# The effect of male parallel dispersal on the kin composition of groups in white-faced capuchins

Eva C. Wikberg [a, *], Katharine M. Jack [b], Fernando A. Campos [a, c], Linda M. Fedigan [c], Akiko Sato [a], Mackenzie L. Bergstrom [c], Tomohide Hiwatashi [a], Shoji Kawamura [a]

[a] Department of Integrated Biosciences, University of Tokyo, Kashiwa, Chiba, Japan
[b] Department of Anthropology, Tulane University, New Orleans, LA, U.S.A.
[c] Department of Anthropology, University of Calgary, Calgary, Alberta, Canada

Sex-biased dispersal can reduce kin cooperation and kin competition in the dispersed sex. However, this may not be the case when group-living animals engage in parallel dispersal, which occurs when an individual transfers between groups together with other animals or immigrates alone into a group that contains familiar animals. Despite this potential effect on kin cooperation and competition, few studies have thoroughly investigated how parallel dispersal affects the kin composition of groups. To further our understanding of this topic, we investigated the effect of parallel dispersal on access to coresident kin in male white-faced capuchins, *Cebus capucinus*. Between 2006 and 2013, we collected demographic and genetic data from two to five groups in Sector Santa Rosa, Costa Rica. We genotyped 41 females and 39 males at 14 short tandem repeat loci, and we calculated their estimated relatedness values. The majority of males dispersed in parallel, and parallel dispersing males were more closely related to one another than were other males. Parallel immigrant males and natal females resided with a similar number of same-sex kin. Single immigrant males in multimale groups rarely resided with male kin, and they resided with fewer same-sex kin than did parallel immigrant males and natal females. Because parallel dispersal offers an opportunity for males to form long-lasting cooperative relationships with familiar kin, this dispersal pattern should be taken into account in future models of the evolution of social structure.
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Dispersal can be costly because it may increase predation risk and aggression from conspecifics while reducing foraging efficiency and access to familiar social partners (Bonte et al., 2012; Isbell & Van Vuren, 1996). Perhaps to mitigate these costs, dispersing individuals in some birds (reviewed in Riehl, 2013), social carnivores (Frame, Malcolm, Frame, & Vanlawick, 1979; Packer, Gilbert, Pusey, & O'Brien, 1991) and primates (reviewed in Schoof, Jack, & Isbell, 2009) engage in parallel dispersal. Parallel dispersal occurs when animals transfer between groups together with familiar animals or when they immigrate alone into a group that contains familiar animals (van Hooff, 2000). The potential benefits of parallel dispersal include lowered predation risk while transferring between groups, reduced aggression from resident animals in the new group, continued access to familiar coalitionary partners (Alberts & Altmann, 1995; Cheney & Seyfarth, 1983; Schoof et al., 2009) and enhanced inclusive fitness (Pope, 1990).

Because parallel dispersal enables dispersing animals to maintain long-term bonds with familiar animals, it may have important fitness consequences, particularly when the dispersing sex relies on coalitions to gain mating opportunities. In some species with male parallel dispersal, coalitions of males have greater success at procuring groups of females and high-quality territories, higher survival and/or greater reproductive success (red howler, *Alouatta seniculus*: Pope, 1990; Sekulic, 1983; tamarins, *Saguinus* spp.: Baker, 1991; Garber, Encarnación, Moya, & Pruetz, 1993; Löttker, Huck, & Heymann, 2004; lion, *Panthera leo*: Packer et al., 1991; white-faced capuchin, *Cebus capucinus*: Fedigan & Jack, 2004; Jack & Fedigan, 2004a, 2004b; acorn woodpecker, *Melanerpes formicivorus*: Koenig, Walters, & Haydock, 2011; Arabian babbler, *Turdoides squamiceps*: Ridley, 2012). Despite the formation of coalitions, it is often only the most dominant male that experiences immediate gains in terms of reproductive opportunities (Díaz-Muñoz, 2011; Jack & Fedigan, 2006; Krakauer, 2005; Krutzen, Barre, Connor, Mann, & Sherwin, 2004; Muniz et al., 2010; Packer et al., 1991; Pope, 1990; Ridley, 2012). None the less, weaker males may be unable to take over or gain membership within a bisexual group on their own, and their best strategy may be to

\* Correspondence: E. C. Wikberg, Department of Integrated Biosciences, University of Tokyo, Bioscience Building 502, 5-1-5 Kashiwanoha, Kashiwa, Chiba 277-8562, Japan.
*E-mail address:* wikberg@ib.k.u-tokyo.ac.jp (E. C. Wikberg).

cooperate with a dominant male and remain subordinate with relatively few mating opportunities (Emlen, 1995; Hatchwell, Sharp, Beckerman, & Meade, 2013; Pope, 1990; Riehl, 2013; Snyder-Mackler, Alberts, & Bergman, 2012; Vehrencamp, 1983). Subordinate males may get a chance to reproduce if they increase their rank after the group take-over (reviewed in Bourke, 2014; Díaz-Muñoz, DuVal, Krakauer, & Lacey, 2014; Riehl, 2013) or if several females are in oestrus simultaneously and the dominant male is unable to guard them all (Alberts, Watts, & Altmann, 2003). This form of reproductive queuing may therefore result in delayed direct fitness benefits (Kokko & Johnstone, 1999). The evolution of male coalitions could also be based on inclusive fitness benefits (Hamilton, 1964) that males gain from cooperating with dominant male kin (reviewed in Bourke, 2014; Díaz-Muñoz et al., 2014; Riehl, 2013). These two hypotheses are not mutually exclusive because a subordinate male can gain immediate inclusive fitness benefits from cooperating with dominant male kin and delayed direct fitness benefits if he eventually acquires reproductive opportunities in the group (Bourke, 2014; Díaz-Muñoz, 2011; Díaz-Muñoz et al., 2014). Theoretical studies suggest that these potential fitness benefits may not outweigh the increased risk of inbreeding and kin competition that continued coresidency with male kin would entail (Hamilton & May, 1977; Queller, 1992; Taylor, 1992; West, Pen, & Griffin, 2002; but see Gardner & West, 2006). However, few empirical studies have rigorously investigated whether or not parallel dispersal results in a higher than expected proportion of coresident kin in the dispersing sex (rhesus macaque, *Macaca mulatta*: Meikle & Vessey, 1981; dwarf mongoose, *Helogale parvula*: Keane, Creel, & Waser, 1996; long-tailed tit, *Aegithalos caudatus*: Sharp, Simeoni, & Hatchwell, 2008). Data from a wider range of species are needed to understand which factors affect the occurrence of kin-biased dispersal and the resulting kin composition of groups.

The white-faced capuchin is an ideal study species for investigating how male parallel dispersal affects the kin composition of groups. On average, white-faced capuchin males disperse from their natal group at around 4 years of age (Jack, Sheller, & Fedigan, 2012), and they continue to disperse between breeding groups at approximately 4-year intervals throughout their lives (Fedigan & Jack, 2004; Jack & Fedigan, 2004b). Males frequently disperse in parallel (Jack & Fedigan, 2004a, 2004b; Perry, Godoy, & Lammers, 2012), and coalitions of males are better at taking over and maintaining access to groups of females than singly immigrating males (Fedigan & Jack, 2004). Despite the importance of male coalitions in this species, male reproductive skew remains high (Jack & Fedigan, 2006; Muniz et al., 2010). The combination of repeated individual dispersal events, reliance on same-sex coalitionary partners, and high reproductive skew makes the white-faced capuchin a particularly interesting species to investigate the possibility of males gaining indirect fitness benefits from cooperating with other males.

The objectives of this study were to determine whether male capuchins show kin-biased dispersal, and to clarify how dispersal patterns affect the kin composition of groups. First, we investigated whether or not males show kin-biased dispersal. If kin cooperation leads to direct (Chapais, 2001) and/or inclusive fitness benefits (Hamilton, 1964), we predicted that males who disperse together would be more closely related to each other than to other males (P1a). In contrast, if the costs of increased kin competition and inbreeding risk offset or outweigh the benefits of kin cooperation (Hamilton & May, 1977; Queller, 1992; Taylor, 1992; West et al., 2002), we expected that males who disperse together would be similarly or less closely related to each other than to other males (P1b). Second, we examined the spatial distribution of related males across groups. If dispersal is kin-biased and males remain together after the immigration event, we expected mean

male—male relatedness to be higher within than between groups (P2a). However, if dispersal is not kin-biased or if male kin do not remain together after the immigration event, we expected mean relatedness to be similar or lower within than between groups (P2b). Third, we investigated how the number of same-sex kin in the group is affected by the animal's sex, dispersal status and the number of coresident same-sex animals. Because most females do not leave their natal group (Jack & Fedigan, 2009), we predicted that females would reside with a higher number of same-sex kin than males (P3). If male dispersal is kin-biased and males remain together after the immigration event, we also expected parallel immigrant males to reside with a higher number of male kin than single immigrant males (P4a). In contrast, we expected parallel immigrant males and single immigrant males to reside with a similar number of kin if male dispersal is not kin-biased or if male kin do not remain together after the immigration event (P4b).

## METHODS

### Data Collection

We studied four groups of white-faced capuchins in the Sector Santa Rosa of the Área de Conservación Guanacaste, Costa Rica (Table 1). One of these groups (CP) fissioned into two groups (AD and RM) in 2013. This population has been studied nearly continuously since 1983 (Fedigan & Jack, 2012). Here we used data from years in which we had genetic relatedness information for all group members (2006—2013). Members of L.M.F.'s and K.M.J.'s research teams collected demographic data from each study group at least once per month. The exact ages of animals born in the study groups were known from the demographic records. Experienced observers estimated ages based on physical appearance for individuals originating in nonstudy groups and for individuals that were already present in the study group when it was first contacted. Using the demographic data, we determined the dispersal status for each resident male and female: natal, parallel or single immigrant, or parallel or single emigrant. Parallel dispersal events involved two or more animals moving simultaneously to a different social group (i.e. simultaneous parallel dispersal) or lone animals transferring to social groups that already contained at least one familiar, previously coresident animal (i.e. delayed parallel dispersal). All other dispersal events were classified as single dispersals. We did not consider short visits (<3 days) to neighbouring groups as dispersal events in our analyses. The males that we classified as immigrants remained at least 6 months in their new group. All adult females (>5 years) and immigrant males (regardless of their age) were included in our analyses (Table 1). We did not include natal males in our analyses unless they dispersed during the study period. We categorized males that were younger than 7 years as juvenile, males between 7 and 9 years as subadult, and males 10 years or older as adult (Fedigan, Rose, & Avila, 1996). Each group contained

**Table 1**
Group composition and male-male mean relatedness (R) throughout the study period

| Group | Study years | Number of adult females | Number of immigrant males | Male-male mean R |
|---|---|---|---|---|
| CP | 2006—2012 | 7—14 | 2—6 | 0.00—0.10 |
| AD[a] | 2013 | 5 | 7 | 0.11 |
| RM[a] | 2013 | 5 | 2 | 0.00 |
| EX | 2006—2013 | 3—4 | 1—5 | 0.00—0.27 |
| GN | 2006—2013 | 8—12 | 3—9 | 0.17—0.49 |
| LV | 2006—2013 | 4—7 | 1—5 | 0.00—0.13 |

[a] AD and RM are fission products of CP.

one to nine immigrant males of different ages (juvenile, subadult or adult) and 3–14 adult females (Table 1).

We collected at least two faecal samples noninvasively from each study animal. We extracted DNA from the samples using the QIAamp stool kit (Qiagen, Crawley, U.K.) and quantified the amount of genomic DNA using real-time quantitative polymerase chain reactions (PCRs; Hiramatsu et al., 2005). We used PCRs to amplify 14 short tandem repeat (STR) loci that consist of tetra-nucleotide repeat units specifically designed for white-faced capuchins (Ceb01, Ceb02, Ceb03, Ceb04, Ceb07, Ceb08, Ceb09, Ceb10, Ceb11, Ceb105, Ceb120, Ceb127, Ceb128, and Ceb130; see Muniz & Vigilant, 2008 for details regarding primers and cycling protocol). Diluted PCR products were combined with a size standard (GeneScan 600 LIZ, Applied Biosystems, Tokyo, Japan) and capillary electrophoresed on an ABI PRISM3130 (Applied Biosystems). Allele sizes were assigned automatically by GeneMapper v3.7 (Applied Biosystems) and visually confirmed by inspecting the electropherograms. We confirmed heterozygote loci using at least two replicates of each extract. The number of replicates needed to confirm homozygotes was based on extract quality and locus-specific dropout rates following the methods of Morin, Chambers, Boesch, and Vigilant (2001). We genotyped two faecal samples collected on different occasions from each animal to confirm their identities. We were unable to do this for two males from whom we collected only one working sample before each disappeared. We genotyped the study animals at 98% of the loci. The mean number of alleles was 5 and the mean heterozygosity was 0.63 (also see Muniz & Vigilant, 2008). This study was approved by the University of Calgary's Life and Environmental Sciences Animal Care Committee (BI2005, BI2008-03, BIO8R-03; 2006–2013) and Tulane University's Institutional Animal Care and Use Committee (A4499, 2006–2014).

*Data Analysis*

We used permutation tests to investigate whether immigrant males were more closely related within cohorts of parallel dispersers (P1) and within study groups (P2) than expected at random. We conducted both sets of analyses because kin-biased dispersal may not necessarily lead to kin-based social groups if male kin do not remain together after the dispersal event (Ridley, 2012; Teichroeb, Wikberg, & Sicotte, 2011; Wikberg, Sicotte, Campos, & Ting, 2012). First, we calculated estimated relatedness values ($R$) using ML-Relate (Kalinowski, Wagner, & Taper, 2006). Then, we calculated the mean $R$ of immigrant male–male dyads in each study group (or each parallel dispersing cohort), and we used these values to calculate the observed population mean $R$ for within-group immigrant males (or within-cohort males). Finally, we randomly drew immigrant males from the study population (or the population of parallel dispersing males) regardless of which group (or cohort) they belonged to, and we calculated the permuted population mean. The permuted groups always consisted of the same number of dyads as the observed groups (or cohorts), and we used 10 000 iterations to generate confidence intervals of permuted groups (Di Fiore & Fleischer, 2005). The code to perform these permutations was written by F.A.C. and is available at http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0048740 (see Appendix S2–S3 in Wikberg et al., 2012). We accounted for multiple testing by correcting the significance threshold using Benjamini and Hochberg's (1995) method implemented in R version 3.1.0 (R Core Team, 2014). In 14 cases, an immigrant male resided in more than one group during the same year. For this analysis, we only counted these males as residents of the group in which they had the longest tenure during that year.

We investigated whether the number of same-sex coresident kin was affected by sex and dispersal status (P3–P4). Owing to different levels of inbreeding and sampling biases (i.e. genotyping a very small proportion of the genome), $R$ does not always correspond to the theoretical values expected for definite kin relationships (Csillery et al., 2006; Van Horn, Altmann, & Alberts, 2008). Demographic data and parentage assignments can more accurately distinguish between different categories of kin, and we therefore used these two methods to determine kinship whenever possible. Of the 75 immigrant males and adult females included in this analysis, maternity was known from the demographic records ($N = 33$ individuals) or assigned by parentage analysis in CERVUS (Kalinowski, Taper, & Marshall, 2007; Marshall, Slate, Kruuk, & Pemberton, 1998) at the 95% confidence level ($N = 13$ individuals). Paternity was assigned by parentage analysis in CERVUS for 38 of 75 study animals. We considered all resident males and females that were at least 6 years old at the time of conception as candidate parents. The proportion of genotyped candidate parents ranged from 0.17 to 0.90. For the study animals whose mothers ($N = 29$) or fathers ($N = 37$) remained unknown, we assessed their level of kinship using calculated $R$ values. We used $R$ for known kin to determine the ranges of $R$ that correspond to different kin categories in our study population to further mitigate the problem of $R$ not corresponding to the theoretical values for definite kin categories (modified from Langergraber, Mitani, & Vigilant, 2009; Rollins et al., 2012; Wikberg et al., 2012; Wikberg, Ting, & Sicotte, 2014). We calculated the 99% confidence intervals for three kin categories: (1) nonkin (i.e. two animals that do not have the same parents), (2) half-sibling and grandparent–grandoffspring dyads and (3) full-sibling and parent–offspring dyads. The 99% confidence intervals for $R$ did not overlap between half-siblings and grandparent–grandoffspring ($R$: 0.23–0.30, $N = 142$), parent–offspring and full-siblings ($R$: 0.49–0.53, $N = 128$), and nonkin ($R$: 0.05–0.09, $N = 188$). Therefore, we classified kin as dyads with an $R$ of 0.23 or higher, which corresponds to the lower confidence interval for known half-siblings and grandparent–grandoffspring. We counted the same-sex kin with which each individual resided each year. We used generalized linear mixed models (GLMM) with a Poisson distribution and a log link function to investigate whether the number of same-sex kin was predicted by the number of same-sex animals in the group, sex and sex dispersal status. Sex dispersal status was categorized as natal female, simultaneous parallel immigrant male and lone immigrant male (i.e. delayed parallel immigrant and single immigrant). We combined delayed parallel immigrant and single immigrant males for the purpose of this analysis because their access to kin was similar (see Results), both categories included a low number of males, and it was often difficult to distinguish between these two categories when males immigrated from an unknown group to a study group. We built four models that included animal identity as a random effect and up to two fixed effects (Table 2). We computed the models with the R package lme4 (Bates et al., 2014), and we performed model selection based on Akaike information criterion (AIC) values (Akaike, 1974). To investigate differences between the three sex dispersal status categories, we used the multiple comparison procedure implemented in the R package multcomp (Hothorn, Bretz, Westfall, Heiberger, & Scheutzenmeister, 2014). Note that the conclusions of this analysis remain the same even if we classify kinship using the $R$ threshold for all dyads.

## RESULTS

During our study, the groups contained 33 immigrant males. Only one of these males remained a resident in a single group throughout the study. In addition, five natal males dispersed to a

**Table 2**
Each competing model's fixed effect, AIC value, delta (i.e. difference in AIC between the current model and the best-fit model) and the hypothesis it supports

| Outcome variable | Fixed effects | AIC | Δ | Support of hypothesis |
|---|---|---|---|---|
| Same-sex kin $N = 354$ | Same-sex group size + Sex dispersal status | 1056 | 0 | Single and parallel immigrant males reside with a different number of same-sex kin |
| | Same-sex group size + Sex | 1069 | 12 | Natal females and immigrant males reside with a different number of same-sex kin |
| | Same-sex group size | 1082 | 26 | No support for the alternative hypotheses |
| | — | 1149 | 93 | No support for the alternative hypotheses |

All models contained animal identity as a random effect.

nonstudy group. Together these 38 males engaged in 47 dispersal events during the study period (Table 3).

### Kin-biased Dispersal

Few males ($N = 5$) who entered a study group did so as a single immigrant (13%) or delayed parallel immigrant (3%). These males appeared to have a similar mean $R$ to the immigrant males in the target group (mean = 0.07, 95% CI: 0–0.14) and in the nontarget groups (mean = 0.12, 95% CI: 0.08–0.17), although the low sample size precluded statistical analyses of this data set.

The majority of dispersal events were classified as parallel dispersals (65%). All juvenile, the majority of subadult (83%) and fewer than half of the adult (43%) dispersal events were parallel (Table 3). We observed 10 cases of simultaneous parallel dispersal ($N = 30$ males in 32 male dispersal events) during the study period (Appendix Fig. A1). Each cohort of parallel dispersers included two to six males. Only four of the 30 males that dispersed in parallel did so with a cohort that contained no close male kin ($R \geq 0.23$). These males either did not reside with male kin of similar age ($N = 2$) or originated from a nonstudy group in which their access to male kin was unknown ($N = 2$). The general pattern was for males to have higher $R$ with male dispersal partners (mean = 0.28, 95% CI: 0.21–0.34) than with immigrant males in their pretransfer (mean = 0.11, 95% CI: 0.06–0.16) and post-transfer group (mean = 0.05, 95% CI: 0.03–0.09), although this was not always the case (Appendix Fig. A1). Almost half (13/28) of the simultaneous parallel dispersing males were natal males. The natal males that dispersed in parallel were paternal half-siblings ($N = 7$ dyads), maternal half-siblings ($N = 1$ dyad), distant maternal kin ($N = 4$ dyads), close kin of unknown category ($N = 1$ dyad) or nonkin ($N = 3$ dyads) (Appendix Fig. A2).
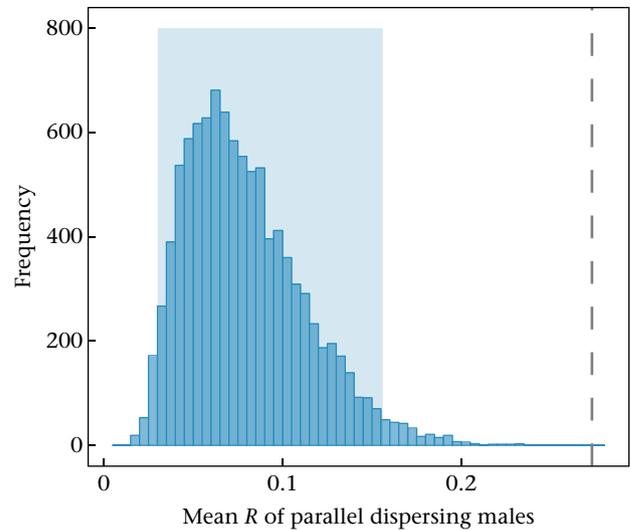


**Figure 1.** Observed mean estimated relatedness ($R$) in cohorts of parallel dispersing males (dashed line). The bars represent the frequency at which each mean $R$ appeared in the permuted population of parallel dispersing males. The shaded area indicates the 95% confidence interval for the permuted population of parallel dispersers.

We investigated whether simultaneous parallel dispersing males ($N = 30$) were more closely related to each other than to other males by comparing the mean $R$ of parallel dispersing cohorts with the mean $R$ of same-size permuted cohorts that consisted of randomly drawn parallel dispersing males, regardless of which cohort they belonged to (P1). The mean $R$ for simultaneous parallel dispersers was 0.27, which was significantly higher than the mean $R$ of permuted cohorts (95% CI: 0.03–0.16; Fig. 1).

### Kin Composition of Groups

During our study, the mean $R$ of coresident immigrant males varied considerably between years in all groups (Table 1). This variation was mostly due to waves of parallel male immigration or emigration. We investigated the spatial distribution of related immigrant males across groups (P2), and the mean $R$ of coresident immigrant males did not differ from the mean $R$ of permuted groups of immigrant males drawn randomly from the study population (Fig. 2). The outcome of these permutations was consistent between years (Fig. 2).

We examined how the number of same-sex kin in the group was affected by the animal's sex, dispersal status and the number of coresident same-sex animals (P3 and P4). The GLMM that best predicted the number of coresident kin included the 'number of same-sex animals' and 'sex dispersal status' variables (Table 2). The number of same-sex animals in the group had a small positive
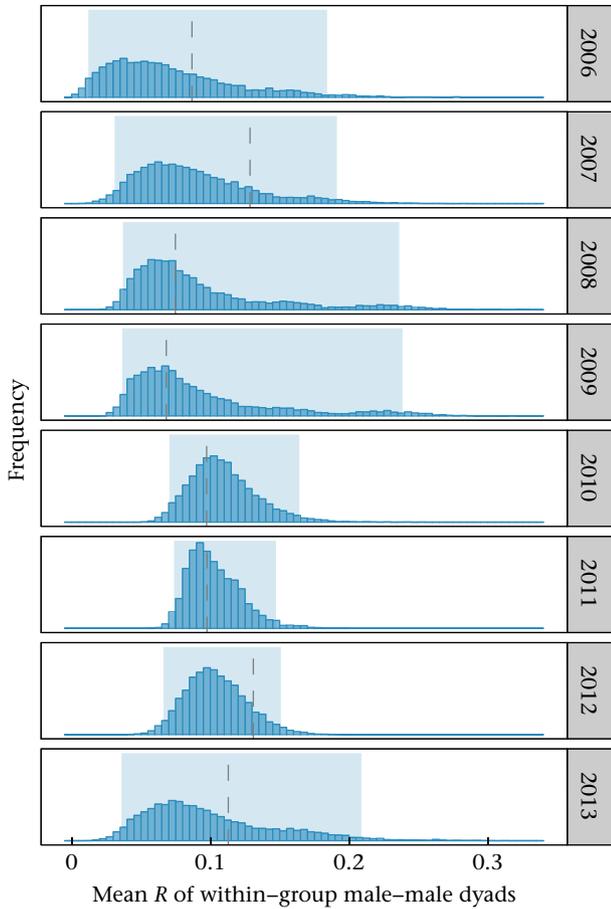
**Table 3**
Number of parallel and single dispersing males in different age classes

| Dispersal type | N | Juvenile | | | Subadult | | | Adult | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Parallel | | Single | Parallel | | Single | Parallel | | Single |
| | | Sim[c] | Del[c] | — | Sim[c] | Del[c] | — | Sim[c] | Del[c] | — |
| Immigration[a] | 12 | 1 | 0 | 0 | 6 | 0 | 0 | 2 | 0 | 3 |
| Emigration and immigration[b] | 18 | 6 | 0 | 0 | 6 | 1 | 1 | 4 | 0 | 0 |
| Emigration suspected | 17 | 1 | 0 | 0 | 2 | 0 | 2 | 3 | 0 | 9 |
| Total | 47 | 8 | 0 | 0 | 15 | 0 | 3 | 9 | 0 | 12 |

[a] Transfers to study groups.
[b] Transfers between study groups.
[c] Sim = simultaneous parallel dispersal; Del = delayed parallel dispersal.

**Figure 2.** Observed mean estimated relatedness ($R$) for within-group male dyads during different years (dashed line). The bars represent the frequency at which each mean $R$ appeared in the permuted population. The shaded areas indicate the 95% confidence interval for the permuted population.

immigrant and single immigrant males) resided with significantly fewer same-sex kin than did natal females (Figs 3, 4, estimate = −1.47, 95% CI: −2.17 to −0.77) and simultaneous parallel immigrant males (Fig. 4; estimate = −1.13, 95% CI: −1.86 to −0.41). The confidence interval for the standard deviation of the random effect was 0.22–0.49.

## DISCUSSION

### Kin-biased Dispersal

We predicted that parallel dispersing males would be more closely related to each other than to other males (P1a), and this prediction was supported (Fig. 1). Similar findings come from several species of birds in which natal animals often disperse in parallel with same-sex siblings (Koenig & Pitelka, 1979; Petrie, 1999; Sharp et al., 2008; Williams & Rabenold, 2005). The majority of natal males in our study dispersed in parallel with their paternal brothers (Appendix Fig. A2). This pattern may be linked to high male reproductive skew leading to a large number of similar-aged paternal siblings (Altmann, 1979; Inoue, 2011). This makes paternal brothers more likely to be available as dispersal partners than are maternal brothers or unrelated similar-aged males (Widdig, 2013). While we cannot differentiate between natal males selectively dispersing with kin versus dispersing with kin by default because of their greater availability, the end result is the same: males frequently reside with close kin after engaging in natal dispersal.

Our preliminary findings suggest that white-faced capuchin males, transferring alone or in parallel, did not preferentially target groups with familiar or unfamiliar immigrant male kin. Similarly, singly dispersing male grey-cheeked mangabeys, *Lophocebus albigena*, rarely join groups that contain male kin, but there are few male kin present in their study population (Chancellor et al., 2011). In contrast, male capuchins frequently have familiar immigrant male kin that reside in surrounding groups. Rather than lacking the option, male capuchins may prefer not to join a group that already contains immigrant male kin, perhaps to reduce the risk of inbreeding and kin competition. However, other studies suggest that it is beneficial for males to join a group that already contains immigrant kin. Singly dispersing male dwarf mongooses bias immigration to groups in which kin occupy a dominant breeding
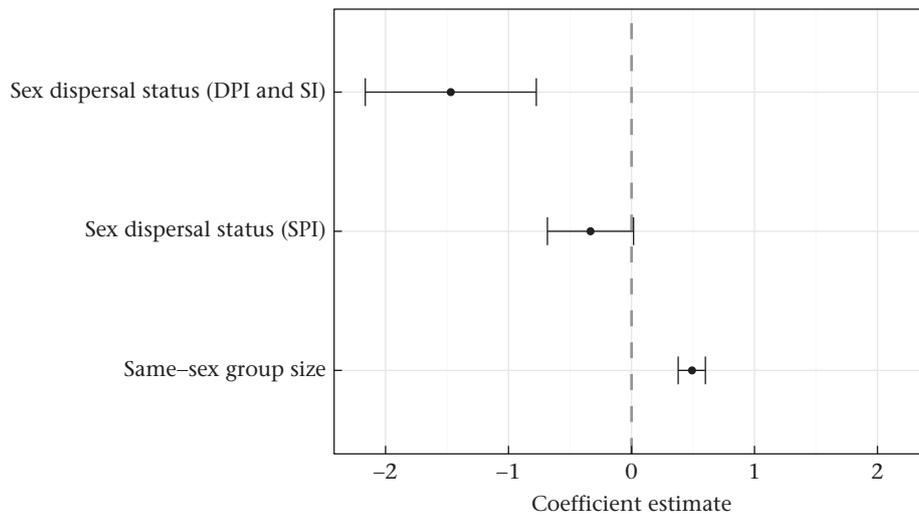
effect on the number of coresident same-sex kin (Fig. 3). Simultaneous parallel immigrant males resided with slightly fewer same-sex kin than did natal females, but this effect was not statistically significant at the 95% confidence level (Figs 3, 4; estimate = −0.33, 95% CI: −0.68 to 0.02). Lone immigrant males (i.e. delayed parallel



**Figure 3.** Coefficient estimates and 95% confidence intervals from the best-fitting model that investigated access to coresident same-sex kin. Same-sex group size is a continuous outcome variable. Sex dispersal status is an ordinal predictor variable with three levels: NF = natal females (which is the baseline level and therefore not included in the figure), SPI = simultaneous parallel immigrant males, and DPI and SI = delayed parallel immigrant males and single immigrant males.
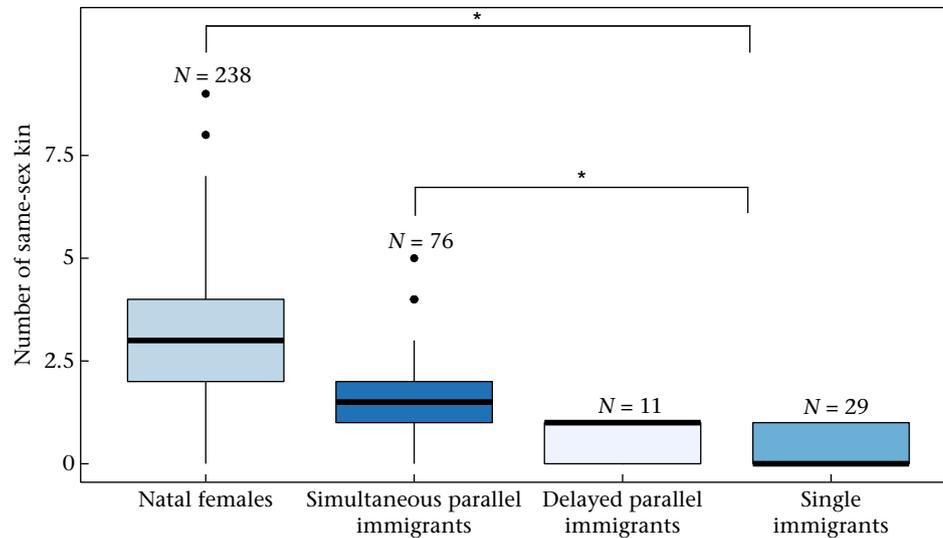
**Figure 4.** The proportion of same-sex group members that are kin for natal females, simultaneous parallel immigrant males, delayed parallel immigrant males and single immigrant males. The box represents the first and third quartiles and the median is marked with a horizontal bar. The range of the data ($1.5 \times$ IQR (interquartile range)) is represented with vertical bars with the exception of outliers which are indicated by dots. Significant differences between natal females, simultaneous parallel immigrant males, and lone immigrant males (i.e. delayed parallel immigrant males and single immigrant males) are indicated with an asterisk.

position (Keane et al., 1996). It is possible that the dwarf mongoose shows a different dispersal pattern because it is a cooperatively breeding species that does not avoid inbreeding (Keane et al., 1996), in contrast to white-faced capuchins (Muniz et al., 2006). Male rhesus macaques are also more likely to join a group that contains their maternal brother than expected by chance (Meikle & Vessey, 1981). Because kinship has a small but significant effect on proximity among familiar immigrant rhesus macaques (Albers & Widdig, 2013), joining a group that contains familiar kin may facilitate social integration in the new group. It is unclear why male rhesus macaques, but not male white-faced capuchins, preferentially join groups with familiar immigrant male kin. The discrepancy may be due to obscure differences in social structure or it may be a by-product of small sample sizes. Further studies with a larger sample size and genetic data from a greater number of possible target groups are necessary to fully investigate how a male's choice of target group is affected by his familiarity and kinship with the resident males.

*Kin Composition of Groups*

We predicted that kin-biased parallel dispersal would lead to higher mean immigrant male relatedness within than between groups (P2a). Despite the prevalence of parallel dispersal involving male kin, mean relatedness among coresident capuchin males remained low, in contrast to our prediction (Fig. 2). There was no difference in relatedness between within-group and between-group male dyads, which conforms to the pattern in other populations with male dispersal (European rabbit, *Oryctolagus cuniculus*: Surridge et al., 1999; lion: Spong, Stone, Creel, & Bjorklund, 2002; Verreaux's sifaka, *Propithecus verreauxi*: Lawler, Richard, & Riley, 2003; white-thighed colobus, *Colobus vellerosus*: Wikberg et al., 2012). These results suggest a weak effect of male parallel dispersal on the distribution of related males in our study population. Such a pattern may arise if parallel immigrant males evict each other after successful immigration, as is often the case in Arabian babblers (Ridley, 2012) and white-thighed colobus (Teichroeb et al., 2011; Wikberg et al., 2012). However, this was not the case in our study, as most of the parallel immigrants formed long-lasting coalitions. Some male dyads dispersed in parallel several times and remained together for up to 6 years. Similar findings come from a

population of long-tailed macaques, *Macaca fascicularis*, in which coresident males have low mean relatedness even though male kin sometimes immigrate in parallel (de Ruiter & Geffen, 1998). The authors suggest that the low mean relatedness is due to a strong dilution effect that occurs when males coreside with other males with which they did not immigrate (de Ruiter & Geffen, 1998). This reasoning can also explain many cases of low mean within-group relatedness in our study. Parallel immigrant males were seldom able to oust the old resident males immediately after entering the group because most cases involved subadult males that had not yet reached adult body size. As a result, groups often consisted of several immigrant males that originated in different groups. In two of three cases, when the parallel immigrant males eventually ousted all of the previously resident males, the group showed exceptionally high mean relatedness among immigrant males ($R$: 0.27−0.49). In addition, males often disperse to neighbouring groups, and they may immigrate to several different neighbouring groups during their lifetime (vervet monkey, *Chlorocebus pygerythrus*: Cheney & Seyfarth, 1983; tufted capuchin, *Sapajus apella*: Izawa, 1994; white-faced capuchin: Jack & Fedigan, 2004a; white-breasted thrasher, *Ramphocinclus brachyurus*: Temple, Hoffman, & Amos, 2006). As a result, the mean between-group relatedness may be relatively high for neighbouring groups compared with more distant groups. Thus, a relatively high number of closely related between-group dyads, in combination with the dilution effect described above, may explain why mean relatedness was not higher within groups than between groups in our study population.

Based on observed dispersal patterns, we predicted that natal females would reside with the highest number of same-sex kin and single immigrant males with the lowest number of same-sex kin (P3 and P4a). These predictions were partially supported. Single immigrant males and delayed parallel immigrant males rarely resided with male kin (Figs 3, 4). Although these males transfer alone, some of them had the option to join a group that contained familiar or unfamiliar male kin. However, our results indicate that this was rarely the case. Simultaneous parallel immigrant males often resided with male kin, and they only resided with slightly fewer same-sex kin than did natal females (Figs 3, 4). Even though we predicted an impact of parallel dispersal on the kin composition of groups, we did not anticipate that its effects would almost offset the sex difference in access to kin. As far as we know, this is one of

the first studies to show such a strong effect of parallel dispersal on the kin composition of groups in a species with near-complete sex bias in dispersal.

*Fitness Benefits Associated with Male Coalitions*

The negative effects of intrasexual kin competition and inbreeding are thought to outweigh the benefits of kin cooperation in male mammals, leading to male-biased dispersal (reviewed in Lawson Handley & Perrin, 2007). However, males may be able to reap the benefits of dispersal while still remaining with male kin by engaging in parallel dispersal. This dispersal pattern is likely to favour cooperation if it reduces competition but maintains high levels of relatedness (Gardner & West, 2006). Because males form coalitions with male kin in bottlenose dolphins, *Tursiops* sp. (Krutzen et al., 2003), lions (Spong et al., 2002), long-tailed tits (Sharp et al., 2008), red howlers (Pope, 1990) and white-faced capuchins (this study), it is possible that male–male coalitions in these species evolved at least partly because of inclusive fitness benefits. However, two cohorts of parallel dispersing males consisted solely of nonkin in our study, and inclusive fitness benefits cannot explain why unrelated males form coalitions. Different patterns of relatedness within male coalitions may reflect that the population has more than one evolutionarily stable strategy (Johnstone, Woodroffe, Cant, & Wright, 1999; Krutzen et al., 2003; Sinervo & Clobert, 2003). According to theoretical and empirical studies, unrelated males share reproductive opportunities more equally than males in kin coalitions (Emlen, 1995; Krutzen et al., 2004; Packer et al., 1991; Vehrencamp, 1983; Wiszniewski, Corrigan, Beheregaray, & Moeller, 2012). Coalitions between nonkin males may therefore lead to direct fitness benefits while coalitions between kin lead to direct fitness benefits for dominant males and inclusive fitness benefits for subordinate males.

Even if male reproductive skew remains high within coalitions of nonkin, the small number of infants sired by subordinate males may still be sufficient to offer incentives for subordinate males to remain in the group and help prevent extragroup males from immigrating (horse, *Equus caballus*: Feh, 1999; gelada, *Theropithecus gelada*: Snyder-Mackler et al., 2012). If competition over breeding opportunities is extreme, subordinates that do not get to sire offspring may still benefit more from remaining in the group rather than dispersing if the chances of successful independent reproduction are small (Baker, 1991; Emlen, 1995; Hatchwell et al., 2013; Riehl, 2013; Vehrencamp, 1983). Male capuchins often disperse from their natal group after the group has been taken over by new immigrant males (Jack et al., 2012), which occurs on average every 4 years (Fedigan & Jack, 2004; Jack & Fedigan, 2004b). As a result, many males disperse from their natal group well before they become fully grown around 10 years of age. These young males reside on average in three groups before reaching adulthood (Jack & Fedigan, 2004b). Initially, they have no chance of becoming a dominant male in a breeding group owing to their small body size. However, they may benefit from establishing residence as a subordinate without mating opportunities if doing so offers them greater access to food and increased protection from predators. As subordinates, these young males can improve their social skills and build strong social relationships that may help them gain the alpha position after they have reached full body size. Thus, the dominant male and relatively weak subordinate males may gain direct fitness benefits from cooperating with each other.

This population of white-faced capuchins may have experienced strong selective pressure for parallel dispersal because of potential direct and inclusive fitness benefits. To further investigate the potential fitness benefits of male coalitions, future studies should focus on how familiarity and kinship affect the quality of cooperative relationships among immigrant males and whether these relationships influence male reproductive success. It is also crucial to determine whether these benefits outweigh the costs of increased kin competition and inbreeding risk. Because parallel dispersal may have important consequences for cooperation for the dispersed sex, in particular for species with high reproductive skew, this dispersal pattern should be taken into account in future models of the evolution of social structure.

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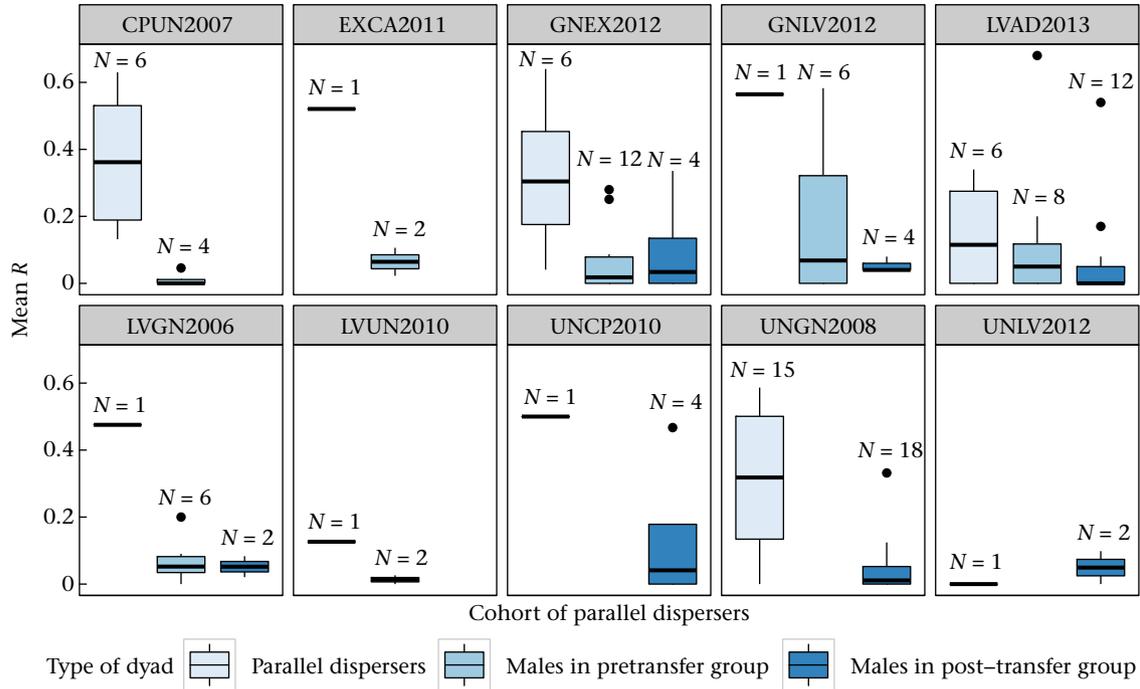
## Appendix



**Figure A1.** Estimated relatedness (*R*) between males belonging to the same cohort of simultaneous parallel dispersers ('Parallel dispersers'), between parallel dispersers and other resident immigrant males in the pretransfer group ('Males in pretransfer group'), and between parallel dispersers and other resident immigrant males in the post-transfer group ('Males in post-transfer group'). The box represents the first and third quartiles and the median is marked with a horizontal bar. The range of the data (1.5 × IQR) is represented with vertical bars with the exception of outliers which are indicated by dots.
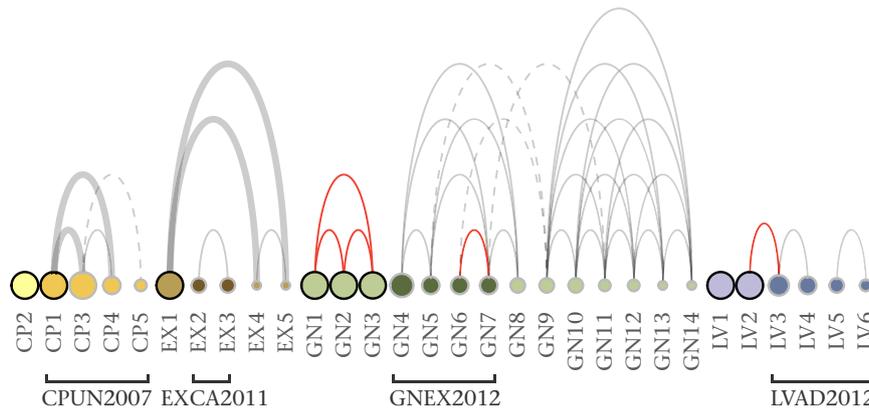


**Figure A2.** The resident males in each group at the time natal males engaged in parallel emigration. Thick lines connect father−son pairs and full-siblings, thin solid lines connect paternal half-siblings and thin dashed lines connect maternal half-siblings. Individuals that are not connected by lines are either distant maternal kin or nonkin. These kinship categories were determined from parentage assignments in CERVUS at the 95% confidence level or were known from the demographic records. The red lines indicate dyads with high *R* but whose exact kinship category remained unresolved. Each circle represents a male, and colours indicate different groups (yellow = CP, brown = EX, green = GN and purple = LV). The hue indicates whether or not the male was part of the cohort of parallel emigrating males (dark = parallel emigrant and light = resident). The emigrating cohort is further indicated by a bracket under which its name is located. The size of the circle indicates male age with increasing sizes from age 2 to 10 years, and circles that represent adult males are of the same size. Black borders represent immigrant males and grey borders represent natal males.