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

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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.


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

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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.