

What traits promote male parallel dispersal in primates?

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Summary

Parallel dispersal occurs when individuals emigrate together with peers or close kin, or immigrate into groups containing familiar or closely related individuals. To understand the evolution of parallel dispersal in male primates, we explore if parallel dispersal co-occurs with male coalitions, or with other traits that may facilitate coalition formation. We conducted a meta-analysis using phylogenetic comparative methods to test for an association between male parallel dispersal and male coalition formation, multi-male social groups, male-biased dispersal, high paternity concentration, and breeding seasonality. These traits were predicted to be correlated with parallel dispersal because they increase the availability of potential dispersal partners, increase individual competitive ability, or provide inclusive fitness benefits for cooperating relatives. Pairwise comparisons revealed that coalitions in general were significantly associated with male parallel dispersal. However, neither intergroup nor intragroup coalitions were associated with parallel dispersal when examined separately, though there was a trend towards significance for intergroup coalitions. Male-biased dispersal was equivocally associated with parallel dispersal, while multi-male social groups, paternity concentration, and breeding seasonality were not. These results suggest that the evolution of male parallel dispersal may be linked with the propensity of males to form coalitions and the need to retain coalition partners.

Keywords: primates, parallel dispersal, coalitions, phylogenetic comparative methods, pairwise comparisons.

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Introduction

Dispersal involves moving from familiar to unfamiliar ecological and/or social environments (locational and social dispersal, respectively; Isbell & Van Vuren, 1996). It is a costly behaviour that is nonetheless undertaken by many individuals. Parallel dispersal occurs when individuals emigrate together with peers or close kin, or immigrate into groups containing familiar or closely related individuals (van Hooff, 2000), and may have evolved as a means to mitigate the costs of dispersal (Pusey & Packer, 1987a). We aim to explore whether the occurrence of male coalitions, and factors that may facilitate coalition formation, may have influenced the evolution of male parallel dispersal in primates.

Parallel dispersal has been reported in a wide range of group-living mammals, including carnivorans (e.g., African wild dogs, *Lycaon pictus*: Frame & Frame, 1976; and lions, *Panthera leo*: Pusey & Packer, 1987b), and primates (e.g., vervet monkeys, *Cercopithecus aethiops*: Cheney & Seyfarth, 1983; white-faced capuchins, *Cebus capucinus*: Jack & Fedigan, 2004a,b; ring-tailed lemurs, *Lemur catta*: Jones, 1983; and Bolivian squirrel monkeys, *Saimiri boliviensis*: Mitchell, 1994). For most group-living mammals, dispersal is male-biased (Greenwood, 1980; Pusey & Packer, 1987a) and parallel dispersal has been reported more often for males than for females (but see Bradley et al., 2007). Although male parallel dispersal is most often documented during dispersal from the natal group it can also occur during secondary dispersal, when males leave the social group into which they had previously immigrated. In moustached tamarins (*Saguinus mystax*) and white-faced capuchins, for example, dispersal coalitions have been observed to last over several secondary dispersal events (Garber, 1994; Jack & Fedigan, 2004a,b).

The costs of dispersal stem largely from greater exposure to predation and starvation during locational dispersal, and from potential aggression from unfamiliar conspecifics during social dispersal (Cheney & Seyfarth, 1983; Pusey & Packer, 1987a; Isbell et al., 1990, 1993; Sussman, 1992; Alberts & Altmann, 1995; Isbell & Van Vuren, 1996; Isbell, 2004). Joint dispersal with conspecifics might reduce the costs of locational dispersal by lowering the probability of predation via greater vigilance or greater defensive strength (Pusey & Packer, 1987a). Travelling with others might also reduce the costs

of social dispersal by providing allies against unfamiliar conspecifics (Pusey & Packer, 1987a; Isbell & Van Vuren, 1996). Coalitions of immigrants provide a collective competitive ability that exceeds individual ability in the face of aggression from unfamiliar conspecifics (e.g., red howler monkeys, *Alouatta seniculus*: Crockett & Pope, 1993; Pope, 2000; white-faced capuchins: Fedigan & Jack, 2004). Lone dispersers can also mitigate the costs of social dispersal by immigrating into groups containing previous group mates, some of whom may be closely related to the dispersers (Isbell et al., 2002; Jack & Fedigan, 2004a,b). Close relatives and familiar conspecifics are likely to be less aggressive towards immigrants and may even assist with group entry (Cheney, 1983; Cheney & Seyfarth, 1983).

The idea that parallel dispersal does indeed reduce the costs of social dispersal for males is suggested by several studies. For example, Cheney & Seyfarth (1983) demonstrated that immature male vervets are more likely than adult males to join groups containing known individuals and these males receive less aggression than those who join groups in which all members are unfamiliar to them. Pope (1990) found that dispersing male red howler monkeys that form coalitions to supplant resident males from female groups have a higher success rate than males attempting to take over groups alone. Similarly, Fedigan & Jack (2004) found that male white-faced capuchins must form aggressive coalitions against other males in order to gain access to, and maintain membership within, a social group. In this species, parallel dispersal is high among both natal (71%) and secondary emigrants (68%), with males dispersing jointly with other group males and/or immigrating into groups containing known individuals (Jack & Fedigan, 2004a,b). These studies suggest that male parallel dispersal may be associated with intergroup coalitions because males dispersing together may increase their competitive ability, which may be important when joining or taking over groups. Furthermore, males may be more likely to participate in group defence if they are familiar with or closely related to other immigrant males. The retention of familiar allies may also be important in the formation of intragroup coalitions, especially if dispersal partners are more willing to form coalitions with one another than with other group members. Thus, the apparent importance of coalition partners may influence the likelihood of males dispersing together. If this is the case, then other factors that make coalition formation more likely may also be correlated with the presence of parallel dispersal.

Parallel dispersers may have a greater chance of gaining membership together in the same group when multiple male residence in groups is the norm. Although it rarely occurs, coalitions of males from all-male bands can evict the sole resident male within female groups in uni-male, multi-female species, such as in Hanuman langurs (*Semnopithecus entellus*: Sommer, 1988). However, coalition formation may be most frequent in multi-male, multi-female groups where multiple males always co-reside and, thus, have greater opportunities to form coalitions with each other both before dispersal and after gaining membership in a new group.

Parallel dispersal may be even more likely in group-living animals when joint dispersers are close genetic relatives and inclusive fitness benefits can accrue from coalitionary behaviour. In most cases, information about relatedness is limited to maternal lines. In species with female philopatry, dispersal is invariably male-biased and groups are comprised of closely related adult females (Pusey & Packer, 1987a; Isbell, 2004). This type of social organization leads to close genetic relatedness among group infants and juveniles along maternal lines, even when offspring are sired by different males. In these species, it is possible that males engaging in parallel dispersal are half-sibs, cousins, nephews, or uncles. Indeed, natal male vervets and white-faced capuchins that engage in parallel dispersal are often maternal siblings (Cheney & Seyfarth, 1983; Jack & Fedigan, 2004b). Thus, we might expect parallel dispersal to be more common in species characterized by male-biased dispersal and female philopatry.

Parallel dispersal may also be more common among paternal siblings, as males may increase inclusive fitness benefits by dispersing with paternal kin. The likelihood of paternal relatedness increases when only one or a few males sire group infants. In a rare study of dispersal and genetic relatedness, Pope (1990) found that paternally related male red howlers that dispersed together formed coalitions that were more stable and resulted in longer group tenure than coalitions comprised of unrelated males. High paternal relatedness is particularly likely in species with low breeding seasonality, because breeding opportunities are more likely to be monopolized by one male when they are spread out over time (Emlen & Oring, 1977; Altmann, 1979). Alternatively, high breeding seasonality likely reduces potential paternal relatedness of males within groups, but van Hooft (2000) suggests that it facilitates familiarity within same-aged cohorts. In addition, high breeding seasonality

increases the availability of same aged dispersal partners, which may also promote parallel dispersal (van Hooff, 2000).

We perform exploratory analyses to examine whether parallel dispersal in male primates is associated with coalitions and factors that may facilitate coalition formation. Thus, we predict male coalitions overall, as well as both intergroup and intragroup coalitions, will be associated with the occurrence of male parallel dispersal. We also anticipate that multi-male, multi-female social groups facilitate coalition formation and will, therefore, be correlated with both parallel dispersal and coalition formation. Since little is known about the genetic relatedness of dispersers, we indirectly investigate it through other factors that might indicate relatedness. We first ask if male parallel dispersal occurs disproportionately in those primate species where dispersal is male-biased rather than bisexual. The prediction is based on the reasoning that dispersers are more closely related in those species with male-biased dispersal because they arise from philopatric females who are themselves related. Additionally, we ask if species classified as having high paternity concentration promote male parallel dispersal. We also ask if low breeding seasonality promotes parallel dispersal by increasing male monopolization potential of ovulatory females and, therefore, paternal relatedness of dispersal partners. However, if paternal relatedness is not important to parallel dispersal, then high breeding seasonality may promote parallel dispersal by increasing peer familiarity and the availability of same aged dispersal partners.

Methods

Data collection

We gathered data on parallel dispersal, coalitions, social system, sex-biased and bisexual dispersal, paternity concentration, and breeding seasonality in primates by using these terms to search the PrimateLit and Web of Science databases (other search terms used include peer migration, aggression, agonism, intergroup encounter, birth seasonality and reproductive skew). In our review of the primate literature, we also searched these databases using both primate Latin binomials and common names (based on Groves, 2001). In addition, we examined records cited within the publications as well as records that cited these publications. Finally, over 100 primate researchers known to

have conducted long-term research on primates were contacted and asked to respond to a brief questionnaire on parallel dispersal, coalitions, breeding seasonality and paternity concentration. All data are presented in Appendix A.

Variables

Sex-biased dispersal, parallel dispersal and coalitions

Species are included in the analyses if published information on dispersal was available. Dispersal can be male-biased, female-biased, or bisexual; however, for our purposes, only male-biased and bisexually dispersing species were included. Since the aim of this manuscript is to elucidate what traits may have promoted the evolution of male parallel dispersal, we did not include species in which only females disperse. A species was categorized as having male parallel dispersal if males from the same group dispersed together and/or they immigrated into groups containing other known males (see van Hooff, 2000). Following de Waal & Harcourt (1992, p. 3), we define coalitions as “the joining of forces by two or more individuals during a conflict of interest with other parties”. For this analysis, we interpreted de Waal and Harcourt’s definition in the broadest of terms: intragroup coalitions were coded as present if two or more males simultaneously directed aggression against another individual from the same group, while intergroup coalitions were coded as present if two or more males from the same group simultaneously directed aggression against an extra-group individual whether or not they appeared to coordinate their actions with one another. We also combined coalitions, so that a species was categorized as having coalitions if they had either or both intergroup and intragroup coalitions. Groups were also broadly defined, and could include transient associations of males (e.g., all-male bands) as well as stable associations. Extra-group individuals were all those who were not part of the male’s own association or group, including lone males and males of other groups. The success rate and purpose of coalitions were considered inconsequential for our purposes (e.g., feeding competition, mate defence, etc.).

Data on the occurrence of parallel dispersal, intergroup coalitions, and intragroup coalitions were available for 29, 43 and 39 of the species for which dispersal was known to be male-biased or bisexual, respectively. Since data

on parallel dispersal or coalition formation were not available for all male-biased or bisexually dispersing species, we chose to assume that species for which no information is reported are not characterized by the behaviour in question, since a behaviour that occurs is often described in the literature whereas one that does not is seldom described as not occurring.

We recognize that the assumption that an unreported behaviour is absent is made at the risk of incorrectly classifying little known species or species for which these types of data are unavailable. The risk of a Type II error may increase as more “error” is introduced into the dataset (Sokal & Rohlf, 1995), which is a possibility when making this assumption. However, our assumption is supported by the fact that 19 of the 20 species in which data on parallel dispersal were published noted the presence of this behaviour, while only one reported its absence. Clearly, there is a strong bias towards reporting when parallel dispersal occurs. To minimize the possibility that parallel dispersal was not observed when it actually does occur in a given species, we included only those species studies for 12 months or longer. Given that the aim of this analysis is exploratory and is designed to elucidate potential variables that may have promoted the evolution of male parallel dispersal, we believe that this dataset is reasonable (total of 57 species).

Social systems, paternity concentration and breeding seasonality

The social system of each species was initially classified as follows: 1 = multi-male, multi-female; 2 = uni-male, multi-female; 3 = extended family groups (often multi-male, uni-female); 4 = monogamous; 5 = solitary. We excluded monogamous and solitary species based on the lack of available dispersal partners in species with these types of social organizations. Given our hypothesis that parallel dispersal occurs more frequently in species with a multi-male, multi-female social system, and the fact that the phylogenetic comparative method (PCM) we employ in our meta-analysis requires binary states for all traits (Maddison, 2000), we combined the three remaining standard social systems into two categories: a ‘multi-male multi-female’ category and an ‘other’, the latter of which included only uni-male, multi-female species and those with extended family group (i.e., callitrichids). In addition to comparing social system with parallel dispersal, we also examined

the dataset for the co-occurrence of coalitions (combined) with social systems.

Paternity concentration was categorized as high if the alpha male sired at least 50% of group offspring, moderate if the alpha male sired more offspring than any other male but less than 50%, and low if a male other than the alpha sired more offspring than any other male (following van Noordwijk & van Schaik, 2004). The majority of data on paternity concentration were obtained from van Noordwijk & van Schaik (2004), and these were supplemented by data published elsewhere and by personal communication. Paternity concentration was assigned based on DNA and/or mating behaviour at the estimated time of conception, and were only used if obtained from wild or non-provisioned free-ranging populations (as per the second dataset in van Noordwijk & van Schaik, 2004). These data were available for 19 species, though low paternity concentration did not occur in the dataset. Therefore, we compared only high versus moderate paternity concentration.

Data on breeding seasonality were obtained primarily from van Schaik et al. (1999), with other sources listed in Appendix A. Species were assigned to the category of low breeding seasonality if fewer than 33% of births occur within a three-month period. Species with 33–67% of births in a 3-month period were assigned to the category of moderate breeding seasonality, while species with greater than 67% of births in a 3-month period were considered to have high breeding seasonality. Breeding seasonality was then converted from a multi-state trait to a binary trait. There were no a priori expectations as to what degree of breeding seasonality, if any, would be correlated with parallel dispersal; low breeding seasonality might promote parallel dispersal by increasing paternal relatedness, whereas high breeding seasonality might promote parallel dispersal by increasing the availability of same aged dispersal partners. Therefore, we excluded moderate breeding seasonality and the analyses were performed comparing low versus high breeding seasonality only (total 31 species).

Data analysis

Phylogenetic comparative methods

Traditional comparative methods assume that data points are independent of one another, i.e., that they are descended from a star phylogeny (Felsen-

stein, 1985). However, due to shared ancestry, closely related species, such as those of the Order Primates, are expected to share more characteristics than distantly related species. This can lead to higher rates of Type I errors, causing an exaggeration of significance, and may also increase Type II errors by not accounting for the evolutionary history of species, which may result in spurious *p* values (Garland et al., 2005). Phylogenetic comparative methods (PCMs) correct for the statistical non-independence of data, and should, therefore, be applied when comparing data on closely related species (Felsenstein, 1985; Maddison, 2000; Nunn & Barton, 2001; Garland et al., 2005).

It has been suggested that PCMs should be used only in instances where species traits are shown to be phylogenetically dependent, and traditional (non-phylogenetic) comparative methods should be used where traits appear to be independent of phylogenetic history (Abouheif, 1999). While some traits may appear to be distributed independently of phylogeny, such as those with high rates of evolution, they are in fact not independent samples because closely related species do have a shared phylogenetic history. In addition, the statistical validity of phylogenetically based comparative tests is not dependent on low rates of evolution, nor does the absence of a phylogenetic signal mean a trait is independent of its phylogenetic history. Not all variables related to character evolution can be measured, so it is possible that some unmeasured variable promoted the evolution of the character of interest (W.P. Maddison, pers. commun.). In this case, not applying a phylogenetic comparative method could lead to incorrect results. PCMs should be applied regardless of whether traits appear to have a phylogenetic signal or not (W.P. Maddison, pers. commun.). Therefore, PCMs were applied for this meta-analysis and phylogenetic independence of traits was not tested.

We used the phylogeny of Smith & Cheverud (2002) with additional phylogenetic information obtained from Purvis (1995), Cortés-Ortiz et al. (2003), Meijaard & Groves (2004), Morales & Melnick (1998) and Pastorini et al. (2001). All branch lengths were set to 1.0, since Mesquite pairwise comparisons do not require this information (Maddison, 2000; see Appendix B). The resulting phylogeny is shown in Figure 1, along with the distributions of parallel dispersal and male coalitions combined (intergroup and/or intragroup coalitions).

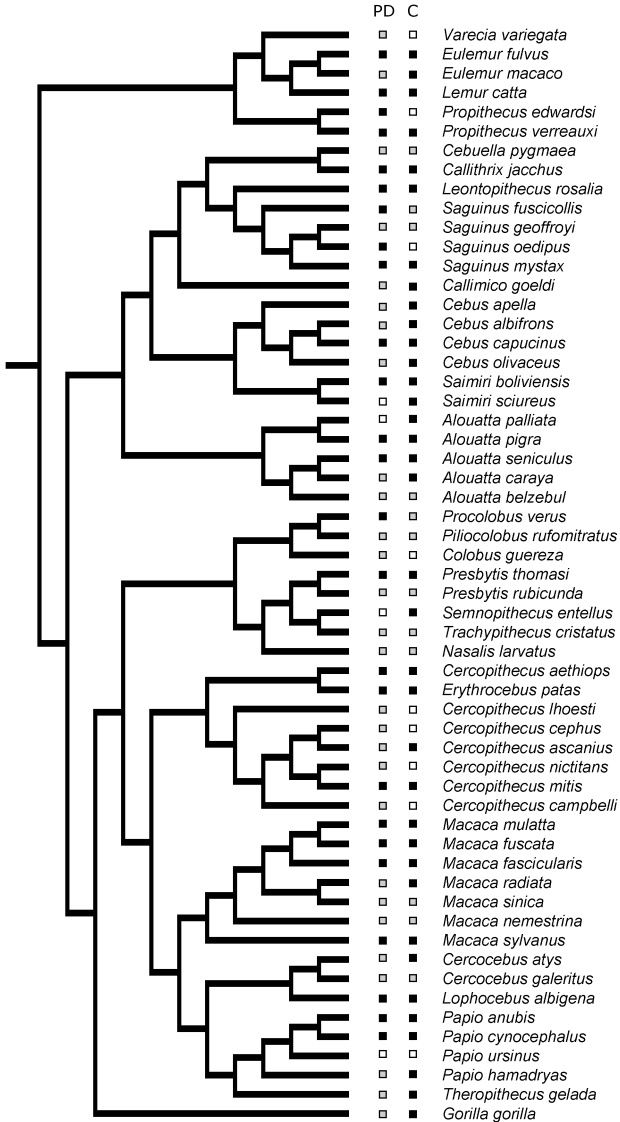


Figure 1. Phylogenetic distribution of parallel dispersal and coalitions combined (inter- and/or intragroup coalitions) in male primates. The left-hand side depicts the distribution of male parallel dispersal (PD), while the right-hand side depicts the distribution of male coalitions combined (C). Black boxes indicate behaviour is present, open boxes indicate behaviour is absent, and grey boxes indicate that no data are available.

Pairwise comparisons

In order to test for an association between parallel dispersal (the dependent variable) and the various socio-ecological variables of interest, comparisons of phylogenetically independent pairs were implemented using the pairwise comparisons module (Maddison, 2006) in Mesquite software version 2.5 (Maddison & Maddison, 2008). Phylogenetically independent (or 'separate') pairs are ones in which the evolutionary paths linking the taxa are not shared (see Maddison, 2000). The pairwise comparisons module in Mesquite has the advantages of not assuming any method of character evolution, not relying on ancestral state reconstruction, and does not require any information on branch lengths (Maddison, 2000). As suggested by Read & Nee (1995) and Maddison (2000), pairwise comparisons were examined for pairs of species (referred to as terminal taxa in the PCM literature; here we use this term interchangeably with 'species') that contrast in both variables being examined. As noted above, the variables compared with parallel dispersal include coalitions, social systems, male-biased and bisexual dispersal, paternity concentration, and breeding seasonality. We chose to compare pairs of taxa that differ in both traits because "if both sister taxa share the same value of X although they vary in Y, this tells us simply that there are factors other than X involved in the evolution of Y" (Read & Nee, 1995, p. 104).

Given the large size of our phylogenetic tree, in some cases it was not feasible to examine all possible maximal sets of pairwise comparisons for certain analyses; therefore, we limited the number of pairwise comparisons to 100 000. Significance levels for all pairwise comparisons were set at $p < 0.05$ and Bonferroni correction was not applied due to the exploratory nature of our analyses (Nakagawa, 2004).

Each pairing of taxa is an alternate way a pair can be chosen for pairwise comparisons (Maddison, 2000). For instance, one pairing might contrast *Papio ursinus* with *P. hamadryas*, while another pairing might contrast *Saguinus oedipus* with *C. capucinus*. These pairings are arbitrary, so long as they contrast in both variables being examined (as described above). These pairs may yield the same result, resulting in a single p value for a comparison. Alternatively, these pairs may yield different results, yielding two p values. In cases where two p values were produced, and one was significant while the other was not, we interpreted the result as equivocal.

Results

Coalitions and parallel dispersal

For coalitions combined, 14 pairs (of 100 000 possible pairings, limit reached) were found, with 11 supporting and 3 contradicting ($p = 0.029$) a positive correlation between coalitions combined and parallel dispersal. For intergroup coalitions only, 14 pairs (of 100 000 possible pairings, limit reached) were found, with 10 supporting and 4 contradicting ($p = 0.089$) the hypothesis of a positive correlation between intergroup coalitions and parallel dispersal. For intragroup coalitions only, 11 pairs (22 560 pairings) were found, and included pairings ranging from 8 supporting and 3 contradicting ($p = 0.113$) to 7 supporting and 4 contradicting ($p = 0.274$) a positive correlation between intragroup coalitions and parallel dispersal (Table 1).

Social system, parallel dispersal, and coalitions combined

For social systems (multi-male, multi-female vs. other) in relation to parallel dispersal, 7 pairs (85 680 pairings) were found, and included pairings ranging from 5 supporting and 2 contradicting ($p = 0.227$) to 4 supporting and 3 contradicting ($p = 0.500$) the hypothesis of a positive correlation between multi-male, multi-female groups and parallel dispersal. For social systems

Table 1. Results of pairwise comparisons.

Independent trait	Dependent trait	Number of taxa	No. of pairs (supporting, contradicting) hypothesis of association	p value
Coalitions combined	Parallel dispersal	57	(11, 3)	0.029*
Intergroup coalitions	Parallel dispersal	57	(10, 4)	0.089
Intragroup coalitions	Parallel dispersal	57	(8, 3)–(7, 4)	0.113, 0.274
Social system	Parallel dispersal	57	(5, 2)–(4, 3)	0.227, 0.500
Social system	Coalitions combined	57	(6, 1)–(4, 3)	0.063, 0.500
Dispersal	Parallel dispersal	57	(7, 1)–(4, 4)	0.035*, 0.637
Paternity conc.	Parallel dispersal	19	(0, 2)–(1, 1)	0.250, 0.750
Breeding seasonality (low vs. high only)	Parallel dispersal	31	(2, 4)–(3, 3)	0.344, 0.656

* significant p value.

in relation to coalitions combined, 7 pairs (38 360 pairings) were found, and included pairings ranging from 6 supporting and 1 contradicting ($p = 0.063$) to 4 supporting and 3 contradicting ($p = 0.500$) the hypothesis of a positive correlation between multi-male, multi-female groups and coalitions combined (Table 1).

Dispersal type and parallel dispersal

For dispersal type (male-biased vs. bisexual dispersal), 8 pairs (of 100 000 possible pairings, limit reached) were found, ranging from 7 supporting and 1 contradicting ($p = 0.035$) to 4 supporting and 4 contradicting ($p = 0.637$) the hypothesis of a positive association between male-biased dispersal and parallel dispersal (Table 1).

Paternity concentration and parallel dispersal

Paternity concentration was separated into high vs. moderate. Given that the data for *C. mitis* were difficult to categorize into either high or moderate paternity concentration (Hatcher, 2007), we conducted the analyses twice, once with *C. mitis* as having high paternity concentration, and once as having moderate paternity concentration; in both analyses, the results were not significant. With *C. mitis* categorized as having moderate paternity concentration, 3 pairs (84 pairings) were found, with 1 supporting and 2 contradicting ($p = 0.500$) the hypothesis that high paternity concentration is positively associated with parallel dispersal. With *C. mitis* categorized as having high paternity concentration, only 2 pairs (84 pairings) were found, ranging from 0 supporting and 2 contradicting ($p = 0.250$) to 1 supporting and 1 contradicting ($p = 0.750$) the hypothesis that high paternity concentration is positively associated with parallel dispersal. Only the latter result is reported in Table 1. However, the extremely small number of pairs (3, 2) results in very low power.

Breeding seasonality and parallel dispersal

Comparison of low versus high breeding seasonality revealed 6 pairs (378 pairings), ranging from 2 supporting and 4 contradicting ($p = 0.344$) to 3 supporting and 3 contradicting ($p = 0.656$) the hypothesis that high breeding seasonality is positively correlated with parallel dispersal (Table 1).

Discussion

The aim of this analysis was to explore what factors co-occur with parallel dispersal in male primates. We predicted that the occurrence of male–male coalitions, both intergroup and intragroup, would be associated with parallel dispersal in male primates. We also examined other factors that are thought to facilitate coalition formation among male primates, including social system, sex-biased dispersal, paternity concentration, and breeding seasonality.

We evaluated the occurrence of multi-male, multi-female social systems because parallel dispersers are expected to have a greater chance of gaining membership together in the same group when multiple male residence in groups is the norm. We found no association between multi-male multi-female social groups and male parallel dispersal. Therefore, males are equally likely to engage in parallel dispersal in species with multi-male multi-female, uni-male multi-female, or extended family social groups. The lack of association suggests that co-residence in a new social group after joint emigration is not necessarily a prerequisite for males to engage in parallel dispersal.

Close genetic relatedness can provide inclusive fitness benefits to males engaging in parallel dispersal if these males form coalitions (van Hooff, 2000). However, high paternity concentration was not associated with parallel dispersal, though it is important to note that few data were available for the analysis of paternity concentration. Data were available for only 19 species, most of which were characterized by high paternity concentration, while not a single species had low paternity concentration. Of course, in many cases, paternity concentration was not confirmed with genetic data but was only inferred from behavioural observations, and perhaps behavioural data are weak indicators of paternity (e.g., Inoue et al., 1993; Jack & Fedigan, 2006; but see Altmann et al., 1996). While the absence of a correlation between high paternity concentration and parallel dispersal may indicate that paternal relatedness among dispersers does not influence the likelihood of parallel dispersal, our analysis suffered from low statistical power and results should be interpreted with caution.

In an attempt to indirectly account for paternity concentration, we also examined whether there was a co-occurrence of parallel dispersal with low breeding seasonality, which may also increase paternal relatedness by spreading out breeding opportunities and increasing male monopolization

potential. Alternatively, high breeding seasonality may promote parallel dispersal by increasing familiarity among same-age cohorts and by increasing the availability of same-aged dispersal partners. Our analyses revealed no association between parallel dispersal and breeding seasonality.

Male-biased dispersal was also considered because it is expected to increase the number of available dispersal partners, some of which may be close male relatives because they arise from philopatric females. The association between male-biased dispersal and parallel dispersal was equivocal, with some pairings suggesting a significant co-occurrence of the two, and other pairings suggesting no co-occurrence. To err on the conservative side, we choose to interpret the results as an indication that relatedness among maternal lines may not be a factor in promoting parallel dispersal in males.

Coalitions were examined because of their apparent value in buffering individuals against aggression, particularly from unfamiliar conspecifics, when entering a new social group or territory. Since aggression is a major potential cost of dispersal, the willingness of males to form coalitions might increase the likelihood of parallel dispersal. Our findings suggest that parallel dispersal may occur because of the benefits gained from coalitionary support. Field studies have indicated that males participating in coalitions do so because they increase their individual competitive ability (e.g., Packer, 1979; Pope, 1990; van Noordwijk & van Schaik, 2001; Fedigan & Jack, 2004). Two main types of coalitions can occur; intragroup coalitions, which are used to compete with other members of one's social group for access to resources (e.g., food or mates), and intergroup coalitions, which may reflect between-group competition for access to these resources (Wrangham, 1980). Interestingly, when we refined our analysis to examine the occurrence of parallel dispersal and each of these two types of coalitions, intragroup coalitions alone were not associated with parallel dispersal, while intergroup coalitions showed a trend toward an association with male parallel dispersal. While further study is needed to directly investigate this topic, these findings suggest that parallel dispersal may assist in the maintenance of long-term cooperative bonds among group males (van Hooff, 2000) and, at least for some species (Cheney & Seyfarth, 1983; Jack & Fedigan, 2004a,b; Pope, 2000), these bonds may be similar to those observed among groups of philopatric females. In addition, the absence of an association between intragroup coalitions and parallel dispersal may also be telling. If parallel

dispersal promotes the retention of kinship among members of the dispersing sex, it makes sense that group males will not band against each other as they may be related. In white-faced capuchins at Santa Rosa National Park, where male parallel dispersal is common during both natal and secondary dispersal, male within-group relationships are tolerant and overt mating competition is rare (Jack, 2003; Jack & Fedigan, 2004a,b). More long-term data are needed on the nature of male–male coalitions, and male–male social relationships in general, in those species that frequently engage in parallel dispersal.

Dispersal is a challenging topic to study, and parallel dispersal may represent only a proportion of all dispersal events, resulting in a limited understanding of the factors promoting its occurrence. We have conducted these exploratory analyses in an attempt to understand what factors may be associated with parallel dispersal in male primates. Our findings suggest that there is an association between the occurrence of male parallel dispersal and coalitions in general, a correlation which may be driven by intergroup coalitions. Dispersal has profound effects on the genetic makeup of groups and populations and despite the difficulties inherent in studying it, we encourage our colleagues to continue publishing their small sample sizes. Over time, a more solid database will accumulate that will enable us to re-assess earlier, more limited analyses such as those presented here, and to pursue new questions as they arise.

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References

- Abouheif, E. (1999). A method for testing the assumption of phylogenetic independence in comparative data. — *Evol. Ecol. Res.* 1: 895-909.
- Alberts, S.C. & Altmann, J. (1995). Balancing costs and opportunities: dispersal in male baboons. — *Am. Nat.* 145: 279-306.
- Altmann, J. (1979). Age cohorts as paternal sibships. — *Behav. Ecol. Sociobiol.* 6: 161-164.
- Altmann, J., Alberts, S.C., Haines, S.A., Dubach, J., Muruthi, P., Coote, T., Geffen, E., Cheesman, J., Mututua, R.S., Saiyalel, S.N., Wayne, R.K., Lacy, R.C. & Bruford, M.W. (1996). Behaviour predicts genetics structure in a wild primate group. — *Proc. Natl. Acad. Sci. USA* 83: 5797-5801.
- Baker, A.J. & Dietz, J.M. (1996). Immigration in wild groups of golden lion tamarins (*Leontopithecus rosalia*). — *Am. J. Primatol.* 38: 47-56.
- Benneton, C. & Noë, R. (2004). Reproductive tactics of adult male sooty mangabeys in Tai National Park, Ivory Coast. — *Folia Primatol.* 75: 169.
- Boinski, S., Kauffman, L., Ehmke, E., Schet, S. & Vreedzaam, A. (2005). Dispersal patterns among three species of squirrel monkeys (*Saimiri oerstedii*, *S. boliviensis* and *S. sciureus*): I. Divergent costs and benefits. — *Behaviour* 142: 525-632.
- Bradley, B.J., Doran-Sheehy, D.M. & Vigilant, L. (2007). Potential for female kin associations in wild western gorillas despite female dispersal. — *Proc. Roy. Soc. Lond. B Biol.* 274: 2179-2185.
- Cheney, D.L. (1981). Inter-group encounters among free-ranging vervet monkeys. — *Folia Primatol.* 35: 124-146.
- Cheney, D.L. (1983). Proximate and ultimate factors related to the distribution of male migration. — In: *Primate social relationships: an integrated approach* (Hinde, R.A., ed.). Blackwell Scientific, Sunderland, MA, p. 241-249.
- Cheney, D.L. (1987). Interactions and relationships between groups. — In: *Primate societies* (Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W. & Struhsaker, T.T., eds). University of Chicago Press, Chicago, IL, p. 267-281.
- Cheney, D.L. & Seyfarth, R.M. (1983). Nonrandom dispersal in free-ranging vervet monkeys: social and genetic consequences. — *Am. Nat.* 122: 392-412.
- Clarke, M. (2005). Testing the model for male-male coalitions: data from male mantled howling monkeys (*Alouatta palliata*). — *Am. J. Phys. Anthropol.* 126: 87.
- Cords, M. (1987). Forest guenons and patas monkeys: male-male competition in one-male groups. — In: *Primate societies* (Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W. & Struhsaker, T.T., eds). University of Chicago Press, Chicago, IL, p. 98-111.
- Cortés-Ortiz, L., Bermingham, E., Rico, C., Rodríguez-Luna, E., Sampaio, I. & Ruiz-García, M. (2003). Molecular systematics and biogeography of the neotropical monkey genus, *Alouatta*. — *Mol. Phylogenet. Evol.* 26: 64-81.
- Crockett, C.M. & Pope, T.R. (1993). Consequences of sex differences in dispersal for juvenile red howler monkeys. — In: *Juvenile primates: life history, development, and behaviour* (Pereira, M.E. & Fairbanks, L.A., eds). Oxford University Press, New York, NY, p. 104-118.
- Digby, L.J., Ferrari, S.F. & Saltzman, W. (2007). Callitrichines: the role of competition in cooperatively breeding species. — In: *Primates in perspective* (Campbell, C.J., Fuentes, A., MacKinnon, K.C., Panger, M. & Bearder, S.K., eds). Oxford University Press, New York, NY, p. 85-105.

- Dittus, W. (1975). Population dynamics of the toque monkey, *Macaca sinica*. — In: Socioecology and psychology of primates (Tuttle, R.H., ed.). Mouton, The Hague, p. 125-151.
- Dittus, W. (1977). The social regulation of population density and age–sex distribution in the toque monkey. — *Behaviour* 63: 281-322.
- Dunbar, R. (1984). Reproductive decisions: an economic analysis of gelada baboon social strategies. — Princeton University Press, Princeton, NJ.
- Emlen, S.T. & Oring, L.W. (1977). Ecology, sexual selection, and the evolution of mating systems. — *Science* 197: 215-223.
- Enstam, K.L. & Isbell, L.A. (2007). The guenons (genus *Cercopithecus*) and their allies: behavioural ecology of polyspecific associations. — In: Primates in perspective (Campbell, C.J., Fuentes, A., MacKinnon, K.C., Panger, M. & Bearder, S.K., eds). Oxford University Press, New York, NY, p. 252-274.
- Escobar-Parámo, P. (2000). Microsatellite primers for the wild brown capuchin monkey *Cebus apella*. — *Mol. Ecol.* 9: 107-108.
- Fashing, P.J. (1999). The behavioural ecology of an African colobine monkey: diet, range use, and patterns of intergroup aggression in eastern black and white colobus monkeys (*Colobus guereza*). — Doctoral thesis, Columbia University, New York, NY.
- Fashing, P.J. (2007). African colobine monkeys: patterns of between-group interactions. — In: Primates in perspective (Campbell, C.J., Fuentes, A., MacKinnon, K.C., Panger, M. & Bearder, S.K., eds). Oxford University Press, New York, NY, p. 201-224.
- Fedigan, L.M. & Jack, K.M. (2004). The demographic and reproductive context of male replacements in *Cebus capucinus*. — *Behaviour* 146: 755-775.
- Felsenstein, J. (1985). Phylogenies and the comparative method. — *Am. Nat.* 125: 1-15.
- Fragaszy, D.M., Visalberghi, E. & Fedigan, L.M. (2004). The complete capuchin: the biology of the genus *Cebus*. — Cambridge University Press, Cambridge.
- Frame, L.H. & Frame, G.W. (1976). Female African wild dogs emigrate. — *Nature* 263: 227-229.
- Garber, P. (1994). Phylogenetic approach to the study of tamarin and marmoset social systems. — *Am. J. Primatol.* 34: 199-219.
- Garland, T.J., Bennett, A.F. & Rezende, E.L. (2005). Phylogenetic approaches in comparative physiology. — *J. Exp. Biol.* 208: 3015-3035.
- Gould, L. (2006). Male sociality and integration during the dispersal process in *Lemur catta*: a case study. — In: Ringtailed lemur biology: *Lemur catta* in Madagascar (Jolly, A., Sussman, R.W., Koyama, N. & Rasamimanana, H., eds). Springer, New York, NY, p. 296-310.
- Gould, L. & Sauther, M. (2007). Lemuriformes. — In: Primates in perspective (Campbell, C.J., Fuentes, A., MacKinnon, K.C., Panger, M. & Bearder, S.K., eds). Oxford University Press, New York, NY, p. 46-72.
- Greenwood, P.J. (1980). Mating systems, philopatry, and dispersal in birds and mammals. — *Anim. Behav.* 28: 1140-1162.
- Groves, C.P. (2001). Primate taxonomy. — Smithsonian Institution Press, Washington, DC.
- Harcourt, A.H., Harvey, P.H., Larson, S.G. & Short, R.V. (1981). Testis weight, body weight and breeding system in primates. — *Nature* 293: 55-57.
- Hatcher, J.L. (2007). Relating paternity and population genetics in blue monkeys, *Cercopithecus mitis stuhlmanni*: empirical results and strategies for obtaining them. — Doctoral thesis, Columbia University, New York, NY.

- Hausfater, G. (1972). Intergroup behaviour of free-ranging rhesus monkeys (*Macaca mulatta*). — *Folia Primatol.* 18: 78-107.
- Henzi, S.P., Weingrill, T. & Barrett, L. (1999). Male behaviour and the evolutionary ecology of chacma baboons. — *S. Afr. J. Sci.* 95: 240-242.
- van Hooff, J.A.R.A.M. (2000). Relationships among non-human primate males: a deductive framework. — In: *Primate males: causes and consequences of variation in group composition* (Kappeler, P.M., ed.). Cambridge University Press, Cambridge, p. 183-191.
- Horwich, R.H., Brockett, R.C. & Jones, C.B. (2000). Alternative male reproductive behaviours in the Belizean black howler monkey (*Alouatta pigra*). — *Neotrop. Primates* 8: 95-98.
- Huck, M., Löttker, P., Heymann, E.W. & Heistermann, M. (2005). Characterization and social correlates of fecal testosterone and cortisol excretion in wild male *Saguinus mystax*. — *Int. J. Primatol.* 26: 159-179.
- Inoue, M., Mitsunaga, F., Nozaki, M., Ohsawa, H., Takenaka, A., Sugiyama, Y., Shimuzu, K. & Takenaka, O. (1993). Male dominance rank and reproductive success in an enclosed group of Japanese macaques: with special reference to post-conception mating. — *Primates* 34: 503-511.
- Isbell, L.A. (2004). Is there no place like home? Ecological bases of dispersal in primates and their consequences for the formation of kin groups. — In: *Kinship and behaviour in primates* (Chapais, B. & Berman, C., eds). Oxford University Press, New York, NY, p. 71-108.
- Isbell, L.A., Cheney, D.L. & Seyfarth, R.M. (1990). Costs and benefits of home range shifts among vervet monkeys (*Cercopithecus aethiops*) in Amboseli National Park, Kenya. — *Behav. Ecol. Sociobiol.* 27: 351-358.
- Isbell, L.A., Cheney, D.L. & Seyfarth, R.M. (1993). Are immigrant vervet monkeys, *Cercopithecus aethiops*, at greater risk of mortality than residents? — *Anim. Behav.* 45: 729-734.
- Isbell, L.A., Cheney, D.L. & Seyfarth, R.M. (2002). Why vervets live in multi-male groups. — In: *The guenons: diversity and adaptation in African monkeys* (Glenn, M. & Cords, M., eds). Kluwer, New York, NY, p. 172-187.
- Isbell, L.A. & Van Vuren, D. (1996). Differential costs of locational and social dispersal and their consequences for female group-living primates. — *Behaviour* 133: 1-36.
- Jack, K.M. (2003). Males on the move: evolutionary explanations of secondary dispersal by male primates. — *Primates* 67: 61-83.
- Jack, K.M. & Fedigan, L.M. (2004a). Male dispersal patterns in white-faced capuchins, *Cebus capucinus*. Part 1: Patterns and causes of natal emigration. — *Anim. Behav.* 67: 761-769.
- Jack, K.M. & Fedigan, L.M. (2004b). Male dispersal patterns in white-faced capuchins, *Cebus capucinus*. Part 2: Patterns and causes of secondary dispersal. — *Anim. Behav.* 67: 771-782.
- Jack, K.M. & Fedigan, L.M. (2006). Why be alpha male? Dominance and reproductive success in wild white-faced capuchins (*Cebus capucinus*). — In: *New perspectives in the study of mesoamerican primates: distribution, ecology, behaviour and conservation* (Estrada, A., Garber, P., Luecke, L. & Pavelka, M.S.M., eds). Springer, New York, NY, p. 367-386.
- Janson, C.H. (1986). The mating system as a determinant of social evolution in capuchin monkeys (*Cebus*). — In: *Primate ecology and conservation* (Else, J.G. & Lee, P.C., eds). Cambridge University Press, Cambridge, p. 169-179.

- Janson, C.H. (1998). Capuchin counterpoint. — In: *The primate anthology: essays on primate behaviour, ecology, and conservation from natural history* (Ciochon, R.L. & Nisbett, R.A., eds). Prentice Hall, Englewood Cliffs, NJ, p. 153-159.
- Jolly, C.J. (2007). Baboons, mandrills, and mangabeys: afro-papionin socioecology in a phylogenetic perspective. — In: *Primates in perspective* (Campbell, C.J., Fuentes, A., MacKinnon, K.C., Panger, M. & Bearder, S.K., eds). Oxford University Press, New York, NY, p. 240-251.
- Jones, K.C. (1983). Inter-troop transfer of *Lemur catta* at Berenty, Madagascar. — *Folia Primatol.* 40: 145-160.
- Kappeler, P.M. (1997). Determinants of primate social organization: comparative evidence and new insights from Malagasy lemurs. — *Biol. Rev.* 72: 111-151.
- Kappeler, P.M. (1999). Lemur social structure and convergence in primate socioecology. — In: *Comparative primate socioecology* (Lee, P.C., ed.). Cambridge University Press, Cambridge, p. 273-299.
- Kawanaka, K. (1973). Intertroop relationships among Japanese monkeys. — *Primates* 14: 113-159.
- Kitchen, D.M., Cheney, D.L. & Seyfarth, R.M. (2004). Factors mediating inter-group encounters in savannah baboons (*Papio cynocephalus ursinus*). — *Behaviour* 141: 197-218.
- Koenig, A., Borries, C., Chalise, M.K. & Winkler, P. (1997). Ecology, nutrition, and timing of reproductive events in an Asian primate, the Hanuman langur (*Presbytis entellus*). — *J. Zool.* 243: 215-235.
- Korstjens, A.H. & Schippers, E.P. (2003). Dispersal patterns among olive colobus in Taï National Park. — *Int. J. Primatol.* 24: 515-539.
- Kowalewski, M.M. (2007). Patterns of affiliation and co-operation in howler monkeys: an alternative model to explain social organization in non-human primates. — Doctoral thesis, University of Illinois, Urbana-Champaign, IL.
- Kowalewski, M.M. & Zunino, G.E. (2004). Birth seasonality in *Alouatta caraya* in Northern Argentina. — *Int. J. Primatol.* 25: 383-400.
- Launhardt, K., Borries, C., Hardt, C., Epplen, J.T. & Winkler, P. (2001). Paternity analysis of alternative male reproductive routes among the langurs (*Semnopithecus entellus*) of Ramnagar. — *Anim. Behav.* 61: 53-64.
- Lawler, R.R., Richard, A.F. & Riley, M.A. (2003). Genetic population structure of the white sifaka (*Propithecus verreauxi verreauxi*) at Beza Mahafaly Special Reserve, southwest Madagascar (1992-2001). — *Mol. Ecol.* 12: 2307-2317.
- Maddison, W.P. (2000). Testing character correlation using pairwise comparisons on a phylogeny. — *J. Theor. Biol.* 202: 195-204.
- Maddison, W.P. (2006). Pairwise comparisons package for Mesquite, version 1.1. — Available at <http://mesquiteproject.org>
- Maddison, W.P. & Maddison, D.R. (2008). Mesquite: a modular system for evolutionary analysis, version 2.5. — Available at <http://mesquiteproject.org>
- Meijaard, E. & Groves, C.F. (2004). The biogeographical evolution and phylogeny of the genus *Presbytis*. — *Primate Rep.* 68: 71-90.
- Meikle, D.B. & Vessey, S.H. (1981). Nepotism among rhesus brothers. — *Nature* 294: 160-161.
- Melnick, D.J. & Pearl, M.C. (1987). Cercopithecines in multimale groups: genetic diversity and population structure. — In: *Primate societies* (Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W. & Struhsaker, T.T., eds). University of Chicago Press, Chicago, IL, p. 121-134.

- Mitchell, C.L. (1994). Migration alliances and coalitions among adult male South American squirrel monkeys (*Saimiri sciureus*). — *Behaviour* 130: 169-190.
- Morales, J.C. & Melnick, D.J. (1998). Phylogenetic relationships of the macaques (Cercopithecoidea: *Macaca*), as revealed by high resolution restriction site mapping of mitochondrial ribosomal genes. — *J. Hum. Evol.* 34: 1-23.
- Morelli, T.L., King, S.J., Pochron, S.T. & Wright, P.C. (2009). The rules of disengagement: takeovers, infanticide, and dispersal in a rainforest lemur, *Propithecus edwardsi*. — *Behaviour* 146: 499-523.
- Nakagawa, S. (2004). A farewell to Bonferroni: the problems of low statistical power and publication bias. — *Behav. Ecol.* 15: 1044-1045.
- Noë, R. (1992). Alliance formation among male baboons: shopping for profitable partners. — In: *Coalitions and alliances in humans and other animals* (Harcourt, A.H. & de Waal, F.B., eds). Oxford University Press, Oxford, p. 285-321.
- van Noordwijk, M.A. & van Schaik, C.P. (1985). Male migration and rank acquisition in long-tailed macaques (*Macaca fascicularis*). — *Anim. Behav.* 33: 849-861.
- van Noordwijk, M.A. & van Schaik, C.P. (2001). Career moves: transfer and rank challenge decisions by male long-tailed macaques. — *Behaviour* 138: 359-395.
- van Noordwijk, M.A. & van Schaik, C.P. (2004). Sexual selection and the careers of primate males: paternity concentration, dominance-acquisition tactics and transfer decisions. — In: *Sexual selection in primates: new and comparative perspectives* (Kappeler, P.M. & van Schaik, C.P., eds). Cambridge University Press, Cambridge, p. 208-229.
- Nunn, C.L. (1999). The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis. — *Anim. Behav.* 58: 229-246.
- Nunn, C.L. & Barton, R.A. (2001). Comparative methods for studying primate adaptation and allometry. — *Evol. Anthropol.* 10: 81-98.
- Olupot, W. & Waser, P.M. (2005). Patterns of male residency and intergroup transfer in gray-cheeked mangabeys (*Lophocebus albigena*). — *Am. J. Primatol.* 66: 331-349.
- Ostner, J. & Kappeler, P.M. (2004). Male life history and the unusual adult sex ratios of redfronted lemur, *Eulemur fulvus rufus*, groups. — *Anim. Behav.* 67: 249-259.
- Packer, C. (1979). Inter-troop transfer and inbreeding avoidance in *Papio anubis*. — *Anim. Behav.* 27: 1-36.
- Pastorini, J., Forstner, M.R.J. & Martin, R.D. (2001). Phylogenetic history of sifakas (*Propithecus*: Lemuriformes) derived from mtDNA sequences. — *Am. J. Primatol.* 53: 1-17.
- Paul, A. & Kuester, J. (1985). Intergroup transfer and incest avoidance in semifree-ranging Barbary macaques (*Macaca sylvanus*) at Salem (FRG). — *Am. J. Primatol.* 8: 317-322.
- Perry, S. (1998). Male-male social relationships in wild white-faced capuchins, *Cebus capucinus*. — *Behaviour* 135: 139-172.
- Plavcan, J.M. (1999). Mating systems, intrasexual competition and sexual dimorphism in primates. — In: *Comparative primate socioecology* (Lee, P.C., ed.). Cambridge University Press, Cambridge, p. 241-260.
- Pope, T.R. (1990). The reproductive consequences of male cooperation in the red howler monkey: paternity exclusion in multi-male and single-male troops using genetic markers. — *Behav. Ecol. Sociobiol.* 27: 439-446.
- Pope, T.R. (2000). The evolution of male philopatry in neotropical monkeys. — In: *Primate males: causes and consequences of variation in group composition* (Kappeler, P.M., ed.). Cambridge University Press, Cambridge, p. 219-235.

- Porter, L.M., Hanson, A.M. & Becerra, E.N. (2001). Group demographics and dispersal in a wild group of goeldi's monkeys (*Callimico goeldii*). — *Folia Primatol.* 72: 108-110.
- Purvis, A. (1995). A composite estimate of primate phylogeny. — *Philos. Trans. Roy. Soc. Lond. B Biol. Sci.* 348: 405-421.
- Pusey, A.E. & Packer, C. (1987a). Dispersal and philopatry. — In: *Primate societies* (Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W. & Struhsaker, T.T., eds). University of Chicago Press, Chicago, IL, p. 250-266.
- Pusey, A.E. & Packer, C. (1987b). The evolution of sex-biased dispersal in lions. — *Behaviour* 101: 275-310.
- Ramirez-Llorens, P., Di Bitetti, M.S., Baldovino, M.C. & Janson, C.H. (2008). Infanticide in black capuchin monkeys (*Cebus apella nigrilus*) in Iguazu National Park, Argentina. — *Am. J. Primatol.* 70: 473-484.
- Read, A.F. & Nee, S. (1995). Inference from binary comparative data. — *J. Theor. Biol.* 173: 99-108.
- Richard, A.F., Rakotomanaga, P. & Schwartz, M. (1993). Dispersal by *Propithecus verreauxi* at Beza Mahafaly, Madagascar. — *Am. J. Primatol.* 30: 1-20.
- Robbins, M.M. (1995). A demographic analysis of male life-history and social structure of mountain gorillas. — *Behaviour* 132: 21-47.
- Robinson, J. (1988). Group size in wedge-capped capuchin monkeys *Cebus olivaceus* and the reproductive success of males and females. — *Behav. Ecol. Sociobiol.* 23: 187-197.
- Rowell, T.E. (1988). The social system of guenons, compared with baboons, macaques and mangabeys. — In: *A primate radiation: evolutionary biology of the African guenons* (Gautier-Hion, A., Bourlière, F., Gautier, J.-P. & Kingdon, J., eds). Cambridge University Press, Cambridge, p. 439-451.
- van Schaik, C.P., van Noordwijk, M.A. & Nunn, C.L. (1999). Sex and social evolution in primates. — In: *Comparative primate socioecology* (Lee, P.C., ed.). Cambridge University Press, Cambridge, p. 204-240.
- Sekulic, R. (1983). Male relationships and infant deaths in red howler monkeys (*Alouatta seniculus*). — *Z. Tierpsychol.* 61: 185-202.
- Sigg, H., Stolba, A., Abegglen, J.J. & Dasser, V. (1982). Life history of hamadryas baboons: physical development, infant mortality, reproductive parameters and family relationships. — *Primates* 23: 473-487.
- Silk, J. (1992). Patterns of intervention in agonistic contests among male bonnet macaques. — In: *Coalitions and alliances in humans and other animals* (Harcourt, A.H. & De Waal, F.B., eds). Oxford University Press, Oxford, p. 216-232.
- Smith, R.J. & Chaverud, J.M. (2002). Scaling of sexual dimorphism in body mass: a phylogenetic analysis of Rensch's Rule in primates. — *Int. J. Primatol.* 23: 1095-1135.
- Smuts, B.B. (1987). Sexual competition and mate choice. — In: *Primate societies* (Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W. & Struhsaker, T.T., eds). University of Chicago Press, Chicago, IL, p. 385-399.
- Snowdon, C.T. & Pickhard, J.J. (1999). Family feuds: severe aggression among cooperatively breeding cotton-top tamarins. — *Int. J. Primatol.* 20: 651-663.
- Sokal, R.R. & Rohlf, F.J. (1995). Biometry: the principles and practice of statistics in biological research, 3rd edn. — W.H. Freeman, New York, NY.
- Sommer, V. (1988). Male competition and coalitions in langurs (*Presbytis entellus*) at Jodhpur, Rajasthan, India. — *Hum. Evol.* 3: 261-278.

- Stammach, E. (1987). Desert, forest and montane baboons: multilevel societies. — In: Primate societies (Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W. & Struhsaker, T.T., eds). University of Chicago Press, Chicago, IL, p. 112-120.
- Steenbeek, R., Sterck, E.H.M., de Vries, H. & van Hooff, J.A.R.A.M. (2000). Costs and benefits of the one-male, age-graded and all-male phase in wild Thomas's langur groups. — In: Primate males: causes and consequences of variation in group composition (Kappeler, P.M., ed.). Cambridge University Press, Cambridge, p. 130-145.
- Sterck, E.H.M. (1997). Determinants of female dispersal in Thomas langurs. — *Am. J. Primatol.* 42: 179-198.
- Sterck, E.H.M. & van Hooff, J.A.R.A.M. (2000). The number of males in langur groups: monopolizability of females or demographic processes? — In: Primate males: causes and consequences of variation in group composition (Kappeler, P.M., ed.). Cambridge University Press, Cambridge, p. 120-129.
- Strier, K.B. (1999). Why is female kin bonding so rare? Comparative sociality of neotropical primates. — In: Comparative primate socioecology (Lee, P.C., ed.). Cambridge University Press, Cambridge, p. 300-319.
- Struhsaker, T.T. & Leland, L. (1987). Colobines: infanticide by adult males. — In: Primate societies (Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W. & Struhsaker, T.T., eds). University of Chicago Press, Chicago, IL, p. 83-97.
- Sugiyama, Y. (1976). Life history of male Japanese monkeys. — In: Advances in the study of behaviour (Rosenblatt, J.S., Hinde, R.A., Shaw, E. & Beer, C., eds). Academic Press, New York, NY, p. 255-284.
- Sussman, R.W. (1992). Male life history and intergroup mobility among ringtailed lemurs (*Lemur catta*). — *Int. J. Primatol.* 13: 395-413.
- Thierry, B. (2007). The macaques: a double-layered social organizations. — In: Primates in perspective (Campbell, C.J., Fuentes, A., MacKinnon, K.C., Panger, M. & Bearder, S.K., eds). Oxford University Press, New York, NY, p. 224-239.
- de Waal, F.B. & Harcourt, A.H. (1992). Coalitions and alliances: a history of ethological research. — In: Coalitions and alliances in humans and other animals (Harcourt, A.H. & de Waal, F.B., eds). Oxford University Press, Oxford, p. 1-19.
- Watanabe, K. (1979). Alliance formation in a free-ranging troop of Japanese macaques. — *Primates* 20: 459-474.
- Widdig, A., Streich, W.J. & Tembrock, G. (2000). Coalition formation among male Barbary macaques (*Macaca sylvanus*). — *Am. J. Primatol.* 50: 37-51.
- Wrangham, R.W. (1980). An ecological model of female-bonded primate groups. — *Behaviour* 75: 262-300.
- Yeager, C.P. & Kool, K. (2000). The behavioural ecology of Asian colobines. — In: Old world monkeys (Whitehead, P.F. & Jolly, C.J., eds). Cambridge University Press, Cambridge, p. 496-521.

Appendix A. Data compiled for species used in pairwise comparisons of male parallel dispersal (0 = absent, 1 = present), intergroup coalitions (0 = absent, 1 = present), intragroup coalitions (0 = absent, 1 = present), coalitions combined (0 = absent, 1 = present), sex-biased dispersal (0 = bisexual, 1 = male-biased), social system (M = multi-male multi-female, O = other), breeding seasonality (L = low, M = moderate, H = high) and paternity concentration (L = low, M = moderate, H = high).

	Male parallel dispersal	Inter-group coalitions	Intra-group coalitions	Coalitions combined	Sex-biased dispersal	Social system	Breeding seasonality	Pat conc.
<i>Varecia variegata</i>		0 ¹	0 ¹	0	1 ²	M ^{3,4}	H ^{5, A}	
<i>Eulemur fulvus</i>	1 ⁶	1 ^{1,6}	0 ¹	1	0 ⁶	M ^{3,4}	H ⁵	
<i>Eulemur macaco</i>		1 ¹		1	0 ²	M ⁴	H ⁵	
<i>Lemur catta</i>	1 ⁷	1 ⁸	0 ¹	1	1 ⁷	M ^{3,4}	H ^{5, B}	
<i>Propithecus verreauxi</i>	1 ⁹	1 ¹	0 ¹	1	1 ¹⁰	M ^{3,4}	H ⁵	
<i>Propithecus edwardsi</i>	1 ^C	0 ^C	0 ^C	0	0 ¹¹	M ⁴	H ¹¹	H ¹¹
<i>Cebuella pygmaea</i>					0 ¹²	O ³	L ⁵	
<i>Callithrix jacchus</i>	1 ^{12, 13}	1 ^D	0 ^D	1	0 ¹²	O ^{14, 15}	L ⁵	
<i>Callimico goeldi</i>		1 ^E	0 ^E	1	0 ¹⁶	M ¹⁵	H ^E	
<i>Leontopithecus rosalia</i>	1 ¹³	1 ¹⁷	0 ¹⁷	1	0 ¹³	M ¹⁵	M ⁵	
<i>Saguinus fuscicollis</i>	1 ¹³				0 ¹²	O ^{3, 15}	M ⁵	
<i>Saguinus geoffroyi</i>					0 ¹²	M ¹⁵		
<i>Saguinus oedipus</i>	1 ¹³	0 ¹⁸	0 ¹⁸	0	0 ¹²	O ^{3, 15}	M ⁵	
<i>Saguinus mystax</i>	1 ^{13, F, G}	1 ^{F, G}	0 ^{F, G}	1	0 ¹²	M ¹⁵	M ^{F, G}	H ^{19, F}
<i>Cebus apella</i>		1 ²¹	1 ²⁰	1	1 ¹²	M ¹⁵	H ⁵	H ²²
<i>Cebus albifrons</i>		1 ²³		1	1 ¹²	M ²⁴	M ⁵	
<i>Cebus capucinus</i>	1 ^{25, 26}	1 ²⁸	1 ²⁷	1	1 ¹²	M ²⁴	M ^H	H ²⁹
<i>Cebus olivaceus</i>		1 ³⁰		1	1 ¹²	M ²⁴	H ⁵	H ³¹
<i>Saimiri boliviensis</i>	1 ³²	1 ³²	1 ³²	1	1 ³²	M ³²		
<i>Saimiri sciureus</i>	0 ³³	1 ³³	1 ³³	1	0 ³³	M ³	H ⁵	
<i>Alouatta pigra</i>	1 ³⁴	1 ³⁴		1	0 ³⁴	M ³		
<i>Alouatta palliata</i>	0 ¹	1 ^{35, I}	1 ^I	1	0 ¹²	M ³	H ^I	
<i>Alouatta seniculus</i>	1 ³⁶	1 ³⁶	1 ³⁷	1	0 ¹²	M ³	L ⁵	H ³¹
<i>Alouatta belzebul</i>					0 ¹²	M ³		
<i>Alouatta caraya</i>		1 ³⁸		1	0 ¹²	M ³	L ³⁹	
<i>Ptilocolobus rufomitatus</i>					0 ⁴⁰	O ⁴⁰		
<i>Procolobus verus</i>	1 ⁴¹				0 ⁴¹	M ³	M ⁵	
<i>Colobus guereza</i>		0 ⁴²	0 ^J	0	1 ⁴³	O ³	L ⁵	
<i>Presbytis rubicunda</i>					1 ⁴⁴	O ^{3, 44}		
<i>Presbytis thomasi</i>	1 ^{45, K}	1 ^{46, K}	0 ^K	1	1 ^{44, 45}	O ⁴⁴	L ^K	H ^{47, K}
<i>Semnopithecus entellus</i>	0 ^L	1 ⁴⁸	0 ^L	1	1 ⁴⁹	M ⁴⁸	H ^{50, L}	H ^{51, L}
<i>Trachypithecus cristatus</i>					1 ^{40, 44}	O ^{40, 44}	M ⁵	
<i>Nasalis larvatus</i>					1 ⁴⁴	O ^{3, 44}	M ⁵	
<i>Erythrocebus patas</i>	1 ^M	1 ^M	0 ^{52, M}	1	1 ⁵³	O ³	H ⁵	H ³¹

Appendix A. (Continued.)

	Male parallel dispersal	Inter-group coalitions	Intra-group coalitions	Coalitions combined	Sex-biased dispersal	Social system	Breeding seasonality	Pat conc.
<i>Cercopithecus aethiops</i>	1 ^{54, N}	1 ⁵⁵	1 ⁵⁴	1	1 ⁵⁴	M ³	H ⁵	H ³¹
<i>Cercopithecus lhoesti</i>		0 ⁵²	0 ⁵²	0	1 ⁵³	O ³		
<i>Cercopithecus cephus</i>		0 ⁵²	0 ⁵²	0	1 ⁵³	O ³		
<i>Cercopithecus ascanius</i>		1 ⁵³	0 ⁵²	1	1 ⁵³	O ³	H ⁵	
<i>Cercopithecus nictitans</i>		0 ⁵²	0 ⁵²	0	1 ⁵³	O ³		
<i>Cercopithecus mitis</i>	1 ^O	1 ^O	0 ⁵²	1	1 ⁵³	O ³	M ⁵	H/M ⁵⁶
<i>Cercopithecus campbelli</i>		0 ⁵²	0 ⁵²	0	1 ⁵⁷	O ⁵⁸		
<i>Macaca fascicularis</i>	1 ^{59, P}	1 ^{60, P}	1 ^{60, P}	1	1 ⁵⁹	M ³	M ^{5, P}	H ^{31, P}
<i>Macaca mulatta</i>	1 ⁶¹	1 ⁶²	1 ⁶¹	1	1 ⁶¹	M ³	H ⁵	H ³¹
<i>Macaca fuscata</i>	1 ⁶³	1 ⁶⁵	1 ⁶⁴	1	1 ⁶³	M ³	H ⁵	M ³¹
<i>Macaca radiata</i>			1 ⁶⁶	1	0 ⁶⁷	M ⁵⁸	H ⁵	
<i>Macaca sinica</i>					1 ^{68, 69}	M ³	H ⁵	M ³¹
<i>Macaca nemestrina</i>					1 ⁶⁷	M ³	M ⁵	
<i>Macaca sylvanus</i>	1 ⁷⁰		1 ⁷¹	1	1 ⁷⁰	M ⁵⁸	H ⁵	
<i>Lophocebus albigena</i>	1 ^Q	1 ^Q	1 ^Q	1	1 ⁷²	M ⁷²	L ^Q	
<i>Cercocebus atys</i>		1 ⁷³	1 ⁷³	1	1 ⁷⁴	M ³	M ⁵	
<i>Cercocebus galeritus</i>					1 ⁷⁵	M ⁵⁸		
<i>Papio anubis</i>	1 ^R	1 ^R	1 ^{76, R}	1	1 ⁴⁹	M ⁵⁸	L ^{5, R}	H ³¹
<i>Papio cynocephalus</i>	1 ^S	1 ^S	1 ^{76, S}	1	1 ⁴⁹	M ³	L ⁵	M ^S
<i>Papio ursinus</i>	0 ^T	0 ⁷⁸	0 ^{76, 77}	0	1 ⁷⁵	M ⁵⁸	L ⁵	H ³¹
<i>Papio hamadryas</i>		1 ⁸⁰	1 ⁷⁹	1	0 ⁸¹	M ³	M ⁵	
<i>Theropithecus gelada</i>		1 ⁸²		1	1 ⁸¹	M ³	M ⁵	
<i>Gorilla gorilla</i>		1 ⁸⁴	1 ⁸³	1	0 ⁴⁹	O ³	L ⁵	H ³¹

^AA. Britt, pers. commun.; ^BL. Gould, pers. commun.; ^CP. Wright & T.L. Morelli, pers. commun.; ^DL. Digby, pers. commun.; ^EL. Porter, pers. commun.; ^FE. Heymann, pers. commun.; ^GP. Garber, pers. commun.; ^HL.M. Fedigan, pers. commun.; ^IM. Clarke, pers. commun.; ^JP. Fashing, pers. commun.; ^KE.H.M. Sterck, pers. commun.; ^LC. Borries, pers. commun.; ^MJ. Chism, pers. commun.; ^NL.A. Isbell, pers. commun.; ^OM. Cords, pers. commun.; ^PM.A. van Noordwijk, pers. commun.; ^QM. Arlet, pers. commun.; ^RR. Palombit, pers. commun.; ^SJ. Altmann & S. Alberts, pers. commun.; ^TD.L. Cheney, pers. commun.

¹Kappeler (1999); ²Kappeler (1997); ³Plavcan (1999); ⁴Gould & Sauther (2007); ⁵van Schaik et al. (1999); ⁶Ostner & Kappeler (2004); ⁷Jones (1983); ⁸Gould (2006); ⁹Lawler et al. (2003); ¹⁰Richard et al. (1993); ¹¹Morelli et al. (2009: this issue); ¹²Strier (1999); ¹³Garber (1994); ¹⁴Harcourt et al. (1981); ¹⁵Digby et al. (2007); ¹⁶Porter et al. (2001); ¹⁷Baker & Dietz (1996); ¹⁸Snowdon & Pickhard (1999); ¹⁹Huck et al. (2005); ²⁰Ramirez-Llorens et al. (2008); ²¹Janson (1998); ²²Escobar-Parámo (2000); ²³Janson (1986); ²⁴Fragaszy et al. (2004); ²⁵Jack & Fedigan (2004a); ²⁶Jack & Fedigan (2004b); ²⁷Perry (1998); ²⁸Fedigan & Jack (2004); ²⁹Jack & Fedigan (2006); ³⁰Robinson (1988); ³¹van Noordwijk & van Schaik (2004); ³²Mitchell (1994); ³³Boinski et al. (2005); ³⁴Horwich et al. (2000); ³⁵Clarke (2005); ³⁶Pope (1990); ³⁷Sekulic (1983); ³⁸Kowalewski (2007); ³⁹Kowalewski & Zunino (2004); ⁴⁰Struhsaker & Leland (1987); ⁴¹Korstjens & Schippers (2003); ⁴²Fashing (1999); ⁴³Fashing (2007); ⁴⁴Yeager & Kool (2000); ⁴⁵Sterck (1997); ⁴⁶Steenbeek et al. (2000); ⁴⁷Sterck & van Hooff (2000); ⁴⁸Sommer (1988); ⁴⁹Pusey & Packer (1987a); ⁵⁰Koenig et al. (1997); ⁵¹Launhardt et al. (2001); ⁵²Rowell (1988); ⁵³Enstam & Isbell (2007); ⁵⁴Cheney & Seyfarth (1983); ⁵⁵Cheney (1981); ⁵⁶Hatcher (2007); ⁵⁷Cords (1987); ⁵⁸Nunn (1999); ⁵⁹van Noordwijk & van Schaik (1985); ⁶⁰van Noordwijk & van Schaik (2001); ⁶¹Meikle & Vessey (1981); ⁶²Hausfater (1972); ⁶³Kawanaka (1973); ⁶⁴Watanabe (1979); ⁶⁵Sugiyama (1976); ⁶⁶Silk (1992); ⁶⁷Thierry (2007); ⁶⁸Dittus (1975); ⁶⁹Dittus (1977); ⁷⁰Paul & Kuester (1985); ⁷¹Widdig et al. (2000); ⁷²Olupot & Waser (2005); ⁷³Benneton & Noë (2004); ⁷⁴Jolly (2007); ⁷⁵Melnick & Pearl (1987); ⁷⁶Noë (1992); ⁷⁷Henzi et al. (1999); ⁷⁸Kitchen et al. (2004); ⁷⁹Sigg et al. (1982); ⁸⁰Cheney (1987); ⁸¹Stammach (1987); ⁸²Dunbar (1984); ⁸³Smuts (1987); ⁸⁴Robbins (1995).

Appendix B. Phylogeny used in the analyses, in Newick format with all branch lengths set to 1.0. (((*Varecia variegata*:1.0 ((*Eulemur fulvus*:1.0, *Eulemur macaco*:1.0):1.0, *Lemur catta*:1.0):1.0):1.0 (*Propithecus edwardsi*:1.0, *Propithecus verreauxi*:1.0):1.0):1.0 ((((((*Cebuella pygmaea*:1.0, *Callithrix jacchus*:1.0):1.0 (*Leontopithecus rosalia*:1.0 (*Saguinus fuscicollis*:1.0 ((*Saguinus geoffroyi*:1.0, *Saguinus oedipus*:1.0):1.0, *Saguinus mystax*:1.0):1.0):1.0):1.0, *Callimico goeldi*:1.0):1.0 ((*Cebus apella*:1.0 ((*Cebus albifrons*:1.0, *Cebus capucinus*:1.0):1.0, *Cebus olivaceus*:1.0):1.0):1.0 (*Saimiri boliviensis*:1.0, *Saimiri sciureus*:1.0):1.0):1.0):1.0 ((*Alouatta palliata*:1.0, *Alouatta pigra*:1.0):1.0 ((*Alouatta seniculus*:1.0, *Alouatta caraya*:1.0):1.0, *Alouatta belzebug*:1.0):1.0):1.0):1.0 ((((*Procolobus verus*:1.0, *Piliocolobus rufomitratus*:1.0):1.0, *Colobus guereza*:1.0):1.0 ((*Presbytis thomasi*:1.0, *Presbytis rubicunda*:1.0):1.0 (*Semnopithecus entellus*:1.0, *Trachypithecus cristatus*:1.0):1.0):1.0, *Nasalis larvatus*:1.0):1.0):1.0 (((*Cercopithecus aethiops*:1.0, *Erythrocebus patas*:1.0):1.0 (*Cercopithecus lhoesti*:1.0 ((*Cercopithecus cephus*:1.0, *Cercopithecus ascanius*:1.0):1.0 (*Cercopithecus nictitans*:1.0, *Cercopithecus mitis*:1.0):1.0):1.0, *Cercopithecus campbelli*:1.0):1.0):1.0):1.0 ((((((*Macaca mulatta*:1.0, *Macaca fuscata*:1.0):1.0, *Macaca fascicularis*:1.0):1.0 (*Macaca radiata*:1.0, *Macaca sinica*:1.0):1.0):1.0, *Macaca nemestrina*:1.0):1.0, *Macaca sylvanus*:1.0):1.0 (((*Cercocebus atys*:1.0, *Cercocebus galeritus*:1.0):1.0, *Lophocebus albigena*:1.0):1.0 (((*Papio anubis*:1.0, *Papio cynocephalus*:1.0):1.0, *Papio ursinus*:1.0):1.0, *Papio hamadryas*:1.0):1.0, *Theropithecus gelada*:1.0):1.0):1.0):1.0):1.0, *Gorilla gorilla*:1.0):1.0):1.0):1.0.