Network cohesion, group size and neocortex size in female-bonded Old World primates

Julia Lehmann¹ and R. I. M. Dunbar^{2,*}

¹*Human and Life Sciences, Whitelands College, Roehampton University, London SW15 4JD, UK*

²*Institute of Cognitive and Evolutionary Anthropology, University of Oxford, Oxford OX2 6PN, UK*

Most primates are intensely social and spend a large amount of time servicing social relationships. In this study, we use social network analysis to examine the relationship between primate group size, total brain size, neocortex ratio and several social network metrics concerned with network cohesion. Using female grooming networks from a number of Old World monkey species, we found that neocortex size was a better predictor of network characteristics than endocranial volumes. We further found that when we controlled for group size, neocortex ratio was negatively correlated with network density, connectivity, relative clan size and proportional clan membership, while there was no effect of neocortex ratio on change in connectivity following the removal of the most central female in the network. Thus, in species with larger neocortex ratios, females generally live in more fragmented networks, belong to smaller grooming clans and are members of relatively fewer clans despite living in a closely bonded group. However, even though groups are more fragmented to begin with among species with larger neocortices, the removal of the most central individual does cause groups to fall apart, suggesting that social complexity may ultimately involve the management of highly fragmented social groups while at the same time maintaining overall social cohesion. These results emphasize a need for more detailed brain data on a wider sample of primate species.

Keywords: primates; social brain; social cohesion; social complexity; neocortex ratio

1. INTRODUCTION

Most primates live in closely bonded social groups in which individuals have differentiated social relationships (Cheney & Seyfarth 1990; Silk 2007). Group size itself correlates with relative neocortex size in primates (Dunbar 1998; Lindenfors *et al.* 2004; Dunbar & Shultz 2007). While this has been interpreted as being synonymous with greater social complexity, analyses of group structure have suggested that large social groups are not simply small groups writ large: rather, large groups seem to be more sub-structured (Kudo & Dunbar 2001), mainly because, in large groups, animals deliberately reduce their social engagement in order to invest in core coalition partners. This ought to have the effect of destabilizing the group, if only because it must reduce social connectivity among the members.

One reason why animals might concentrate their social effort on fewer partners as group size increases is that the costs of group-living increase with group size, especially for low-ranking females who typically experience increasing frequencies of anovulatory menstrual cycles as a result of high levels of harassment in large groups (Dunbar 1980, 1988; Abbott *et al.* 1986). Primates seek to buffer themselves against these costs by forming grooming-based coalitions that help to reduce the intrusiveness of these effects (Dunbar *in press*). In most cases, this probably involves passive effects (e.g. the threat implied by

alliances signalled by grooming partnerships (Cheney & Seyfarth 1980; Bergman *et al.* 2003); reduced stress levels (Crockford *et al.* 2008; Wittig *et al.* 2008)), but can sometimes involve active defence (Dunbar 1989).

Wittig *et al.* (2008) showed that, at least in baboons, females who belong to smaller social networks—or who reduce network size by cutting out more casual interactions—cope better (as indexed by serum corticosteroid titres) with stressful events (such as the immigration of a potentially infanticidal male) than do females who have larger networks. Similarly, Dunbar & Dunbar (1988) found that, in gelada, lactating females progressively withdrew from casual interactions to focus increasingly on their core grooming partner(s) as the costs of lactation placed increasing stress on their time budgets.

Although primate groups become increasingly sub-structured as their size increases, the fact that this also correlates with both increasing neocortex volume (Dunbar & Shultz 2007; Lehmann *et al.* *in press*) and indices of social skill (Pawlowski *et al.* 1998; Byrne & Corp 2004) suggests that a large neocortex might enable social coherence to be maintained in larger groups, despite the inevitably disruptive effects of sub-structuring. Since cognitive ability might thus play an important role in allowing species to cope with the socio-logical stresses of living in a large social group, it is important to distinguish between the effects of group size and brain size.

In this study, we investigate the relationship between brain size, group size and primate social network cohesion in order to ask whether large brains might be used to offset the effects that increasing group size might have on group

* Author for correspondence (robin.dunbar@anthro.ox.ac.uk).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2009.1409> or via <http://rspb.royalsocietypublishing.org>.

network structure. We focus our analysis on species in which females are philopatric and form female-bonded matriline. By concentrating on female–female social relationships in species in which females remain within their natal communities throughout their lives, we avoid the complicating issues of reproductive relationships and different dispersal patterns which would be hard to control for in such analyses. Since there are no theoretical grounds for expecting any specific network metrics to reflect a particular pattern of social organization, we use a number of network metrics in our analysis that aim at measuring the level of overall network cohesion. We also test between two alternative indices of brain volume (endocranial volume versus neocortex size) as predictor for network metrics in primates since there remains some ambivalence as to which might be the better predictor of sociality (Deaner *et al.* 2000).

2. MATERIAL AND METHODS

(a) Data

Data on grooming patterns in 11 species (representing guenons, macaques, baboons and gelada) included in this analysis are given in the electronic supplementary material, table S1. The average number of females in a group was 11 (range 5–18, $n = 11$ species), well within the normal range for these species. All the social groups were stable through time, and showed no indication of fragmentation. In addition to group size, brain size indices and network variables, we include two other potential covariates, namely female body mass and sexual dimorphism (male/female body mass).

We used two brain measures, namely total endocranial volumes (taken from Isler *et al.* 2008) and neocortex ratio (volume of the neocortex/volume of the rest of the brain: Dunbar 1992). Whenever possible, we calculated neocortex ratios based on actual brain tissue volumes as given by Stephan *et al.* (1981). For those species for which no published data on neocortex volumes were available, we estimated neocortex ratio from female endocranial volume using the equations given by Kudo & Dunbar (2001). Because the majority of our dataset is based on neocortex ratio estimates, we made an additional effort to validate the equations used for calculating neocortex ratio. We used the comprehensive dataset from Isler *et al.* (2008) to calculate the estimated neocortex ratios using the equations from Kudo & Dunbar (2001) and correlated those estimates with ‘real’ neocortex ratios based on Stephan *et al.* (1981). We found that estimates correlate highly with real neocortex measures ($r^2 = 0.86$, $n = 36$, $p < 0.001$) with a slope parameter very close to $\beta = 1$ ($\beta = 0.94$), indicating that estimates of neocortex ratios are very close to real values (see the electronic supplementary material, figure S1).

(b) Network parameters

For all grooming matrices, we calculated the percentage of total individual grooming effort directed towards a particular partner. These percentages represent the distribution of individual grooming effort across same-sex group members. Using these matrices, we calculated network density by dividing the number of existing grooming relationships by the total number of possible relationships ($N^2 - N$ in the case of directed relationships; Wasserman & Faust 1994). Network density therefore allows us to assess what proportion of the existing dyads actually interacted. To examine the structure of grooming networks in more detail,

we first made the matrices symmetric and then dichotomized them, using UCInet (6.170, Analytic Technologies, Lexington, USA). Matrices were made symmetrical using the maximum effort rules (i.e. any particular dyad was given its maximum value, irrespective of whether this was grooming given or grooming received, assuming that a social bond exists irrespective of the direction of the behaviour exchanged). In addition, following standard practice in analyses of this kind, dichotomized matrices were filtered so as to include only significant grooming relationships in the analyses: this is considered advisable in order to avoid the problem of unnecessary error variance introduced by too many casual interactions (James *et al.* 2009). We only considered relationships in which one of the partners invested more than 10 per cent of their total grooming effort as ‘real’ relations (or edges) and included these in the network analysis. The value of 10 per cent was determined by plotting for each population the mean number of grooming partners against a range of discriminant values (DV). The DV at which there was a steep drop-off in the number of grooming partners per individual was chosen as the cut-off value (Lehmann *et al.* in press). Across populations, the mean and the modal DV value was 0.1 (see also Dunbar 1984; Kudo & Dunbar 2001). This edge-filtering technique allows us to concentrate on relatively strong relationships, thereby reducing the problem of the distorting effects that casual relationships can have on network metrics, especially in short-term studies (James *et al.* 2009). More importantly, this procedure does not suffer from the weak links problem that can be important in some biological contexts such as disease transmission (James *et al.* 2009): in the present context, social grooming is of interest not for its weak link properties, but only to the extent that it provides an index of the strength of social relationships. Hence, our interest lies mainly with dyads that groom frequently rather than rarely.

The transformed symmetric binary matrices were then used to analyse sub-grouping patterns. Network analysis provides a multitude of different algorithms to analyse subgrouping patterns. In this study, we used an algorithm to identify all subgroups in which each individual is connected to each other individual by a maximum distance of two links (n -clans in UCInet). In line with network terminology, we refer to these subgroups as grooming clans. The use of two-clans is a common network algorithm that allows sub-grouping patterns to be identified in larger networks. Because very few Old World monkeys have grooming clusters that contain more than three individuals (Kudo & Dunbar 2001), we do not consider larger distances to be meaningful for these animals. We determined average clan size in relation to overall female group size and the average percentage of all clans that a particular female belonged to. In addition, we also calculated individual connectivity (i.e. the number of links that need to be deleted so that there is no longer a connection between any two individuals) as an indicator of network cohesiveness (a cohesive network is assumed to be less vulnerable to the removal of any one individual). Individual values were averaged within populations.

Finally, in order to determine how important individual females are for the average network connectivity, we analysed the change (expressed as percentage of total) in the overall network connectivity after the (statistical) removal of the most central female from the network. We have shown

elsewhere that there is a significant decrease in overall connectivity following the removal of the most but not the least central individual (Lehmann *et al.* in press), indicating that the overall network structure in these primates is typically dominated by a few very central individuals. Centrality was measured using Freeman's 'between-ness value' (i.e. the number of shortest paths between any dyad involving individual i): an individual with a high between-ness value links a large number of otherwise unconnected females and is hence highly central (Wasserman & Faust 1994). Such individuals are often referred to as 'brokers' (Lusseau & Newman 2004) and it has been hypothesized that socially more complex species rely more on weak links (Kudo & Dunbar 2001), which are functionally brokers. Thus, networks that are highly dependent on brokers are expected to 'fall apart' when such central individuals are removed.

Whenever possible, we collated networks for more than one population per species, thereby avoiding the pitfall of the representativeness of single networks (see James *et al.* 2009). Whenever grooming matrices were available from more than one study/population per species (six of the 11 species), we averaged values across those studies for all between-species comparisons. The dataset includes data from both wild and captive populations. We initially treated these as two different datasets, but as there were no significant differences between them in any analyses (Andrews 2008), they were combined for all the analyses reported here.

(c) Statistical analysis

We controlled for phylogenetic non-independence in cross-species comparisons by using the method of independent contrasts (CAIC: Purvis & Rambaut 1995). Log-transformed data were used in independent contrast analysis. Phylogeny was based on a Bayesian consensus tree, available from <http://10ktrees.fas.harvard.edu/index.html>. Because comparative analyses are potentially sensitive to branch lengths, we ran the analysis twice, once using mean branch lengths averaged across all trees in the consensus analysis and once assuming equal branch length between species. Since results were identical, we only report those based on mean branch length. Data were analysed using a multivariate general linear model (SPSS 15), with network parameters as dependent variables and group size, sexual dimorphism index and neocortex ratio, female body mass and female endocranial volume, respectively, as covariates. In order not to over-parameterize the model, only main effects were included. Finally we used stepwise regression to evaluate which of the correlated parameters (body mass or neocortex ratio) was the better predictor of social network structure in primates.

3. RESULTS

Because endocranial volume, neocortex ratio and female body mass are highly correlated, we ran the analysis three times, each time including just one of these variables together with the other two covariates (female group size and sexual dimorphism index). Results for all three models were found to be broadly similar (which is to be expected given that endocranial volume, female body mass and neocortex ratios are highly correlated) (table 1). Interestingly, female body mass was a better predictor for network parameters than endocranial

volumes (table 1), but model r -values (which indicate the amount of variance explained by the model) were highest for the models containing neocortex ratios for all the five variables analysed (table 1). This suggests that neocortex ratio is the more important predictor of female network parameters. This is also supported by the finding that a stepwise regression procedure always excluded body mass but included neocortex ratio for those variables where neocortex ratio was found to be significant in the multivariate analysis. Given these results, we focus on the remainder of the paper on model 3, which uses neocortex ratio as a predictor.

Overall, sexual dimorphism only had a significant effect on the percentage change in connectivity following the removal of the most central female ($F_{\text{body mass}} = 7.9$, $p_{\text{body mass}} < 0.03$, $F_{\text{endocranial}} = 9.34$, $p_{\text{endocranial}} < 0.02$; $F_{\text{neocortex}} = 7.9$, $p_{\text{neocortex}} < 0.03$; figure 1). Networks of highly sexual dimorphic species are more affected by the removal of a central female than less dimorphic species.

With neocortex ratio and sexual dimorphism controlled for, group size was found to be positively related only to two network metrics (table 1): average connectivity and percentage change in connectivity following the removal of the most central female. Females in larger groups form more strongly connected social networks (higher connectivity; figure 2), which are less affected by the removal of a central female. Density, relative clan size and relative clan membership were not affected by group size (after controlling for neocortex ratio).

By contrast, with group size and sexual dimorphism partialled out, neocortex ratio was negatively related to most of the network parameters: species with larger neocortices form relatively smaller clans and were members of relatively fewer clans (figure 3*a,b*). In addition, the networks of these species were found to be significantly less dense and had a lower connectivity (figure 4*a,b*). This indicates that, when group size is partialled out, grooming networks in species with larger neocortices are more fragmented, even in stable social groups. Interestingly, there was no relationship between neocortex size and the percentage of reduction in connectivity following the removal of the most central individual, indicating that the networks of large brained species do not lose their overall connectivity, despite the fact that they are more fragmented in the first place (table 1).

4. DISCUSSION

Our analysis shows that, in female-bonded Old World monkey species, social network parameters are correlated with both group size and brain size, especially neocortex size, with both variables having independent effects. Overall, our analysis supports previous findings (Dunbar & Shultz 2007) that it is indeed relative neocortex size and not the overall brain size that is related to primate social complexity. Endocranial volume, female body mass and neocortex size are strongly correlated, but for all dependent variables the models including relative neocortex ratio produced stronger results, followed by female body mass, while endocranial volume produced the weakest models. It is important to note that these relationships hold over a narrow range of neocortex volumes and

Table 1. Multivariate general linear model analysis of individual network indices. (NCr, neocortex ratio; Grpsz, group size; clan size (%), average clan size as percentage of total group size; % membership, relative number of clans an individual belongs to; % delta connectivity, change in the overall network connectivity (in per cent) following the statistical removal of the most central female; adjusted model $r =$ adjusted r -value of the model as an indicator for model performance (explained variance). Bold values indicate significant results ($p < 0.05$). Sexual dimorphism index was also included into all three models but since it only had a significant effect on % delta connectivity we did not include its statistical values in the table (see text). All the analyses are based on independent contrasts and models did not include an intercept.)

		density			connectivity			clan size (%)			% membership			% delta connectivity		
		<i>F</i>	<i>p</i>		<i>F</i>	<i>p</i>		<i>F</i>	<i>p</i>		<i>F</i>	<i>p</i>		<i>F</i>	<i>p</i>	
model 1	Grpsz	0.002	> 0.9		9.997	< 0.02		1.570	> 0.2		2.28	> 0.15		41.738	< 0.001	
	body mass	3.739	> 0.09		4.129	> 0.08		8.228	< 0.03		4.685	> 0.06		0.532	> 0.4	
	adjusted model r	$r = 0.41$	> 0.08		$r = 0.438$	> 0.07		$r = 0.591$	< 0.05		$r = 0.52$	< 0.05		$r = 0.834$	< 0.002	
model 2	Grpsz	0.037	> 0.8		9.821	< 0.02		0.367	> 0.5		4.246	> 0.05		33.658	< 0.002	
	endocranial	2.02	> 0.1		3.659	> 0.09		6.123	< 0.05		4.068	> 0.08		0.368	> 0.5	
	adjusted model r	$r = 0.3$	> 0.1		$r = 0.413$	> 0.08		$r = 0.525$	< 0.05		$r = 0.493$	> 0.05		$r = 0.830$	< 0.002	
model 3	Grpsz	3.127	> 0.1		17.4	< 0.01		0.285	> 0.6		0.077	> 0.7		26.65	< 0.002	
	NCr	12.18	$p < 0.01$		8.481	< 0.03		13.634	< 0.01		13.83	< 0.01		0.529	> 0.4	
	adjusted model r	$r = 0.669$	< 0.002		$r = 0.596$	< 0.03		$r = 0.698$	< 0.01		$r = 0.731$	< 0.01		$r = 0.834$	< 0.002

Figure 1. Relationship between sexual dimorphism index and percentage change in connectivity following the removal of the most central female. Graphs represent partial plots, controlling for group size and neocortex ratio; calculations are based on independent contrasts. For statistical values see table 1.

Figure 2. Relationship between group size and (a) connectivity, (b) per cent change in connectivity. Graphs represent partial plots, controlling for sexual dimorphism and neocortex ratio; calculations are based on independent contrasts. For statistical values see table 1.

quite a modest range in group sizes (relative to the overall distributions for all primates).

Once we controlled for brain size, there was relatively little effect of group size on network parameters. However, group size was found to be positively correlated to overall connectivity and this relationship remained significant even after the removal of the most central female in the group. This suggests that females in large groups are better connected and less affected by the removal of a central individual and that there may be a dissociation

Figure 3. Relationship between neocortex ratio and (a) clan size (as % of total female group size) and (b) per cent clan membership. Graphs represent partial plots, controlling for group size and sexual dimorphism; calculations are based on independent contrasts. For statistical values see table 1.

between the effects of group size and those of social cognition *per se* (as measured by neocortex size), indicating that group size may not always be a reliable proxy for social complexity. However, the significance of these relationships in the present analysis remains uncertain because of the possibility that some network metrics may scale with group size (James *et al.* 2009).

By contrast, after controlling for group size, neocortex size seems to be a very strong predictor of network structure: species with larger neocortices have less dense and less connected networks, with individuals being members of smaller and relatively fewer grooming clans. The fact that these relationships are all negative is important: as relative neocortex size increases, primate groups become more deeply structured, with females concentrating their social effort on an increasingly smaller subset of core social partners, as indicated by the fact that relative clan size and relative individual involvement in clans reduces with increasing neocortex ratio. This also results in overall reduced network density and connectivity, suggesting that social complexity may ultimately involve the management of highly fragmented social groups while at the same time maintaining overall social cohesion (see also Lehmann *et al.* in press). In other words, species with larger neocortices seem to be able to use their greater social skills to maintain cohesion in large groups despite the fact that larger groups will inevitably become more fragmented.

It has been suggested that weak ties become increasingly important in socially more complex systems, because they link otherwise unlinked subgroups (Maryanski 1987). Although, in general, removing the most central female (i.e. the most connected individual)

Figure 4. Relationship between neocortex ratio and (a) network density and (b) connectivity. Graphs represent partial plots, controlling for group size and sexual dimorphism; calculations are based on independent contrasts. For statistical values see table 1.

in this sample of species results in groups becoming significantly less connected than if the female with the lowest between-ness index is removed (Lehmann *et al.* in press; see also Kudo & Dunbar 2001), our finding that this effect is not correlated with neocortex ratio suggests that the networks of species with larger neocortex ratios are not more vulnerable to the removal of individual group members, despite the fact that their networks are less dense and have a lower connectivity value. This supports the hypothesis that brokers are indeed increasingly important in larger brained species, in line with Maryanski's (1987) prediction that one function of weak ties may be that they allow for greater social flexibility.

We suggest that it is this capacity that allows these species of primates to maintain large coherent social groups. Thus, despite having more concentrated ego-networks (perhaps because of the need to buffer themselves against the costs of living in large groups), it seems that species with large neocortices are still able to maintain coherence in the network as a whole, through exploiting weak links. Thus, in socially complex species, we should expect a high degree of social flexibility and hence individual group members should be able to adjust their networks relatively quickly to the new conditions (Flack *et al.* 2006), thereby maintaining overall group cohesion.

We have concentrated here on only one social behaviour, namely grooming; however, it has been suggested (Lehmann & Boesch 2009; Lehmann *et al.* in press) that one characteristic of social complexity may be that networks based on different behaviours are highly divergent, and that this may buffer highly structured and fragmented groups against the effects of the removal of weak ties. It may be that species with large neocortices

are better able to manage relationships based on several different metrics (see Bergman *et al.* 2003) and it is this that allows them to manage greater social structuring. Finally, we should note that, while the correlation between estimated and actual neocortex values is very reasonable ($r = 0.92$, slope $\beta \approx 1$), it is far from perfect, such that some error variance is necessarily introduced into the analyses. While any such bias ought to act conservatively by reducing the significance of the results, it is always possible that these estimates might have introduced a consistent bias; that aside, our results at worst emphasize the need for brain region data on a wider sample of primate species so that more refined analyses can be carried out.

J.L. was funded by the British Academy Centenary Research Project. We would also like to thank several colleagues who generously shared their unpublished data with us, as well as Katherine Andrews for collating the data and Susanne Shultz for discussions about data analysis.

REFERENCES

- Abbott, D. H., Keverne, E. B., Moore, G. F. & Yodyingud, U. 1986 Social suppression of reproduction in subordinate talapoin monkeys, *Miopithecus talapoin*. In *Primate ontogeny* (eds J. Else & P. C. Lee), pp. 329–341. Cambridge, UK: Cambridge University Press.
- Andrews, K. 2008 Social cohesion in primate societies, MPhil thesis, University of Liverpool, UK.
- Bergman, T. J., Beehner, J. C., Cheney, D. L. & Seyfarth, R. M. 2003 Hierarchical classification by rank and kinship in baboons. *Science* **302**, 1234–1236. (doi:10.1126/science.1087513)
- Byrne, R. W. & Corp, N. 2004 Neocortex size predicts deception rate in primates. *Proc. R. Soc. Lond. B* **271**, 1693–1699. (doi:10.1098/rspb.2004.2780)
- Cheney, D. L. & Seyfarth, R. M. 1980 Vocal recognition in free-ranging vervet monkeys. *Anim. Behav.* **28**, 362–367. (doi:10.1016/S0003-3472(80)80044-3)
- Cheney, D. L. & Seyfarth, R. M. 1990 *How monkeys see the world*. Chicago, IL: University of Chicago Press.
- Crockford, C., Wittig, R. M., Whitten, P. L., Seyfarth, R. M. & Cheney, D. L. 2008 Social stressors and coping mechanisms in wild female baboons (*Papio hamadryas ursinus*). *Horm. Behav.* **53**, 254–265. (doi:10.1016/j.yhbeh.2007.10.007)
- Deaner, R. O., Nunn, C. L. & Van Schaik, C. P. 2000 Comparative tests of primate cognition: different scaling methods produce different results. *Brain Behav. Evol.* **55**, 44–52. (doi:10.1159/000006641)
- Dunbar, R. I. M. 1980 Determinants and evolutionary consequences of dominance among female gelada baboons. *Behav. Ecol. Sociobiol.* **7**, 253–265. (doi:10.1007/BF00300665)
- Dunbar, R. I. M. 1984 *Reproductive decisions: an economic analysis of gelada baboon social strategies*. Princeton, NJ: Princeton University Press.
- Dunbar, R. I. M. 1988 Habitat quality, population dynamics and group composition in colobus monkeys (*Colobus guereza*). *Int. J. Primatol.* **9**, 299–329.
- Dunbar, R. I. M. 1989 Reproductive strategies of female gelada baboons. In *Sociobiology of sexual and reproductive strategies* (eds A. Rasa, C. Vogel & E. Volland), pp. 74–92. London, UK: Chapman & Hall.
- Dunbar, R. I. M. 1992 Neocortex size as a constraint on group size in primates. *J. Hum. Evol.* **20**, 469–493.
- Dunbar, R. I. M. 1998 The social brain hypothesis. *Evol. Anthropol.* **6**, 178–190. (doi:10.1002/(SICI)1520-6505(1998)6:5<178::AID-EVAN5>3.0.CO;2-8)
- Dunbar, R. I. M. In press. Brain and behaviour in primate evolution. In *Mind the gap: tracing the origins of human universals* (eds P. Kappeler & J. Silk). Berlin, Germany: Springer.
- Dunbar, R. I. M. & Dunbar, P. 1988 Maternal time budgets of gelada baboons. *Anim. Behav.* **36**, 970–980. (doi:10.1016/S0003-3472(88)80055-1)
- Dunbar, R. I. M. & Shultz, S. 2007 Understanding primate brain evolution. *Phil. Trans. R. Soc. B* **362**, 649–658. (doi:10.1098/rstb.2006.2001)
- Flack, J. C., Girvan, M., de Waal, F. B. M. & Krakauer, D. C. 2006 Policing stabilizes construction of social niches in primates. *Nature* **439**, 426–430. (doi:10.1038/nature04326)
- Isler, K., Kirk, E. C., Miller, J. M. A., Albrecht, G. A., Gelvin, B. R. & Martin, R. D. 2008 Endocranial volumes of primate species: scaling analyses using a comprehensive and reliable data set. *J. Hum. Evol.* **55**, 967–978. (doi:10.1016/j.jhevol.2008.08.004)
- James, R., Croft, D. P. & Krause, J. 2009 Potential banana skins in animal social network analysis. *Behav. Ecol. Sociobiol.* **63**, 989–997. (doi:10.1007/s00265-009-0742-5)
- Kudo, H. & Dunbar, R. I. M. 2001 Neocortex size and social network size in primates. *Anim. Behav.* **62**, 711–722. (doi:10.1006/anbe.2001.1808)
- Lindfors, P., Fröberg, L. & Nunn, C. L. 2004 Females drive primate social evolution. *Biol. Lett.* **1**, 101–103. (doi:10.1098/rsbl.2003.0114)
- Lehmann, J. & Boesch, C. 2009 Sociality of the dispersing sex: the nature of social bonds in west African female chimpanzees (*Pan troglodytes*). *Anim. Behav.* **77**, 377–387. (doi:10.1016/j.anbehav.2008.09.038)
- Lehmann, J., Andrews, K. & Dunbar, R. I. M. In press. Social networks and social complexity in female-bonded primates. In *Social brain, distributed mind* (eds R. I. M. Dunbar, C. Gamble & J. A. Gowlett). Oxford, UK: Oxford University Press.
- Lusseau, D. & Newman, M. E. J. 2004 Identifying the role that animals play in their social networks. *Proc. R. Soc. Lond. B* **271**, S477–S481. (doi:10.1098/rsbl.2004.0025)
- Maryanski, A. R. 1987 African ape social structure: is there strength in weak ties? *Social Netw.* **9**, 191–215. (doi:10.1016/0378-8733(87)90020-7)
- Pawlowski, B. P., Lowen, C. B. & Dunbar, R. I. M. 1998 Neocortex size, social skills and mating success in primates. *Behaviour* **135**, 357–368.
- Purvis, A. & Rambaut, A. 1995 Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Comput. Appl. Biosci.* **11**, 247–251.
- Silk, J. B. 2007 Social components of fitness in primate groups. *Science* **317**, 1347–1351. (doi:10.1126/science.1140734)
- Stephan, H., Frahm, H. & Baron, G. 1981 New and revised data on volumes in brain structures in insectivores and primates. *Folia Primatol.* **35**, 1–29. (doi:10.1159/000155963)
- Wasserman, S. & Faust, K. 1994 *Social network analysis: methods and applications*. Cambridge, UK: Cambridge University Press.
- Wittig, R. M., Crockford, C., Lehmann, J., Whitten, P. L., Seyfarth, R. M. & Cheney, D. L. 2008 Focused grooming networks and stress alleviation in wild female baboons. *Horm. Behav.* **54**, 170–177. (doi:10.1016/j.yhbeh.2008.02.009)