Females drive primate social evolution

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Within and across species of primates, the number of males in primate groups is correlated with the number of females. This correlation may arise owing to ecological forces operating on females, with subsequent competition among males for access to groups of females. The temporal relationship between changes in male and female group membership remains unexplored in primates and other mammalian groups. We used a phylogenetic comparative method for detecting evolutionary lag to test whether evolutionary change in the number of males lags behind change in the number of females. We found that change in male membership in primate groups is positively correlated with divergence time in pairwise comparisons. This result is consistent with male numbers adjusting to female group size and highlights the importance of focusing on females when studying primate social evolution.

1. INTRODUCTION

A fundamental question in social evolution concerns the factors that influence group size and composition. What factors influence variation in group size across species, and how do these factors affect the numbers of adult males and females within groups? These questions have been addressed by focusing on the ecological variables that determine the spatio-temporal distribution of females, based on the expectation that resources and predation account for variation in female reproductive success. By comparison, access to females is generally the major factor influencing male reproductive success (Trivers 1972; Wilson 1975; Emlen & Oring 1977). Thus, after risks and resources determine the spatio-temporal distribution of females, the distribution of females is expected to influence the degree of male intrasexual competition (Emlen & Oring 1977). The general framework is therefore one of female-driven social evolution.

Comparative tests of this general framework have been conducted across species of primates, with results showing that the number of males in primate groups correlates with the number of females (Andelman 1986; Ridley 1986; Dunbar 1988; Altmann 1990; Mitani *et al.* 1996; Nunn 1999). A common interpretation of this pattern is that as female group size increases owing to the ecological advantages of group-living, it becomes more difficult for a single male to defend access to the group of females, resulting in multimale–multifemale groups. Recently, it has been shown that additional variation in male membership can be accounted for by female mating behaviour; species in which females mate more synchronously exhibit relatively more males in the group (Nunn 1999). This effect is expected if it is more difficult for a single male to monopolize access when two or more females are mating simultaneously in the group.

These comparative tests, along with similar tests within species (Altmann 2000), support one prediction of models based on female-driven social evolution: the number of males in primate groups varies according to the degree of competition over females (sexual selection). Thus, males are adjusting to variation in female spatial and temporal availability, or, as stated by Altmann (1990), 'primate males go where the females are' (p. 193).

In this paper, we test another prediction of female-driven social evolution that has yet to be investigated empirically and focuses on the causal links between males and females. Specifically, female-driven social evolution predicts sequential effects, with the number of females influencing the number of males in primate groups. Thus, evolutionary changes in the number of males are expected to lag behind changes in the number of females. When investigating patterns across species, at least three factors may cause the number of males (male group size) to lag behind the number of females (female group size). First, changes in the number of males may be sensitive to female sexual behaviour, such as oestrous synchrony, which may not evolve instantaneously as female group size increases. Selection for such adjustments in female sexual behaviour may result from variation in the degree of predation or infanticide risk (van Schaik & Hörstermann 1994; van Schaik & Janson 2000). Second, individuals may require time to evolve defences to infectious disease risk that are expected to increase in multimale–multifemale groups, including risks of acquiring socially or sexually transmitted diseases (Freeland 1976; Møller *et al.* 1993; Nunn *et al.* 2000; Nunn & Altizer 2004). Finally, cognitive constraints may limit the number of individuals in groups (Dunbar 1988). For example, male alliances in multimale primate groups require a degree of cooperation that is unlikely to exist in strictly polygynous systems (Sommer 1988).

2. MATERIAL AND METHODS

To test the hypothesis that male group size lags behind female group size in primate groups, we acquired data on the number of males and the number of females in groups, and primate phylogeny. Data on group composition were taken from Nunn & Barton (2000), to which we added data on solitary strepsirhines and tarsiers from Kappeler & Heymann (1996). Group sizes were log-transformed prior to analyses. Analyses were carried out using both the full dataset and a dataset with solitary species removed, as evolutionary analyses of social animals should provide the strongest tests of the hypothesis. Phylogenetic information was taken from Purvis (1995), which is a dated supertree synthesized using both morphological and molecular information.

To test the lag hypothesis, we used a phylogenetic method described in Deaner & Nunn (1999), which was originally used to test whether primate brain size lags behind body size. The method is implemented by first calculating unstandardized independent contrasts (Felsenstein 1985) in female number (ΔX_n) and male number (ΔY_n) using only the tips of the phylogeny. Contrasts are constructed such that ΔX_n is forced to be positive, based on the fact that the direction of subtraction is arbitrary for independent contrasts (Garland *et al.* 1992). The second step calculates residuals from a regression through the origin of ΔY_n against ΔX_n. The final step involves regressing these residuals on time since the taxa diverged.

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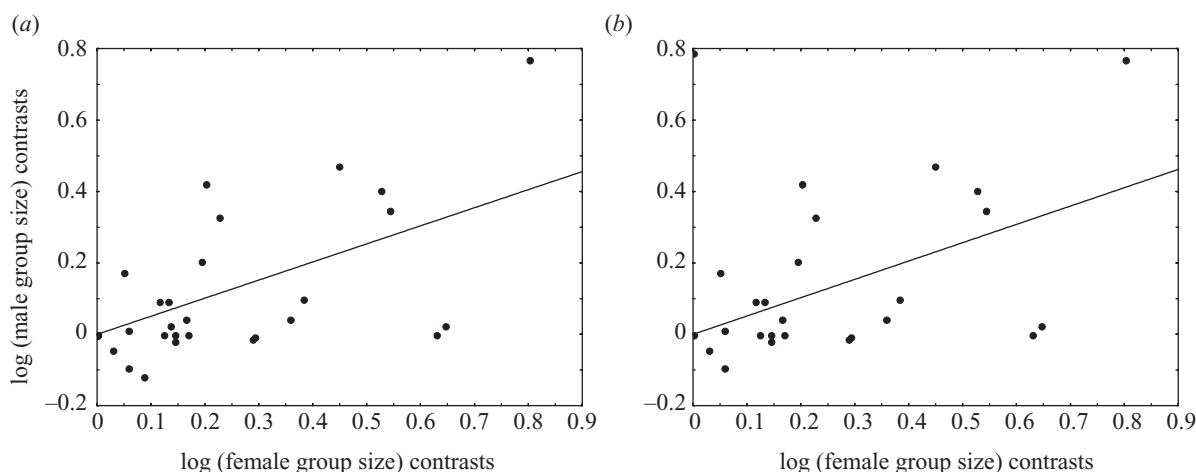DOI 10.1098/rsbl.2003.0114

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(a)

(b)

Figure 1. The relationship between male group size and female group size in primates. Plots show independent contrasts calculated at the tips of the tree only, with the least-squares regression line forced through the origin. (a) Using the full dataset, (b) solitary species excluded. See § 3 for statistical results.

Evolutionary lag is indicated by larger residuals on contrasts characterized by longer branches, which indicates that relative to ΔX_n, ΔY_n increases when there is more time available for change to take place. In other words, we are testing whether male group size is larger than expected on longer branches and smaller than expected on shorter branches. We used only pairwise contrasts calculated using extant trait values because the method relies on accurate estimates of time since divergence and the amount of evolutionary change since two species last shared a common ancestor. Following Deaner & Nunn (1999), we also checked whether more change occurs on longer branches, but found no significant relationship between pairwise contrasts in female group size and divergence dates ($b = 0.009$, $R^2 = 0.020$, $n = 37$, $p = 0.407$; after excluding solitary species: $b = 0.012$, $R^2 = 0.012$, $n = 27$, $p = 0.593$). Further information on the method and its application is available in Deaner & Nunn (1999). All statistical results reported are from two-tailed tests.

3. RESULTS

Groups sizes of males and females were significantly correlated, both when using the full dataset ($b = 0.506$, $R^2 = 0.506$, $n = 37$, $p < 0.001$) and when excluding solitary species ($b = 0.508$, $R^2 = 0.359$, $n = 28$, $p < 0.001$) (figure 1). To test the lag hypothesis, we calculated residuals from the regression of male number on female number. Residual male group size scaled positively with the divergence dates of pairwise comparisons, both when using all available data ($y = 0.017x - 0.064$, $R^2 = 0.167$, $n = 37$, $p = 0.012$) and when excluding solitary species ($y = 0.025x - 0.069$, $R^2 = 0.178$, $n = 28$, $p = 0.025$). These results are consistent with the hypothesis that male group size lags behind female group size (figure 2).

The results can be summarized as occurring due to reduced variation in male group size on shorter branches of the primate tree, leading to negative residuals on the left-hand sides of figure 2a,b and positive residuals on the right-hand sides of these figures. This pattern could arise if comparisons among two unimale–multifemale primate species, as compared with pair-living, unifemale–multimale or multimale–multifemale species, are characterized by shorter branch lengths. Specifically, contrasts involving male group size among two unimale–multifemale sister species would be expected to be small, owing to the fact that these species by definition have a similar number of males, whereas contrasts in female group size would exhibit a greater degree of variation and would be larger. On the contrasts plot (figure 1), unimale–multifemale species

therefore would be more likely to have negative residuals. If this alternative explanation accounts for the results in figure 2, then contrasts linking unimale–multifemale species should have shorter branches than other contrasts used in our analyses. Out of the 37 contrasts available in the complete dataset, there were only nine contrasts linking two unimale–multifemale species. We found, however, no statistically significant differences between the branch lengths involving unimale–multifemale species as related to other contrasts in the dataset. In addition, we repeated the analyses after excluding these nine pairwise comparisons. Residual male group size scaled positively with divergence date when using this subset of all available data ($y = 0.018x - 0.060$, $R^2 = 0.193$, $n = 28$, $p = 0.019$), with results approaching significance after further excluding the solitary species ($y = 0.021x - 0.057$, $R^2 = 0.128$, $n = 25$, $p = 0.078$).

4. DISCUSSION

In this study we confirmed previous results (Andelman 1986; Dunbar 1988; Altmann 1990; Mitani *et al.* 1996; Nunn 1999) that male and female group sizes are tightly correlated across species of primates. Our results also support predictions of the lag hypothesis: change in the number of males lags behind change in the number of females. These results point to females as the driving sex in primate social evolution, with female group size changing first and male group size subsequently adjusting to female number.

Alternatives to the female-driven model, or variations on this general model, have been proposed. For example, females may seek protection from predation, sexual coercion or infanticide by forming associations with males (Wrangham 1979; Smuts & Smuts 1993; van Schaik 1996; van Schaik & Kappeler 1997). Such hypotheses require the opposite pattern to that found here, with female group size predicted to lag behind male group size. We cannot rule out such effects in individual species and there is much variation left unexplained (figure 2). Our results nevertheless indicate that, in general, female-driven social evolution accounts for significant variation in patterns of group membership across primates.

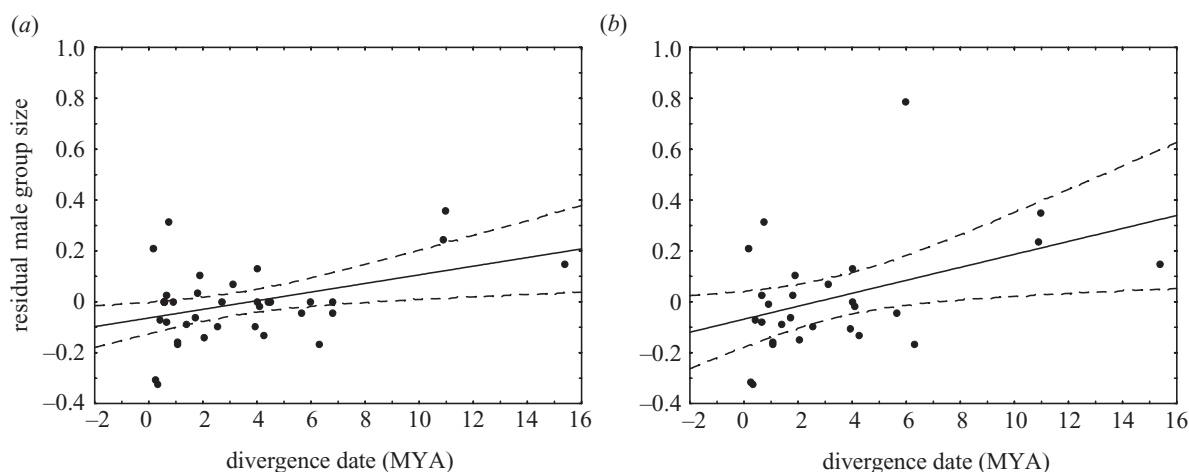The ecological model proposed by Emlen & Oring (1977) is expected to account for variation both across

Figure 2. Evolutionary lag in male group size. Residual male group size (see figure 1) correlates with divergence date, indicating that male group size lags behind female group size evolution. (*a*) Using the full dataset, (*b*) solitary species excluded. Plots show regression lines with 95% confidence intervals (dashed lines). See § 3 for statistical results.

and within species, and previous work on primates has shown that intraspecific variation also supports the general prediction of the female-driven model, namely that male and female numbers are correlated (Altmann 2000). Because the processes that produce these patterns operate within species, it may be surprising that lag would exist across species. As noted in § 1, however, several factors may account for this pattern at the interspecific level, including the time required for males and females to evolve sexual, behavioural and physiological adaptations to living in groups of different size and composition.

In conclusion, these results highlight the importance of focusing on females when studying primate social evolution. It is female group size that apparently responds to natural selection, and it is consequently their group size that holds the key to understanding what drives social evolution in the first place. Future research should continue to integrate the patterns linking male and female group size to the ecological variation that ultimately underlies cross-species variation in primate sociality.

Acknowledgements

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