group) for 13 months (June 2009 – June 2010). The group was followed from approximately 0800 hours–1600 hours, 20 days/month. Fifteen-minute focal observations of agonistic and affiliative interactions with other group members were conducted opportunistically on each of the 39 adult females. Ad libitum notes on these kinds of interactions were recorded to supplement the focal data. Aggressive (chases, physical assaults, shaking branches threateningly), submissive (the 'present type I', 'rapid glance' and 'gape' described by Struhsaker, 1975) and grooming interactions were recorded. A total of 588 focal observation hours (mean ± SD = 15.08 ± 4.99 per female) and 1920 contact hours were collected. One female red colobus was not observed to interact with any other female and was excluded from analyses. Long-term demographic data were used to calculate birth rates and infant survivorship from 2006, when all group members were first individually identified, through January 2011.

All fieldwork was strictly observational and the monkeys spent the vast majority of the time in trees, although in the event that they came to the ground, they were given a wide berth to avoid disturbing their activities. No signs of distress or disturbance was noticeable from the monkeys during observation periods. Our study procedures were approved by McGill University's Animal Care Committee (MUACC No. 5041).

Assigning Age, Reproductive State and Residency Status

At the beginning of this study, ages were estimated to the nearest year based on an individual's known history and external appearance by experienced researchers and field assistants. Their independent estimations were then averaged for each monkey and, to reduce error, females were placed into two broad age categories: young (<10 years old) and old (≥10 years). Of the 39 adult female red colobus, 26 were old, 12 were young and one could not be confidently aged.

Female reproductive state was divided into three categories: without dependent offspring; carrying an infant less than 3 months old; and accompanied by a juvenile 3–6 months old. Female primates with infants may be more aggressive and can receive extra attention, including grooming, from other females (Frank & Silk, 2009; Gumert, 2007; Henzi & Barrett, 2002; Muroyama, 1994; Seyfarth, 1976, 1980; Tiddi et al., 2010; Wei et al., 2013), prompting us to distinguish between females with infants with neonatal coloration (<3 months) and those with older dependent juveniles.

Precise residency status was available for only five females because all others had already immigrated by 2006, when group members were individually identifiable. We therefore used a binary variable with 'short-term residents' comprising all known immigrants since 2006 and 'long-term residents' comprising the rest (4+ years of residency). Females typically disperse from their natal group as adolescents at around 2–3 years of age, but as is the case in several colobines, they have been known to undergo additional group transfers in adulthood (Struhsaker, 2010). Age is therefore not necessarily correlated with residency status and may have independent effects on social interactions, but in our data set they were associated with each other (Wilcoxon two-sample test: $W = 44.5$, $N = 38$, $P < 0.001$): all old females were long-term residents. Most young females were also long-term residents, but of the five short-term residents, four were young and one could not be aged. This potential confound was taken into account in the analyses (see The Transitory States and Reciprocity Hypotheses below).

Calculating Reproductive Fitness

We measured fitness as the number of surviving infants produced per year since the mother's first recorded birth, calculated from the long-term data (February 2006 – January 2011). In determining when to count an offspring as having 'survived', we followed Struhsaker and Pope (1991), considering an offspring large enough to survive on its own at 34 months for females and 38 months for males. We chose the higher age limit as the cutoff for infants without available sex data (49 of the 89 infants born in the group since 2006). None of the adult females included in our data set matured from a subadult (sexually inactive) to an adult (having had her first copulation or menarche) over the long-term data collection period.

Analysis

Dominance, coalitions and submission in female red colobus

We determined whether the red colobus females formed a dominance hierarchy with a significant and high linearity index (few circular triads where A dominates B, B dominates C, but C dominates A; Appleby, 1983), a high directional consistency (low rate of dominance interactions contradicting the hierarchy; van Hooff & Wensing, 1987), a short latency (number of contact hours necessary) to detect a hierarchy and a steep slope (difference in dominance between adjacent ranks), all considered indicative of a strong dominance hierarchy (Bergstrom & Fedigan, 2010; Isbell & Young, 2002; Wikberg, Teichroeb, Bădescu, & Sicotte, 2013). We lacked the long-term data necessary to assess hierarchical stability (permanent changes in dominance rank over time). The Zumpe and Michael (1986) method was used to rank the red colobus females into a hierarchy because aggressive interactions were rare and this method is suitable for sparse data sets (Bayly, Evans, & Taylor, 2006; Zumpe & Michael, 1986). The method calculates, within each dyad, the percentage of aggression given and submission received by each member and computes the mean of these two values for each member. An individual's overall rank is the average of its dyadic ranks (Zumpe & Michael, 1986).

We used MatMan v.1.1 (de Vries, 1993, 1995) to calculate the statistical significance of the linearity, the Landau's modified linearity index h' and the directional consistency index (DCI) of the hierarchy. To calculate hierarchical steepness based on dyadic proportion of wins, we used the R package 'steepness' (Leiva & de Vries, 2014). We tallied all occurrences of coalition formation and formal submission signals in interfemale interactions observed during focal and ad libitum data collection.

The transitory states and reciprocity hypotheses

We built generalized linear mixed models (GLMMs) with the R package 'lme4' (Bates, Maechler, Bolker, & Walker, 2015), following the principles of the information-theoretic Akaike information criterion method (IT-AIC, Burnham & Anderson, 2002). In contrast to a null hypothesis testing approach, which produces a dichotomous conclusion on the basis of failing or succeeding to reject the null hypothesis, the IT-AIC method emphasizes strength of evidence for

each of multiple alternative hypotheses (Garamszegi, 2011). Techniques for implementing IT-AIC analyses include considering all model variants of the global model (which contains all predictors of interest that make biological sense to include) that lie within a certain range of AIC (or some other information criterion) scores from the lowest-AIC model. Models that do not fit the data, that do not make sense in the study system or that are more complex than any lower-AIC model can be pruned from the candidate model set (Grueber, Nakagawa, Laws, & Jamieson, 2011; Richards, Whittingham, & Stephens, 2011). Inference is then based on the remaining models, with the option of weighting models in the candidate set by their delta AIC (dAIC) values, evidence ratios, Akaike weights or model likelihoods, and using model averaging to generate estimates and errors for each parameter (Burnham & Anderson, 2002; Burnham, Anderson, & Huyvaert, 2011; Garamszegi, 2011; Symonds & Moussalli, 2010; but see Richards et al., 2011, where weighting models within the candidate set is not recommended).

For this study, two model sets were run, one for predicting the total number of aggressive actions that individual A directed at individual B ($Aggs_{AB}$) and the other for predicting the square root-transformed total number of times individual A groomed individual B ($sqrtGrooms_{AB}$; note that this is the amount of grooming received, which was the variable of interest, from individual B's perspective). We started with a global GLMM model for each, including only variables that pertained to the predictions from the reciprocity hypothesis and the transitory states hypothesis, comprising the following fixed effects: total number of aggressive acts or grooms observed in the other direction ($Aggs_{BA}$ or $sqrtGrooms_{BA}$) as a test for reciprocity, following Gomes, Mundry, and Boesch (2009), as well as the age and residency status of each interactant (Age_A, Age_B, $Res.Status_A$, $Res.Status_B$), and the number of months that each individual spent carrying an infant ($monthsI_A$, $monthsI_B$) to test for the effect of transitory states. We could not include all three measures of reproductive state (number of months carrying an infant, accompanied by a juvenile and unaccompanied by dependent offspring) because they were highly collinear. For example, if a female spent many months without a dependent offspring, she would by definition spend fewer months carrying an infant or being accompanied by a juvenile. To avoid feeding the models redundant information, only one reproductive measure was included and we chose the number of months spent carrying an infant because we had reason to believe a priori that mothers with infants would be more likely to be protective and aggressive towards other females and to be attractive groomees (if grooming is traded for access to infants). For the grooming model, we additionally included an interaction between $sqrtGrooms_{BA}$ and $monthsI_B$ as an evaluation of the hypothesis that grooming is traded for access to infants (which is really a special case of both the reciprocity and the transitory states hypotheses). Random intercepts for the individual identities of A and B (ID_A and ID_B) were included in the models to control for individual variation in baseline tendency to interact (Grueber et al., 2011). Because of the rarity of aggression, $Aggs_{AB}$ was either 1 or 0, and a binomial model with a probit link function best fit the data. For the grooming model, we used a negative binomial error model using the 'glmer.nb' function. The global models were initially run with the number of focal minutes for each interactant as additional fixed effects, but this increased AIC or decreased model fit as most interactions were observed during ad libitum data sampling, and so these terms were excluded from the global models. Predictors were standardized to a mean of 0 and an SD of 0.5 (and binary predictors were rescaled to a mean of 0 and a range of -0.5 to 0.5) using the 'standardize' function in the 'arm' package prior to model selection (Balasubramaniam et al., 2018; Gelman & Su, 2008).

The global models were used to generate a list of possible nested models (including null models with intercept and random effects only), ranked by AIC calculated by maximum likelihood, using the 'dredge' function from the package 'MuMIn' (Bartoń, 2018). A shortlist of candidate models within a dAIC of 3 from the lowest AIC was extracted (Richards et al., 2011, recommend a delta of between 2 and 6 to ensure 95% confidence that the true model is retained). Because age and residency status were associated with each other, we followed a strategy by Freckleton (2011) of rerunning any candidate models that included either term with a combined age–residency predictor (a factor with three levels: young short-term resident, young long-term resident, old long-term resident) replacing age and residency status to see whether model AIC was improved. None of the models were improved by more than 1 AIC point, so we kept these fixed effects (age and residency status) separate in all models. All candidate models that converged were evaluated for fit by assessing the distribution of scaled residuals and testing for overdispersion and zero inflation using the 'DHARMa' R package, and testing for singularity with the 'isSingular' function from the 'lme4' package (Bates et al., 2015; Hartig, 2018). Finally, model averaging using the 'zero' method was conducted on only the candidate models that passed these tests with the 'model.avg' function in the 'MuMIn' package (Balasubramaniam et al., 2018; Burnham & Anderson, 2002; Grueber et al., 2011; Nakagawa & Freckleton, 2011).

The number of months an individual spent carrying an infant over the study period does not necessarily correspond well to the probability of carrying an infant while interacting with other females and cannot be used to estimate the effect of the other reproductive states on social interactions. For these reasons, we additionally tallied the frequencies with which aggressors/groomers and aggressees/groomees were in any of the three reproductive states (carrying an infant, accompanied by a juvenile or unaccompanied by dependent offspring). The difference in the tallied counts and their expected counts (calculated based on the number of female-months in each state over the study period) were compared visually across aggressor–aggressee and groomer–groomee reproductive state pair combinations (see Results, Fig. 1). As an additional investigation of the hypothesis that grooming is traded for access to infants, we ran a chi-square test to determine whether groomees were more or less likely than expected to be carrying an infant. Significance of the chi-square test was evaluated using 10 000 Monte Carlo simulations with the 'chisq.test' command in the base R package (R Core Team, 2018).

Fitness implications of transitory states and social interactions

We ran a linear model to predict an individual female's birth rate of surviving offspring using counts of aggression given and grooming received as predictor variables, along with age and residency status. We did not run an IT-AIC model selection process as above for this simpler model.

Given the high standard used for counting a juvenile as having survived (34–38 months), results may be biased in favour of older females because maternal inexperience and lower milk quality often hinder offspring survival for primiparous mothers (Anderson, 1986; Hinde, 2009; Robbins, Robbins, Gerald-Steklis, & Steklis, 2006). Accordingly, we ran a second linear model to predict a female's birth rate of live offspring (excluding stillbirths) over the 5-year long-term data set. Because the birth rate data were somewhat zero-inflated, we verified that using linear models did not alter our inference by running permutation tests using the 'lmp' command in the 'lmPerm' package (Wheeler & Torchiano, 2016). All models were run in R v.3.5.1 (R Core Team, 2018).

Cross-species comparison of traits that skew social interactions

We searched the primate literature for examples of where despotic factors (dominance rank and kinship) and transitory states (age and residency status) have been found to correlate with
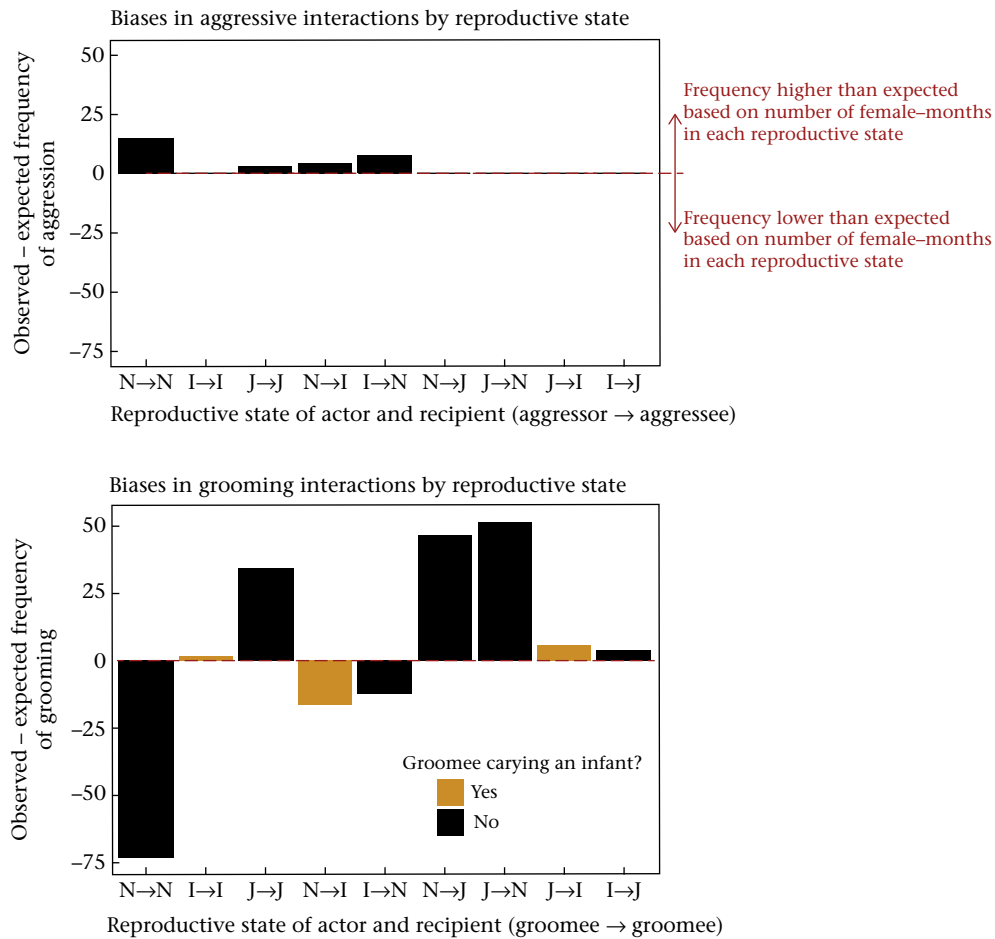
Figure 1. Differences in observed and expected frequencies of aggression and grooming between females in each reproductive state (N: not accompanied by offspring; I: carrying an infant; J: accompanied by a juvenile). Interactions relevant to the 'trading grooming for access to infants' hypothesis are shown in orange.

aggression and grooming behaviour among adult females in wild, unprovisioned primate groups. Reproductive state was not included in this broader analysis because of how commonly grooming is traded for access to infants, a commodity whose value (in grooming time) often depends on the mother's dominance status and/or kinship relations, stratifying the effect of this equalizing factor (Barrett et al., 2002; Bădescu, Sicotte, Ting, & Wikberg, 2015; Fruteau, van de Waal, van Damme, & Noë, 2011; Gumert, 2007; Henzi & Barrett, 2002; Seyfarth, 1977; Wei et al., 2013). We searched for examples from species that were classified by Sterck et al. (1997) as egalitarian (including their subcategories of 'dispersal-egalitarian', 'resident-egalitarian') or despotic ('resident-nepotistic'). Many species categorized as 'resident-nepotistic-tolerant' are considered to be more on the egalitarian end of the spectrum and were classified here as egalitarian (e.g. macaques in grades 3 and 4; Thierry, 2007). While differences between species are better explained by phylogeny than by ecological context for some taxa (Thierry, 2007), the degree of despotism or egalitarianism can also be ecologically dependent and flexible within a species (Rowell, 1967; Strier, 1994). We therefore used Sterck et al.'s (1997) classification at the species level as a guide but in a few cases we made adjustments where reports on the population in question challenged Sterck et al.'s (1997) assignment. For macaques, we generally defaulted to Thierry's (2007) grade classifications, as Sterck et al. (1997) were vague in classifying 'most' *Macaca* as resident-nepotistic. White-thighed colobus groups with strong dominance hierarchies were placed in the despotic column while

those with no detectable hierarchies were kept in the egalitarian column. Sterck et al. (1997) tentatively classified wedge-capped capuchins, *Cebus olivaceus,* as 'resident-egalitarian', but here we considered them despotic following O'Brien (1993), who described them as female-bonded with linear dominance hierarchies (see Appendix Table A3). Finally, Hanuman langurs (*Semnopithecus entellus*) were also tentatively categorized as resident-egalitarian by Sterck et al. (1997), but have been described as having despotic (albeit unstable, individualistic and age-inversed) hierarchies, so we considered them despotic for our purposes, although in reality they are most likely in an intermediate state between egalitarianism and despotism (Koenig, Borries, Caselli, & Lu, 2013).

Reciprocity was compared in a more quantitative analysis wherein the effect of competition regime category on the correlation coefficient r between grooming given and received within female dyads for 24 wild, unprovisioned primate groups was tested with a two-way t test. Twenty-two of these correlation coefficients were obtained from a review by Schino and Aureli (2008), one from another by Lukas and Clutton-Brock (2018) and one from the present study on red colobus (data in Table A3). Deviations from Sterck et al.'s (1997) classifications in the grooming reciprocity analysis included blue monkeys, *Cercopithecus mitis,* which was placed in the despotic category despite Sterck et al.'s (1997) classification of this species as resident-egalitarian because Cords (2000) found stable, linear hierarchies among females in this population. In addition, while capped langurs, *Trachypithecus pileatus,* were not classified by Sterck et al. (1997), we used the grooming reciprocity

value available for this population and classified the population as egalitarian based on the rarity of feeding contests and weakly differentiated agonistic relationships reported for the same population (Stanford, 1991). Alpha was set to 0.05 for all statistical interpretations.

RESULTS

Dominance, Coalitions and Submission in Female Red Colobus

Only 15 aggressive events between red colobus females were observed during 588 h of focal sampling, but an additional 92 events from ad libitum sampling (1920 contact hours) were observed and analysed. We observed 561 grooming interactions (269 from focal and 292 from ad libitum data) and a total of 17.6 h of grooming between females (focal data only).

No linear dominance hierarchy was detectable in the red colobus group due to a very high number of circular triads (MatMan hierarchy analysis: $P = 0.46$, Landau's $h' = 0.078$, number of circular triads = 2444.5 of a maximum of 2470, DCI = 0.94, $N = 38$). Hierarchical steepness was only 0.013 (intercept = 19.26, right $P = 0.42$, left $P = 0.58$, $N = 1000$ simulations). Given the absence of a discernible hierarchy, additional metrics (e.g. latency to detection of a hierarchy, hierarchical stability) were not quantifiable, although we can say that it would require many more than 49 contact hours/female to detect a hierarchy, should a weakly expressed one exist in this group. No linear hierarchy was present even when young females were removed from the data set, rejecting the idea that a hierarchy may exist only among old females ($P = 0.53$, Landau's $h' = 0.11$, number of circular triads = 810.8 of a maximum of 819; DCI = 0.91, $N = 24$; and steepness was not much higher: 0.015, right $P = 0.36$, left $P = 0.64$, $N = 1000$ simulations). Female coalitions were never observed, and submissive behaviours were observed only once during focal observations and three times during ad libitum data collection.

The Transitory States and Reciprocity Hypotheses

Dyadic aggression was somewhat higher when the aggressor was an old female, but none of the other transitory states were influential, nor was reciprocal aggression (Table 1). However, the grooming model supported both the reciprocity and transitory states hypotheses. Reciprocal grooming as well as the age and residency status of the groomee all predicted grooming to similar degrees: females that were enthusiastic groomers received more grooming, as did older and short-term resident females (Table 2). Trading grooming for access to infants was not supported by the grooming model: the sqrtGrooms$_{BA}$ * monthsI$_B$ interaction did not make it into any candidate models.

Table 1
Model-averaged results for predicting dyadic aggression (Aggs$_{AB}$)

Factor	Estimate	SE$_{adj}$	z	Pr (>|z|)	95% CIs
Intercept	-1.86	0.14	13.13	<0.001***	-2.14, -1.58
Age$_A$	0.89	0.38	2.30	<0.05*	0.13, 1.64
Res.Stat$_A$	-0.43	0.50	0.86	0.39	-0.18, 1.63
monthsI$_B$	-0.12	0.19	0.61	0.54	-0.68, 0.16
Age$_B$	-0.12	0.20	0.59	0.55	-0.73, 0.16
Aggs$_{BA}$	0.12	0.16	0.79	0.43	-0.062, 0.52
Res.Stat$_B$	-0.029	0.14	0.20	0.84	-0.45, 0.92
monthsI$_A$	0.025	0.10	0.25	0.80	-0.25, 0.55

Random effects: intercepts for female identity (ID$_A$ and ID$_B$). See Table A1 for the full candidate model set from which these model-averaged values were derived. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Table 2
Model-averaged results for predicting dyadic grooming (sqrtGrooms$_{AB}$)

Factor	Estimate	SE$_{adj}$	z	Pr (>|z|)	95% CIs
Intercept	-1.64	0.12	14.18	<0.001***	-1.87, -1.42
Age$_B$	1.26	0.41	3.10	<0.01**	0.46, 2.06
Res.Stat$_B$	-1.15	0.48	2.39	<0.05*	0.21, 2.10
monthsI$_A$	-0.028	0.14	0.20	0.84	-0.44, 0.32
sqrtGrooms$_{BA}$	1.06	0.11	9.59	<0.001***	0.85, 1.28
Res.Stat$_A$	-0.07	0.25	0.29	0.77	-0.52, 0.80
Age$_A$	0.13	0.22	0.56	0.57	-0.21, 0.79

Random effects: intercepts for female identity (ID$_A$, and ID$_B$). See Table A2 for the full candidate model set from which these model-averaged values were derived. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Fitness Implications of Transitory States and Social Interactions

The median number of surviving offspring produced per year was 0.24 for short-term resident females (all of them young), 0 for young long-term residents and 0.28 for old long-term residents (means were 0.23, 0.04 and 0.26, respectively). Because fitness by this measure was low for young long-term residents, birth rate of surviving offspring was positively predicted by a female's age and negatively by her residency status; both age and residency status had similarly moderate effects (Table 3). However, when fitness was calculated by live birth rate, it was not well predicted by any of our predictor variables (Table 4; median live birth rate per year was 0.51 for short-term residents, 0 for young long-term residents and 0.55 for old long-term residents; means were 0.53, 0.30 and 0.52, respectively).

Grooming patterns did not indicate widespread trading of grooming for access to infants. Attraction to handle an infant is typically most intense towards neonates (Bădescu et al., 2015; Fruteau et al., 2011; Wei et al., 2013), but in red colobus, grooming received by mothers carrying infants <3 months old was actually significantly lower than the null expectation based on the number of female-months spent carrying infants in the group (chi-square test: $\chi^2 = 4.6$, $N = 38$, $P = 0.03$). Females without dependent offspring appeared to groom females with juveniles more than expected, but grooming in the other direction in these dyads was equally over-represented and no obvious bias in reproductive state for either interactant appeared in aggressive interactions (Fig. 1). Notably, all reproductive state pairs with counts of grooming that were much greater than expected involved a female accompanied by a juvenile.

Cross-species Comparison of Traits that Skew Social Interactions

Species classified as egalitarian show a wide range of factors that structure aggression and grooming within their groups, encompassing all four predictor variables assessed. However, all egalitarian species in our analysis have at least one of the transitory states (age or residency status) as a structuring factor, while we found only one example among the despotic societies of social interactions being skewed by these transitory states (Table 5). Grooming reciprocity was higher in despotic societies in the analysis of dyadic grooming correlation coefficients ($t_{21} = -2.2$, $N = 24$, $P = 0.037$; Fig. 2; data in the Appendix, Table A3), while correlation coefficients in egalitarian societies spanned a wider range.

DISCUSSION

Female social behaviour in red colobus was consistent with a highly egalitarian social system. No linear hierarchy was found among female red colobus, but a linear hierarchy is also difficult to detect in a group where aggression is rare (Galimberti, Fabiani, &

Table 3
Linear model results for predicting fitness (birth rate of surviving offspring)

Factor	Estimate	SE	t	P	95% CIs	Model R^2_{adj}	Model P
Intercept	0.044	0.054	0.82	0.42	-0.066, 0.15	0.26	<0.01**
Res.Stat	-0.27	0.094	2.83	<0.01**	0.075, 0.46		
Age	0.20	0.075	2.71	<0.05*	0.050, 0.35		
Aggression out	0.018	0.016	1.14	0.26	-0.014, 0.050		
Grooming in	-0.0025	0.0040	-0.62	0.54	-0.011, 0.0056		

Res.Stat = residency status. * $P < 0.05$; ** $P < 0.01$.

Boitani, 2003; Klass & Cords, 2011). Koenig and Borries (2006) set the minimum sample size for reliably constructing a hierarchy at five interactions per dyad. For Kibale red colobus, female—female aggression rates are so low that observing the requisite number of aggressive interactions in a group of 39 females would take approximately 34.6 years (working 8 h/day, 300 days/year). The rarity of aggression, very low hierarchical steepness, absence of female coalitions and extreme rarity of formal submission displays indicate that the group is highly egalitarian.

In our red colobus group, reciprocity and transitory states were strong predictors of grooming, indicating that social interactions are not randomly distributed, even in highly egalitarian primates. While the reciprocity hypothesis could not account for patterns of aggression, one transitory state — age — was predictive of aggression rates. We found no evidence of trading grooming for access to infants. However, there was a tendency for females accompanied by a juvenile to be involved in grooming interactions more than expected, possibly in an effort to integrate their maturing offspring into the group's social network. We also found that social status indicators (aggression output or grooming received) were not associated with reproductive success. This could arise if there is no link between social advantages and fitness, or if social advantage is evenly distributed across females in the group over time. The greater success that older females had in rearing surviving offspring may be attributable to the disadvantage of primiparity and maternal inexperience. However, young females had a similar boost in offspring survival if they were short-term residents. Young females that are long-term residents are less likely to have undergone secondary dispersal, and some may not even have dispersed from their natal group. Taken together, the results on reproductive success may simply indicate that females have lower offspring survival unless they disperse, presumably to avoid inbreeding, which secondary dispersal can help avoid further if each group transfer lowers the number of related male groupmates. This suggestion could be further investigated by comparing the level of heterozygosity of surviving offspring and offspring that die at an early age.

Our comparative analysis indicated that transitory states commonly structure social interactions in egalitarian societies across the primate order. On the other hand, reciprocity, at least as measured through a simple correlation of dyadic grooming given and received, was higher in despotic societies than egalitarian ones. At first glance, this seems surprising as rank differences should generate dyadic grooming asymmetries (Seyfarth, 1977). However, females in many despotic societies prefer to groom kin (Butovskaya, 1993; Silk, Seyfarth, & Cheney, 1999), which should not only encourage more cooperation but, if rank and kinship covary, should also mean that grooming tends to occur between individuals of adjacent or similar rank, where strong asymmetries would be less expected (Seyfarth, 1977). The results indicate more stringent matching of grooming effort in reciprocal relationships in despotic societies.

Overall, egalitarian societies showed more variation, both in reciprocity (Fig. 2) and in the factors that influenced their social interactions, which included despotic social drivers (dominance and kinship). In striking contrast, despotic species seem to be restricted to dominance ranks and kinship as the predominant factors structuring their social networks (Isbell & Young, 2002). The one exception, Hanuman langurs, is easily explained because their age-inversed hierarchies most likely render age a contributor to aggressive interactions through its effect on rank, suggesting dominance rank is the primary predictor of aggression (Koenig et al., 2013). The divide in the variety of factors that structure social interactions in egalitarian and despotic societies may indicate that despotism represents a state reached once contest competition for resources pushes a society past a threshold, beyond which ranks and kinship are so influential that the effects of transitory states on social interactions are relatively negligible (Thierry, 1990). Alternatively, it may reflect the tendency for researchers to classify species that lie somewhere in between despotic and egalitarian as egalitarian.

Whether the diversity of factors that structure female—female interactions in egalitarian populations suggests a variety of ways to be an egalitarian society or different degrees of egalitarianism, research on this diversity is a promising path to a deeper understanding of primate social evolution. If transitory states rise in their influence on social interactions, they should act to destabilize dominance hierarchies, which can occur through multiple means. Social status may be skewed through transitory state-dependent tendencies for aggression (e.g. testosterone rises during pregnancy and changes with female age in many primates; Altmann, Lynch, Nguyen, Alberts, & Gesquiere, 2004; Beehner, Phillips-Conroy, & Whitten, 2005; Behringer, Deschner, Deimel, Stevens, & Hohmann, 2014; Castracane, 1998; Chambers & Hearn, 1979). Age-dependent dominance hierarchies may come about this way and have been recognized for their potential to even out lifetime reproductive success (hence the suggestion that the age-inversed nature of despotic Hanuman langur hierarchies places them at an intermediate position between an egalitarian and a despotic society; Lu, Borries, Gustison, Larney, & Koenig, 2016). Alternatively, a given transitory state may confer status by attracting groomers if it signals potential for learning from an older female (e.g. in elephants, matriarchs possess important social knowledge and skill in predation risk assessment; McComb, Moss, Durant, Baker, & Sayialel, 2001; McComb et al., 2011), a mother with a new infant (as suggested by the 'learning to mother' hypothesis; Lancaster, 1971), or a recently immigrated female that may possess ecological knowledge new to the group. While reciprocity was high in despotic societies, the level of reciprocity may rise again at the other end of the spectrum as egalitarianism increases if Seyfarth's (1977) prediction of closer reciprocity between individuals of similar rank can be extended to comparisons among egalitarian societies. Under conditions of very low food competition, the marginal benefits of enacting any aggression may become trivial and reciprocity may become as prominent as favouring females in certain transitory states as grooming partners, as appears to be the case in our highly egalitarian red colobus group. Across mammals, similar forces or additional mechanisms may give rise to egalitarian societies. For example, female herb-field mice, *Apodemus uralensis*, groom reciprocally, age largely determines aggressive interaction outcomes in female bighorn sheep, *Ovis canadensis*, and lionesses,

Table 4
Linear model results for predicting fitness (live birth rate)

Factor	Estimate	SE	t	P	95% CIs	Model R^2_{adj}	Model P
Intercept	0.30	0.097	3.05	<0.01**	0.099, 0.50	0.097	0.12
Age	0.13	0.13	0.99	0.33	-0.14, 0.41		
Res.Stat	-0.25	0.17	1.45	0.16	-0.099, 0.59		
Grooming in	-0.0031	0.0071	-0.44	0.66	-0.018, 0.011		
Aggression out	0.049	0.028	1.74	0.092	-0.0085, 0.11		

Res.Stat = residency status. **$P < 0.01$.

Table 5
Examples of where despotic traits (dominance rank and access to kin) and transitory states (age and residency status) predict aggression or grooming interactions among females in egalitarian and despotic societies

Dependent variable	Predictor trait	Egalitarian societies	Despotic societies
Aggression	Dominance rank	Chimpanzees, *Pan troglodytes*[f]	White-faced capuchins, *Cebus capucinus*[a] Tibetan macaques, *Macaca thibetana*[b] Longtailed macaques, *Macaca fascicularis*[c] White-thighed colobus, *Colobus vellerosus*, groups with strong hierarchies[d] Hanuman langurs (*Semnopithecus entellus*)[e]
	Kinship	Mountain gorillas, *Gorilla beringei beringei*[h]	Japanese macaques, *Macaca fuscata*[g]
	Age	—	Hanuman langurs (through rank)[e]
	Residency status	Spider monkeys, *Ateles geoggroyi*[i] Chimpanzees[j] Mountain gorillas[h]	—
Grooming	Dominance rank	Sooty mangabeys, *Cercocebus atys*[n]	Geladas, *Theropithecus gelada*[k] White-faced capuchins[a] Longtailed macaques[c] Tufted capuchins, *Cebus apella*[l] Vervet monkeys, *Cercopithecus aethiops*[m] Wedge-capped capuchins, *Cebus olivaceus*[t]
	Kinship	Chimpanzees[p] Mountain gorillas[h] White-thighed colobus with access to >1 female kin[q]	Geladas[k] Japanese macaques[g] Tibetan macaques[b] Chacma baboons, *Papio hamadryas ursinus*[o]
	Age	Bonobos, *Pan paniscus*[r]	—
	Residency status	Chimpanzees[j] White-thighed colobus[s]	—

[a] Perry (1996).
[b] Berman, Ionica, and Li (2004).
[c] van Noordwijk and van Schaik (1987).
[d] Wikberg et al. (2013).
[e] Koenig et al. (2013).
[f] Wittig and Boesch (2003) (dominant females won more aggressive contests for food in Taï NP, where contest competition is higher than at other chimpanzee sites).
[g] Kurland (1977).
[h] Watts (1994).
[i] Riveros, Schaffner, and Aureli (2017).
[j] Pusey (1980).
[k] Tinsley Johnson, Snyder-Mackler, Beehner, and Bergman (2014).
[l] Tiddi et al. (2010).
[m] Seyfarth (1980).
[n] Range and Noë (2002).
[o] Silk et al. (1999).
[p] Foerster et al. (2015).
[q] Wikberg et al. (2014a).
[r] Idani (1991).
[s] Wikberg et al. (2014b).
[t] O'Brien (1993).

Panthera leo, operate on a first-come, first-served basis at carcasses (Festa-Bianchet, 1991; Packer, Pusey, & Eberly, 2001; Stopka & Graciasová, 2001). More research comparing how a variety of egalitarian societies are structured may reveal patterns rooted in phylogeny or ecological circumstances with implications for how egalitarianism evolves.

A general theory for what should govern female relationships in egalitarian groups can be pushed beyond the assumption that they are unstructured, with relatively undifferentiated relationships, more individualism and more tolerance. Here we argue that biased interactions can lead to evenly distributed social benefits over time

if they are biased by reciprocity or by traits that are transitory, and we demonstrate that such mechanisms may be at work across egalitarian primate societies. If social interactions have any fitness consequences, a relatively even distribution of social advantage over time in egalitarian societies would promote lower overall skew in lifetime reproductive success. This can set egalitarian societies apart from despotic societies in their evolutionary trajectories, because dominance- and kinship-regulated social behaviour render bias in social advantage more static, promoting greater skew in lifetime reproductive success in despotic groups (Lu et al., 2016). Determining whether feedback loops mediated by equalizing
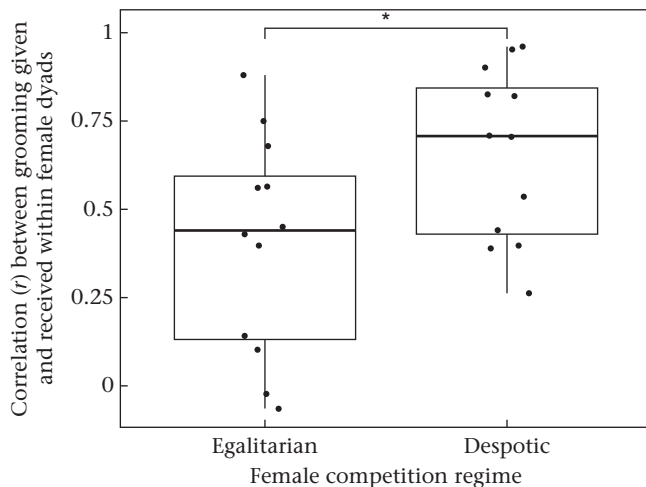
Figure 2. Grooming reciprocity as measured by correlations in dyadic grooming frequency in despotic societies and egalitarian societies (horizontal bars = means; horizontal box edges = SEs). *$P < 0.05$.

factors or despotic factors are at work in mammalian social systems would be an intriguing line of inquiry to illuminate the mechanisms by which social systems evolve.

Acknowledgments

References

Ahumada, J. A. (1992). Grooming behavior of spider monkeys (*Ateles geoggroyi*) on Barro Colorado Island, Panama. *International Journal of Primatology, 13*, 33—49.

Altmann, J., Lynch, J. W., Nguyen, N., Alberts, S. C., & Gesquiere, L. R. (2004). Life-history correlates of steroid concentrations in wild peripartum baboons. *American Journal of Primatology, 64*, 95—106. https://doi.org/10.1002/ajp.20064.

Anderson, C. M. (1986). Female age: Male preference and reproductive success in primates. *International Journal of Primatology, 7*, 305—326.

Appleby, M. C. (1983). The probability of linearity in hierarchies. *Animal Behaviour, 31*, 600—608.

Balasubramaniam, K. N., Beisner, B. A., Berman, C. M., Marco, A. De, Duboscq, J., Koirala, S., et al. (2018). The influence of phylogeny, social style, and socio-demographic factors on macaque social network structure. *American Journal of Primatology, 80*, 1—15. https://doi.org/10.1002/ajp.22727.

Barrett, L., Gaynor, D., & Henzi, P. (2002). A dynamic interaction between aggression and grooming reciprocity among female chacma baboons. *Animal Behaviour, 63*(6), 1047—1053. https://doi.org/10.1006/anbe.2002.3008.

Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E., & Hill, R. A. (1999). Market forces predict grooming reciprocity in female baboons. *Proceedings of the Royal Society B: Biological Sciences, 266*(1420), 665—670. https://doi.org/10.1098/rspb.1999.0687.

Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E., & Hill, R. A. (2000). Female baboons do not raise the stakes but they give as good as they get. *Animal Behaviour, 59*(4), 763—770. https://doi.org/10.1006/anbe.1999.1361.

Bartoń, K. (2018). *MuMIn: Multi-Model Inference. R Package Version 1.42.1.* https://cran.r-project.org/package=MuMIn.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 67*, 1—48. https://doi.org/10.18637/jss.v067.i01.

Bayly, K. L., Evans, C. S., & Taylor, A. (2006). Measuring social structure: A comparison of eight dominance indices. *Behavioural Processes, 73*(1), 1—12. https://doi.org/10.1016/j.beproc.2006.01.011.

Beehner, J. C., Phillips-Conroy, J. E., & Whitten, P. L. (2005). Female testosterone, dominance rank, and aggression in an Ethiopian population of hybrid baboons. *American Journal of Primatology, 67*, 101—119. https://doi.org/10.1002/ajp.20172.

Behringer, V., Deschner, T., Deimel, C., Stevens, J. M. G., & Hohmann, G. (2014). Age-related changes in urinary testosterone levels suggest differences in puberty onset and divergent life history strategies in bonobos and chimpanzees. *Hormones and Behavior, 66*, 525—533. https://doi.org/10.1016/j.yhbeh.2014.07.011.

Bergman, T., & Beehner, J. (2003). Hybrid zones and sexual selection: Insights from the Awash baboon hybrid zone (Papio hamadryas anubis, P. h. hamadryas). In C. B. Jones (Ed.), *Sexual selection and reproductive competition in primates: New insights and directions* (Vol. 3, pp. 503—537). Norman, OK: American Society of Primatologists.

Bergstrom, M. L., & Fedigan, L. M. (2010). Dominance among female white-faced capuchin monkeys (*Cebus capucinus*): Hierarchical linearity, nepotism, strength and stability. *Behaviour, 147*(7), 899—931. https://doi.org/10.1163/000579510X497283.

Berman, C. M., Ionica, C. S., & Li, J. (2004). Dominance style among *Macaca thibetana* on Mt. Huangshan, China. *International Journal of Primatology, 25*(6), 1283—1312.

Burnham, K. P., & Anderson, D. R. (2002). *Model Selection and Multimodel Inference: A Practical Information-theoretic Approach* (2nd ed.). New York, NY: Springer.

Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. *Behavioral Ecology and Sociobiology, 65*(1), 23—35. https://doi.org/10.1007/s00265-010-1029-6.

Butovskaya, M. (1993). Kinship and different dominance styles in groups of three species of the genus *Macaca. Folia Primatologica, 60*, 210—224.

Bădescu, I., Sicotte, P., Ting, N., & Wikberg, E. C. (2015). Female parity, maternal kinship, infant age and sex influence natal attraction and infant handling in a wild colobine (*Colobus vellerosus*). *American Journal of Primatology, 77*(4), 376—387. https://doi.org/10.1002/ajp.22353.

Castracane, V. D. (1998). The effect of dexamethasone administration at different stages of gestation on maternal plasma steroid concentrations in the baboon (*Papio cynocephalus*). *Human Reproduction, 13*, 2282—2285.

Chambers, P. L., & Hearn, J. P. (1979). Peripheral plasma levels of progesterone, oestradiol-17beta, oestrone, testerone, androstenedione and chorionic gonadotrophin during pregnancy in the marmoset monkey, *Callithrix jacchus. Journal of Reproduction and Fertility, 56*, 23—32.

Chapman, C. A., Bortolamiol, S., Matsuda, I., Omeja, P. A., Paim, F. P., Reyna-Hurtado, R., et al. (2017). Primate population dynamics: Variation in abundance over space and time. *Biodiversity & Conservation, 27*(5), 1221—1238. https://doi.org/10.1007/s10531-017-1489-3.

Chapman, C. A., & Chapman, L. J. (n.d.). [Long-term rainfall data for Kanyawara, Kibale National Park]. (Unpublished raw data).

Chapman, C. A., & Chapman, L. J. (1999). Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. *Primates, 40*, 215—231.

Chapman, C. A., Chapman, L. J., Bjorndal, K. A., & Onderdonk, D. A. (2002). Application of protein-to-fiber ratios to predict colobine abundance on different spatial scales. *International Journal of Primatology, 23*, 283—310. https://doi.org/10.1023/A.

Cheney, D., Seyfarth, R., & Fischer, J. (2006). Reproduction, mortality, and female reproductive success in chacma baboons of the Okavango Delta, Botswana. In L. Swedell, & S. Leigh (Eds.), *Reproduction and Fitness in Baboons: Behavioral, Ecological, and Life History Perspectives* (pp. 147—176). New York, NY: Springer. http://link.springer.com/chapter/10.1007/978-0-387-33674-9_7.

Cords, M. (2000). Agonistic and affiliative relationships in a blue monkey group. In P. F. Whitehead, & C. J. Jolly (Eds.), *Old World Monkeys* (pp. 453—479). Cambridge, U.K.: Cambridge University Press.

Crook, J. H. (1965). The adaptive significance of avian social organizations. *Symposia of the Zoological Society of London, 14*, 181—218.

Demaria, C., & Thierry, B. (2001). A comparative study of reconciliation in rhesus and Tonkean macaques. *Behaviour, 138*, 397—410. https://doi.org/10.1163/15685390152032514.

Emlen, S. T., & Oring, L. W. (1977). Ecology, sexual selection, and evolution of mating systems. *Science, 197*, 215—223.

Fa, J. E. (1986). On the ecological status of the Barbary macaque *Macaca sylvanus* L . in north Morocco: Habitat Influences versus human impact. *Biological Conservation, 35*, 215—258.

Fedigan, L. M. (1983). Dominance and reproductive success in primates. *American Journal of Physical Anthropology, 26*(Suppl. 1), 91—129. https://doi.org/10.1002/ajpa.1330260506.

Festa-Bianchet, M. (1991). The social system of bighorn sheep: Grouping patterns, kinship and female dominance rank. *Animal Behaviour, 42*(1), 71—82. https://doi.org/10.1016/S0003-3472(05)80607-4.

Foerster, S., McLellan, K., Schroepfer-Walker, K., Murray, C. M., Krupenye, C., Gilby, I. C., et al. (2015). Social bonds in the dispersing sex: Partner preferences among adult female chimpanzees. *Animal Behaviour, 105*, 139–152. https://doi.org/10.1016/j.anbehav.2015.04.012.

Frank, R. E., & Silk, J. B. (2009). Grooming exchange between mothers and non-mothers: The price of natal attraction in wild baboons (*Papio anubis*). *Behaviour, 146*, 889–906.

Freckleton, R. P. (2011). Dealing with collinearity in behavioural and ecological data: Model averaging and the problems of measurement error. *Behavioral Ecology and Sociobiology, 65*(1), 91–101. https://doi.org/10.1007/s00265-010-1045-6.

Fruteau, C., van de Waal, E., van Damme, E., & Noë, R. (2011). Infant access and handling in sooty mangabeys and vervet monkeys. *Animal Behaviour, 81*(1), 153–161. https://doi.org/10.1016/j.anbehav.2010.09.028.

Galimberti, F., Fabiani, A., & Boitani, L. (2003). Socio-spatial levels in linearity analysis of dominance hierarchies: A case study on elephant seals. *Journal of Ethology, 21*, 131–136.

Garamszegi, L. Z. (2011). Information-theoretic approaches to statistical analysis in behavioural ecology: An introduction. *Behavioral Ecology and Sociobiology, 65*(1), 1–11. https://doi.org/10.1007/s00265-010-1028-7.

Gelman, A., & Su, Y. (2018). *Arm: Data Analysis using Regression and Multilevel/Hierarchical Models (R Package Version 1.10-1)*. https://CRAN.R-proeject.org/package=arm.

Gomes, C. M., Mundry, R., & Boesch, C. (2009). Long-term reciprocation of grooming in wild West African chimpanzees. *Proceedings of the Royal Society B: Biological Sciences, 276*(1657), 699–706. https://doi.org/10.1098/rspb.2008.1324.

Grueber, C. E., Nakagawa, S., Laws, R. J., & Jamieson, I. G. (2011). Multimodel inference in ecology and evolution: Challenges and solutions. *Journal of Evolutionary Biology, 24*, 699–711. https://doi.org/10.1111/j.1420-9101.2010.02210.x.

Gumert, M. D. (2007). Grooming and infant handling interchange in *Macaca fascicularis*: The relationship between infant supply and grooming payment. *International Journal of Primatology, 28*(5), 1059–1074. https://doi.org/10.1007/s10764-007-9202-0.

Hartig, F. (2018). *DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. R Package* Version 0.2.0. https://cran.r-project.org/package=DHARMa.

Henzi, P., & Barrett, L. (2002). Infants as a commodity in a baboon market. *Animal Behaviour, 63*(5), 915–921. https://doi.org/10.1006/anbe.2001.1986.

Hinde, K. J. (2009). Richer milk for sons but more milk for daughters: Sex-biased investment during lactation varies with maternal life history in rhesus macaques. *American Journal of Human Biology, 21*(4), 512–519. https://doi.org/10.1002/ajhb.20917.

van Hooff, J. A. R. A. M., & Wensing, J. A. B. (1987). Dominance and its behavioral measures. In H. Frank (Ed.), *Man and Wolf* (pp. 219–251). Dordrecht, the Netherlands: Dr W. Junk.

Idani, G. (1991). Social relationships between immigrant and resident bonobo (*Pan paniscus*) females at Wamba. *Folia Primatologica, 57*, 83–95.

Isbell, L. A. (1991). Contest and scramble competition: Patterns of female aggression and ranging behavior among primates. *Behavioral Ecology, 2*, 143–155.

Isbell, L. A., & Young, T. P. (2002). Ecological models of female social relationships in primates: Similarities, disparities, and some directions for future clarity. *Behaviour, 139*, 177–202.

Izawa, K. (1980). Social behavior of the wild black-capped capuchin (*Cebus apella*). *Primates, 21*, 443–467.

Janson, C. (1985). Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). *Behavioral Ecology and Sociobiology, 18*, 125–138.

Janson, C., & van Schaik, C. P. (1988). Recognizing the many faces of primate food competition: Methods. *Behaviour, 105*(1/2), 165–186.

Jones, C. B. (1979). Grooming in the mantled howler monkey, *Alouatta palliata* Gray. *Primates, 20*, 289–292.

Klass, K., & Cords, M. (2011). Effect of unknown relationships on linearity, steepness and rank ordering of dominance hierarchies: Simulation studies based on data from wild monkeys. *Behavioural Processes, 88*(3), 168–176. https://doi.org/10.1016/j.beproc.2011.09.003.

Koenig, A. (2002). Competition for resources and its behavioral consequences among female primates. *International Journal of Primatology, 23*(4), 759–783.

Koenig, A., & Borries, C. (2006). The predictive power of socioecological models: A reconsideration of resource characteristics, agonism, and dominance hierarchies. In G. Hohmann, M. Robbins, & C. Boesch (Eds.), *Feeding Ecology in Apes and Other Primates* (pp. 263–285). Cambridge, U.K.: Cambridge University Press.

Koenig, A., Borries, C., Caselli, A., & Lu, A. (2013). Effects of age, reproductive state, and the number of competitors on the dominance dynamics of wild female Hanuman langurs. *Behaviour, 150*(5), 485–523. https://doi.org/10.1163/1568539X-00003064.

Kurland, J. (1977). *Kin selection in the Japanese Monkey*. Basel, Switzerland: Karger.

Leiva, D., & de Vries, H. (2014). *steepness: Testing Steepness of Dominance Hierarchies* (p. R package version 0.2-2) https://cran.r-project.org/package=steepness.

Lomnicki, A. (1988). *Population Ecology of Individuals*. Princeton, NJ: Princeton University Press.

Lu, A., Borries, C., Gustison, M. L., Larney, E., & Koenig, A. (2016). Age and reproductive status influence dominance in wild female Phayre's leaf monkeys. *Animal Behaviour, 117*, 145–153. https://doi.org/10.1016/j.anbehav.2016.04.020.

Lukas, D., & Clutton-Brock, T. H. (2018). Social complexity and kinship in animal societies. *Ecology Letters, 21*, 1129–1134. https://doi.org/10.1111/ele.13079.

McComb, K., Moss, C., Durant, S. M., Baker, L., & Sayialel, S. (2001). Matriarchs as repositories of social knowledge in African elephants. *Science, 292*, 491–494.

McComb, K., Shannon, G., Durant, S. M., Sayialel, K., Slotow, R., Poole, J., et al. (2011). Leadership in elephants: The adaptive value of age. *Proceedings of the Royal Society B: Biological Sciences, 278*, 3270–3276. https://doi.org/10.1098/rspb.2011.0168.

Muroyama, Y. (1994). Exchange of grooming for allomothering in female patas monkeys. *Behaviour, 128*, 103–119.

Nakagawa, N. (1992). Distribution of affiliative behaviors among adult females within a group of wild patas monkeys in a nonmating, nonbirth season. *International Journal of Primatology, 13*, 73–96.

Nakagawa, S., & Freckleton, R. P. (2011). Model averaging, missing data and multiple imputation: A case study for behavioural ecology. *Behavioral Ecology and Sociobiology, 65*(1), 103–116. https://doi.org/10.1007/s00265-010-1044-7.

Nicholson, A. J. (1954). An outline of the dynamics of animal populations. *Australian Journal of Zoology, 2*, 9–65.

Noë, R., & Hammerstein, P. (1995). Biological markets. *Trends in Ecology & Evolution, 10*, 336–339.

van Noordwijk, M. A., & van Schaik, C. P. (1987). Competition among female long-tailed macaques, *Macaca fascicularis. Animal Behaviour, 35*, 577–589.

Oi, T. (1988). Sociological study on the troop fission of wild Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island. *Primates, 29*, 1–19.

O'Brien, T. G. (1993). Allogrooming behaviour among adult female wedge-capped capuchin monkeys. *Animal Behaviour, 46*, 499–510.

Packer, C., Pusey, A. E., & Eberly, L. E. (2001). Egalitarianism in female African lions. *Science, 293*, 690–693.

Pandit, S. A., & van Schaik, C. P. (2003). A model for leveling coalitions among primate males: Toward a theory of egalitarianism. *Behavioral Ecology and Sociobiology, 55*, 161–168. https://doi.org/10.1007/s00265-003-0692-2.

Perry, S. (1996). Female–female social relationships in wild white-faced capuchin monkeys, Cebus capucinus. *American Journal of Primatology, 40*(2), 167–182. https://doi.org/10.1002/(SICI)1098-2345(1996)40:2<167::AID-AJP43.0.CO;2-W>.

Pusey, A. E. (1980). Inbreeding avoidance in chimpanzees. *Animal Behaviour, 28*(2), 543–552. https://doi.org/10.1016/S0003-3472(80)80063-7.

Pusey, A. E., Williams, J., & Goodall, J. (1997). The influence of dominance rank on the reproductive success of female chimpanzees. *Science, 277*(5327), 828–831. https://doi.org/10.1126/science.277.5327.828.

R Core Team. (2018). *R: A Language and Environment for Statistical Computing.* Vienna, Austria: R Foundation for Statistical Computing.

Range, F., & Noë, R. (2002). Familiarity and dominance relations among female sooty mangabeys in the Taï National Park. *American Journal of Primatology, 56*(3), 137–153. https://doi.org/10.1002/ajp.1070.

Richards, S. A., Whittingham, M. J., & Stephens, P. A. (2011). Model selection and model averaging in behavioural ecology: The utility of the IT-AIC framework. *Behavioral Ecology and Sociobiology, 65*(1), 77–89. https://doi.org/10.1007/s00265-010-1035-8.

Riveros, J. C., Schaffner, C. M., & Aureli, F. (2017). You are not welcome: Social exchanges between female spider monkeys (*Ateles geoffroyi*). *International Journal of Primatology, 38*(5), 856–871. https://doi.org/10.1007/s10764-017-9982-9.

Robbins, A. M., Robbins, M. M., Gerald-Steklis, N., & Steklis, H. D. (2006). Age-related patterns of reproductive success among female mountain gorillas. *American Journal of Physical Anthropology, 131*(4), 511–521. https://doi.org/10.1002/ajpa.20474.

Rowell, T. (1967). Variability in the social organization of nonhuman primates. In D. Morris (Ed.), *Primate Ethology* (pp. 219–235). London, U.K.: Weidenfeld & Nicolson.

Sánchez-Villagra, M. R., Pope, T. R., & Salas, V. (1998). Relation of intergroup variation in allogrooming to group social structure and ectoparasite loads in red howlers (*Alouatta seniculus*). *International Journal of Primatology, 19*(3), 473–491.

van Schaik, C. P. (1989). The ecology of social relationships amongst female primates. In V. Standen, & R. Foley (Eds.), *Comparative Socioecology* (pp. 195–218). Oxford, U.K.: Blackwell.

van Schaik, C. P., Pandit, S. A., & Vogel, E. R. (2006). Toward a general model for male–male coalitions in primate groups. In P. M. Kappeler, & C. P. van Schaik (Eds.), *Cooperation in Primates and Humans* (pp. 151–172). https://doi.org/10.1007/3-540-28277-7.

Schino, G., & Aureli, F. (2008). Grooming reciprocation among female primates: A meta-analysis. *Biology Letters, 4*, 9–11. https://doi.org/10.1007/BF00303714.

Seyfarth, R. M. (1976). Social relationships among adult female baboons. *Animal Behaviour, 24*, 917–938. https://doi.org/10.1016/S0003-3472(76)80022-X.

Seyfarth, R. M. (1977). A model of social grooming among adult female monkeys. *Journal of Theoretical Biology, 65*, 671–698. https://doi.org/10.1016/0022-5193(77)90015-7.

Seyfarth, R. M. (1980). The distribution of grooming and related behaviours among adult female vervet monkeys. *Animal Behaviour, 28*, 798–813.

Silk, J. B. (2002). Kin selection in primate groups. *International Journal of Primatology, 23*(4), 849–875. https://doi.org/10.1023/A:1015581016205.

Silk, J. B. (2007). Social components of fitness in primate groups. *Science, 317*(5843), 1347–1351. https://doi.org/10.1126/science.1140734.

Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social bonds of female baboons enhance infant survival. *Science, 302*(5648), 1231–1234.

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., et al. (2009). The benefits of social capital: Close social bonds among female baboons enhance offspring survival. *Proceedings of the Royal Society B: Biological Sciences, 276*(1670), 3099–3104. https://doi.org/10.1098/rspb.2009.0681.

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., et al. (2010a). Female chacma baboons form strong, equitable, and enduring social bonds. *Behavioral Ecology and Sociobiology, 64*(11), 1733–1747. https://doi.org/10.1007/s00265-010-0986-0.

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., et al. (2010b). Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology, 20*(15), 1359–1361. https://doi.org/10.1016/j.cub.2010.05.067.

Silk, J. B., Seyfarth, R. M., & Cheney, D. L. (1999). The structure of social relationships among female savanna baboons in Moremi Reserve, Botswana. *Behaviour, 134*, 679–703.

Snaith, T. V., & Chapman, C. A. (2007). Primate group size and interpreting socio-ecological models: Do folivores really play by different rules? *Evolutionary Anthropology, 16*(3), 94–106. https://doi.org/10.1002/evan.20132.

Stanford, C. B. (1991). *The Capped Langur in Bangladesh: Behavioral Ecology and Reproductive Tactics*. Basel, Switzerland: Karger.

Sterck, E. H. M., & Steenbeek, R. (1997). Female dominance relationships and food competition in the sympatric Thomas langur and long-tailed macaque. *Behaviour, 134*(9/10), 749–774.

Sterck, E. H. M., Watts, D. P., & van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology, 41*(5), 291–309. https://doi.org/10.1007/s002650050390.

Stopka, P., & Graciasová, R. (2001). Conditional allogrooming in the herb-field mouse. *Behavioral Ecology, 12*(5), 584–589. https://doi.org/10.1093/beheco/12.5.584.

Strier, K. B. (1994). Myth of the typical primate. *Yearbook of Physical Anthropology, 271*, 233–271.

Struhsaker, T. T. (1975). *The Red Colobus Monkey*. Chicago, IL: University of Chicago Press.

Struhsaker, T. T. (2010). *The Red Colobus Monkeys: Variation in Demography, Behavior, and Ecology of Endangered Species*. Oxford, U.K.: Oxford University Press.

Struhsaker, T. T., & Pope, T. R. (1991). Mating system and reproductive success: A comparison of two African forest monkeys (*Colobus badius* and *Cercopithecus ascanius*). *Behaviour, 117*, 182–205.

Sugiyama, Y. (1971). Characteristics of the social life of bonnet macaques (*Macaca radiata*). *Primates, 12*, 247–266.

Sugiyama, Y. (1988). Grooming interactions among adult chimpanzees at Bossou, Guinea, with special reference to social structure. *International Journal of Primatology, 9*, 393–407.

Symonds, M., & Moussalli, A. (2010). A brief guide to model selection, multimodal inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology, 65*, 13–21.

Takahashi, H., & Furuichi, T. (1998). Comparative study of grooming relationships among wild Japanese macaques in Kinkazan A troop and Yakushima M troop. *Primates, 39*, 365–374. https://doi.org/10.1007/BF02573084.

Thierry, B. (1990). Feedback loop between kinship and dominance: The macaque model. *Journal of Theoretical Biology, 145*, 511–521.

Thierry, B. (2007). Unity in diversity: Lessons from macaque societies. *Evolutionary Anthropology, 16*, 224–238. https://doi.org/10.1002/evan.20147.

Tiddi, B., Aureli, F., & Schino, G. (2010). Grooming for infant handling in tufted capuchin monkeys: A reappraisal of the primate infant market. *Animal Behaviour, 79*(5), 1115–1123. https://doi.org/10.1016/j.anbehav.2010.02.008.

Tinsley Johnson, E., Snyder-Mackler, N., Beehner, J. C., & Bergman, T. J. (2014). Kinship and dominance rank influence the strength of social bonds in female geladas (*Theropithecus gelada*). *International Journal of Primatology, 35*(1), 288–304. https://doi.org/10.1007/s10764-013-9733-5.

Vehrencamp, S. (1983). A model for the evolution of despotic versus egalitarian societies. *Animal Behaviour, 31*, 667–682.

Ventura, R., Majolo, B., Koyama, N. F., Hardie, S. M., & Schino, G. (2006). Reciprocation and interchange in wild Japanese macaques: Grooming, cofeeding, and agonistic support. *American Journal of Primatology, 68*, 1138–1149. https://doi.org/10.1002/ajp.20314.

de Vries, H. (1993). The rowwise correlation between two proximity matrices and the partial rowwise correlation. *Psychometrika, 58*, 53–69.

de Vries, H. (1995). An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Animal Behaviour, 50*, 1375–1389.

Watts, D. P. (1994). Social relationships of immigrant and resident female mountain gorillas. II: Relatedness, residence, and relationships between females. *American Journal of Primatology, 32*, 13–30.

Wei, W., Qi, X., Garber, P. A., Guo, S., Zhang, P., & Li, B. (2013). Supply and demand determine the market value of access to infants in the golden snub-nosed monkey (*Rhinopithecus roxellana*). *PLoS One, 8*(6), e65962. https://doi.org/10.1371/journal.pone.0065962.

Wheeler, B., & Torchiano, M. (2016). *lmPerm: Permutation Tests for Linear Models. R Package* Version 2.1.0. https://cran.r-project.org/package=lmPerm.

Wikberg, E. C., Teichroeb, J. A., Bădescu, I., & Sicotte, P. (2013). Individualistic female dominance hierarchies with varying strength in a highly folivorous population of black-and-white colobus. *Behaviour, 150*, 1–26. https://doi.org/10.1163/1568539X-00003050.

Wikberg, E. C., Ting, N., & Sicotte, P. (2014a). Familiarity is more important than phenotypic similarity in shaping social relationships in a facultative female dispersed primate, *Colobus vellerosus*. *Behavioural Processes, 106*, 27–35. https://doi.org/10.1016/j.beproc.2014.04.002.

Wikberg, E. C., Ting, N., & Sicotte, P. (2014b). Kinship and similarity in residency status structure female social networks in black-and-white colobus monkeys (*Colobus vellerosus*). *American Journal of Physical Anthropology, 153*(3), 365–376. https://doi.org/10.1002/ajpa.22435.

Wittig, R. M., & Boesch, C. (2003). Food competition and linear dominance hierarchy among female chimpanzees of the Tai National Park. *International Journal of Primatology, 24*, 847–867.

Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour, 75*(3/4), 262–300.

Zumpe, D., & Michael, R. P. (1986). Dominance index: A simple measure of relative dominance status in primates. *American Journal of Primatology, 10*(4), 291–300. https://doi.org/10.1002/ajp.1350100402.

Appendix

Table A1
Candidate model set for aggression among red colobus females

Intercept	Age$_A$	Age$_B$	Res.Stat$_A$	Res.Stat$_B$	monthI$_A$	monthI$_B$	Agg$_{BA}$	AIC	dAIC	Weight
-1.86	1.02	NA	-0.72	NA	NA	NA	NA	242	0	0.051
-1.88	1.03	NA	-0.75	NA	NA	-0.27	NA	242	0.37	0.043
-1.89	1.05	-0.31	-0.71	NA	NA	NA	0.23	242	0.41	0.042
-1.89	1.03	NA	-0.71	NA	NA	-0.28	0.21	243	0.46	0.041
-1.88	1.05	-0.27	-0.76	NA	NA	NA	NA	243	0.53	0.039
-1.83	0.67	NA	NA	NA	NA	NA	0.23	243	0.66	0.037
-1.90	1.06	-0.30	-0.74	NA	NA	-0.26	0.23	243	0.78	0.035
-1.84	0.67	-0.28	NA	NA	NA	NA	0.25	243	1.07	0.030
-1.84	0.66	NA	NA	NA	NA	-0.26	0.23	243	1.08	0.030
-1.82	0.63	NA	NA	NA	NA	-0.25	NA	244	1.44	0.025
-1.84	0.67	-0.28	NA	NA	NA	-0.24	0.25	244	1.60	0.023
-1.82	0.64	-0.25	NA	NA	NA	NA	NA	244	1.62	0.023
-1.88	1.04	NA	-0.76	-0.30	NA	-0.31	NA	244	1.67	0.022
-1.87	1.02	NA	-0.73	-0.16	NA	NA	NA	244	1.78	0.021
-1.88	1.02	NA	-0.64	NA	0.13	NA	0.21	244	1.80	0.021
-1.88	1.03	NA	-0.68	-0.20	NA	NA	0.21	244	1.88	0.020
-1.84	0.67	NA	NA	NA	0.17	NA	0.22	244	1.92	0.020
-1.89	1.05	-0.31	-0.68	NA	0.13	NA	0.23	244	2.00	0.019
-1.83	0.64	-0.24	NA	NA	NA	-0.23	NA	244	2.30	0.016
-1.85	0.68	-0.29	NA	NA	0.17	NA	0.24	244	2.32	0.016
-1.89	1.05	-0.27	-0.76	NA	0.12	-0.24	NA	244	2.67	0.014
-1.83	0.64	NA	NA	NA	0.17	-0.24	NA	244	2.72	0.013
-1.83	0.64	NA	NA	-0.28	NA	-0.29	NA	244	2.79	0.013
-1.65	0.21	1.27	NA	-1.16	-0.056	NA	1.06	235	1.79	0.017

Variables included the total number of aggressive actions that individual A directed at individual B (Aggs$_{AB}$), the age (Age$_A$, Age$_B$) and residency status (Res.Stat$_A$, Res.Stat$_B$) of each interactant and the number of months that each individual spent carrying an infant (monthsI$_A$, monthsI$_B$). NA indicates that the variable was not included in a candidate model. All candidate models that passed tests of model fit are listed.

Table A2
Candidate model set for grooming among red colobus females

Intercept	Age_A	Age_B	$Res.Stat_A$	$Res.Stat_B$	$monthI_A$	$monthI_B$	$sqrtGroom_{BA}$	sqrt $Groom_{BA}$ $*monthI_B$	AIC	dAIC	Weight
-1.64	NA	1.26	NA	1.15	-0.060	NA	1.08	NA	234	0	0.042
-1.64	NA	1.26	-0.007	1.15	NA	NA	1.08	NA	234	0.12	0.040
-1.65	0.35	1.26	-0.29	1.16	NA	NA	1.04	NA	234	0.30	0.036
-1.65	0.21	1.27	NA	1.16	-0.056	NA	1.06	NA	235	1.79	0.017

Variables included the square root-transformed total number of times that individual B groomed individual A ($sqrtGrooms_{BA}$); all other abbreviations as given in Table A1. All candidate models that passed tests of model fit are listed.

Table A3
Data set for comparing grooming reciprocity across competitive regimes

Species	Competitive regime		Grooming r coeff.	Original source
	Sterck et al. (2007)	This study		
Red howler monkey, *Alouatta seniculus*	DE	Egalitarian	0.14	Sánchez-Villagra, Pope, & Salas (1998) [a]
Mantled howler monkey, *Alouatta palliata*	DE	Egalitarian	-0.023	Jones (1979), group 5[b]
	DE	Egalitarian	-0.064	Jones (1979), group 12[b]
Spider monkey, *Ateles geoffroyi*	DE	Egalitarian	0.396	Ahumada (1992) [b]
Vervet monkey, *Cercopithecus aethiops*	RN	Despotic	0.82	Seyfarth (1980), group A[b]
	RN	Despotic	0.706	Seyfarth (1980), group B[b]
	RN	Despotic	0.535	Seyfarth (1980), group C[b]
Blue monkey, *Cercopithecus mitis*	RE	Despotic	0.441	Cords (2000) [b]
Tufted capuchin, *Cebus apella*	RN	Despotic	0.389	Izawa (1980) [b]
White-faced capuchin, *Cebus capucinus*	RN	Despotic	0.262	Perry (1996) [b]
Wedge-capped capuchin, *Cebus olivaceus*	RE	Egalitarian	0.679	O'Brien (1993), MainGroup[b]
Patas monkey, *Erythrocebus patas*	RE	Egalitarian	0.879	Nakagawa (1992) [b]
Japanese macaque, *Macaca fuscata*	RN	Despotic	0.901	Oi (1988), Hanyama-K[b]
	RN	Despotic	0.952	Oi (1988), Hanyama-M[b]
	RN	Despotic	0.709	Takahashi & Furuichi (1998), Kinkazan-A[b]
	RN	Despotic	0.961	Takahashi & Furuichi (1998), Yakushima-M[b]
	RN	Despotic	0.826	Ventura, Majolo, Koyama, Hardie, & Schino (2006), Kw[b]
	RN	Despotic	0.396	Ventura et al. (2006), Nina-A[b]
Bonnet macaque, *Macaca radiata*	RN	Egalitarian	0.429	Sugiyama (1971) [b]
Barbary macaque, *Macaca sylvanus*	RN	Egalitarian	0.102	Fa (1986) [b]
Capped langur, *Trachypithecus pileatus*	–	Egalitarian	0.565	Stanford (1991) [b]
Bonobo, *Pan paniscus*	DE	Egalitarian	0.75	Idani (1991) [b]
Chimpanzee, *Pan troglodytes*	DE	Egalitarian	0.561	Sugiyama (1988) [b]
Red colobus, *Procolobus rufomitratus*	DE	Egalitarian	0.45	Present study

DE = dispersal-egalitarian; RE = resident-egalitarian; RN = resident-nepotistic; RNT = resident-nepotistic-tolerant (following Sterck et al., 1997).
[a] Sourced from review by Lukas and Clutton-Brock (2018).
[b] Sourced from review by Schino and Aureli (2008).