

Chapter 7

The Effects of Dispersal and Reproductive Patterns on the Evolution of Male Sociality in White-Faced Capuchins



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Abstract In many mammalian species, philopatric females reside with female kin with whom they form long-lasting cooperative bonds, whereas dispersing males rarely form strong bonds with other males. However, males may have the opportunity to disperse and form long-lasting bonds with paternal male kin in species with high male reproductive skew and parallel male dispersal. We used 54 group-years with demographic and genetic data to investigate how male dispersal and reproductive patterns affected the distribution of male kin in the Santa Rosa white-faced capuchins (*Cebus capucinus imitator*). During 41 of 54 group-years, there was a high degree of reproductive monopolization by either the alpha or a subordinate male. Natal males often co-resided with paternal brothers of similar age. The likelihood of parallel dispersal from the natal group increased with age similarity and paternal sibship. Some males may possibly gain inclusive fitness benefits by engaging in parallel dispersal and forming long-term cooperative bonds with other males. However, only one of three groups displayed a positive association between male-male relatedness and time spent co-resident in the breeding group. Inbreeding avoidance between alpha males and their daughters also gives subordinate males an opportunity to gain direct fitness benefits and may provide a strong incentive for cooperation among males that are not close kin. These findings suggest that cooperation between related and unrelated males likely evolved due to different reasons.

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Subordinate males related to the alpha male may gain inclusive fitness benefits, while only unrelated subordinate males gained reproductive opportunities and direct fitness benefits from cooperating.

Keywords Social evolution · Kin cooperation · Kin competition · Inbreeding · Parallel dispersal

7.1 Introduction

Many gregarious mammals show male dispersal and female philopatry (i.e. females remain in their natal group to breed) (Greenwood 1980). As a result, adult females will typically reside with their adult female kin, while adult males will rarely reside with adult male kin after dispersing from their natal group to a breeding group. Having access to related social partners may favour the evolution of social behaviours via kin selection, which occurs when the cost of the behaviour to the actor's own reproductive success is outweighed by an increase in reproductive output by a related recipient (Hamilton 1964a, b). Due to these inclusive fitness benefits, cooperation is more likely to evolve among kin than non-kin (Hamilton 1964a, b). If kin interact with each other more frequently than non-kin, the former may be more reliable allies due to their history of interactions, and long-lasting cooperative relationships with kin may lead to increased reproductive success for both partners (Chapais 2001). Thus, kin cooperation can evolve due to indirect fitness benefits according to Hamilton (1964a, b) or direct fitness benefits according to Chapais (2001).

Several influential socioecological models proposed in the 1980s and 1990s suggested that the sex that relies on cooperative partners to gain high reproductive success should remain in their natal group and cooperate with same-sex kin (Wrangham 1980; van Schaik 1989; Sterck et al. 1997). However, the benefit of kin cooperation does not always compensate the cost of intense competition. Therefore, the sex that experiences high competition for limited resources and does not gain sufficient benefits from forming kin coalitions should disperse from their natal group to avoid kin competition (Griffin and West 2002; West et al. 2002).

These theoretical models explain why many female primates reside with female kin with whom they form long-lasting cooperative bonds, whereas many male primates disperse (Sterck et al. 1997). Female sociality is predicted to have significant fitness benefits, although only a few studies have been able to confirm this prediction in long-lived animals (Silk et al. 2003, 2009; Kalbitzer et al. 2017) due to difficulties in determining fitness outcomes in these populations (Silk et al. 2009). Even though males disperse, they may still form kin-biased affiliative relationships in their natal group. For example, male rhesus macaques (*Macaca mulatta*) form the strongest relationship with their maternal kin, although their relationships were not as strong as those between maternal female kin (Widdig et al. 2016). This difference may be due to mothers biasing affiliation to offspring of the philopatric sex (Kulik et al. 2015; Murray et al. 2016). In contrast, males formed stronger relationships with paternal kin than did females, perhaps because paternal male kin often disperse together (Widdig et al. 2016).

Fedigan (1993) noted early on that although female white-faced capuchins (*Cebus capucinus imitator*) conformed to these expectations, male white-faced capuchins did not. They were unusual in comparison to other male-dispersed primate species, even species in the same genus, by showing frequent affiliation with other males and by forming dominance hierarchies that appeared to be dependent not only on individual traits like body size and strength but also on social factors (Fedigan 1993). Similar reports from other primate species have since appeared. For example, dispersing males benefit from cooperating with each other in Assamese macaques (*Macaca assamensis*) (Schuelke et al. 2010) and Geoffroy's tamarins (*Saguinus geoffroyi*) (Diaz-Munoz and Ribeiro 2014).

Fedigan and Jack (2012) investigated this topic in more detail by using unique longitudinal data sets from the Santa Rosa capuchins. Using decades of behavioural observations from multiple study groups, they found that males benefitted from forming dispersal coalitions (i.e. showing parallel dispersal) because these coalitions were more successful than single males in taking over groups of females (Fedigan and Jack 2004; Jack and Fedigan 2004a, b). From data collected during five park-wide population surveys, they discovered that group productivity (i.e. infant to female ratio) was higher in groups with more males (Fedigan and Jack 2011). These results indicated that it was important for males to cooperate, which can explain why males form tolerant, cooperative, and often affiliative relationships with each other (Jack 2003; Schoof and Jack 2014). What is so remarkable is that male capuchins are able to form cooperative relationships despite dispersing several times during their lifetime (Jack and Fedigan 2004b; Jack and Fedigan (2018), Chap. 6 in this volume) and competing intensely for reproductive opportunities – a combination of traits that is not predicted to co-occur according to theoretical models (Griffin and West 2002; West et al. 2002).

Observational data suggest that white-faced capuchin males may have solved the dilemma of needing to form alliances and dispersing in two ways. First, frequent parallel dispersal leaves open the possibility that males disperse and cooperate with their close kin to gain inclusive fitness benefits (Jack and Fedigan 2004a, b). Following this hypothesis, we predict that male kin will be more likely to disperse in parallel than male non-kin, that immigrant male kin will reside together longer than immigrant male non-kin, and that male reproductive skew will be high (i.e. subordinate males gain indirect rather than direct fitness benefits from cooperating with a related alpha male). Second, cooperating males may share reproductive opportunities in which case all males gain direct fitness benefits from cooperating (Fedigan 1993). Based on this hypothesis, parallel dispersal need not be kin-biased, co-residency times will be longer for co-dispersing males than other males, and reproductive skew will be low. We will evaluate the support for each of the two hypotheses using 20 years of demographic and genetic data from the Santa Rosa white-faced capuchins. Based on the findings of this and previous studies, we will discuss how the costs and benefits associated with kin cooperation and kin competition can explain male sociality during different life history stages.

7.2 Methods

7.2.1 Study Population

This study on white-faced capuchins was conducted in Sector Santa Rosa of the Área de Conservación Guanacaste, Costa Rica. Most females are philopatric (Jack and Fedigan 2009), and they often give birth for the first time at 6.5 years of age (Fedigan and Jack 2012). Males typically leave their natal group at around 4 years of age, but the dispersal age varies from 19 months to 11 years in our study population (Jack and Fedigan 2004b; Jack et al. 2012). Although subadult males (7–10 years) are able to copulate with ejaculation, they have not sired any genotyped offspring in our study population to date (Wikberg et al. 2017). Adult males (>10 years) have gained full body size, but it is only upon becoming alpha males that they develop the full complement of secondary sexual characteristics (Jack et al. 2014; also see Chap. 6 by Jack and Fedigan (2018) in this volume).

7.2.2 Demographic and Behavioural Data Collection

Demographic and ad libitum (Altmann 1974) behavioural data from four groups (Table 7.1) were collected once a month between 1993 and 2013 under the supervision of Linda Fedigan and Katharine Jack. These data were used to determine group composition, age of individuals, mother-offspring relationships, and alpha male status. Alpha males can easily be distinguished by the direction of submissive interactions,

Table 7.1 Group composition and reproductive skew (Nonacs’ B index)

Group	Years	AF ^a	IM ^a	Infants ^a	# years with 1 reproducing male		# years with >1 reproducing male	
					Only alpha	Only subordinate	Skewed/total ^b	B index
CP	1993–2012	2–10 (14/15)	1–6 (9/11)	0–7 (42/53)	9	4	0/4	–0.25–0.05
EX	2006–2010	3–4 (4/4)	1–4 (6/6)	0–4 (10/16)	3	0	0/1	–0.74
GN	1999–2013	4–11 (12/12)	3–9 (9/13)	0–8 (36/46)	7	0	1/5	–0.13–0.50
LV	1993–2013	4–6 (9/10)	2–10 (19/30)	0–4 (33/49)	12	0	0/4	–0.11–0.11
Total					36/40	4/40	1/14	

^aThe range represents the number of adult females (AF), immigrant males (IM), and infants present in any year. The proportions of genotyped animals are indicated in parentheses. Raw data can be found at University of Calgary’s digital repository PRISM

^bNumber of years with reproductive skew/total number of years with two or more reproducing males

such as avoid, fear grin, flee, and supplant (Perry 1998; Jack 2003; Jack et al. 2014). We observed too few submissive interactions between the subordinate males to be able to rank them in relation to each other. Therefore, we will only discuss how alpha versus subordinate status (rather than exact rank number) affects reproductive output.

7.2.3 Genetic Data Collection

Two faecal samples were collected from offspring, mothers, and candidate sires (Wikberg et al. 2014a, 2017). In Shoji Kawamura's laboratory at the University of Tokyo, we performed DNA extractions, DNA quantification using real-time quantitative polymerase chain reactions (PCRs), PCR amplifications of up to 20 short tandem repeat loci, capillary electrophoresis, and confirmation of genotypes (Wikberg et al. 2014a, 2017). Sires were assigned at the 95% confidence interval using the software Cervus (Marshall et al. 1998; Kalinowski et al. 2007), and estimated relatedness values (R -values) were calculated with ML-Relate (Kalinowski et al. 2006) as previously described (Wikberg et al. 2017).

7.2.4 Data Analysis

When multiple resident males reproduced, we assessed whether reproduction was skewed using Nonacs' B index. This index calculates how different the observed reproductive sharing is from being equal while taking into account the number of months each adult male spent resident in the group that year (Nonacs 2000). The index ranges from -1 to 1 , and higher values indicate stronger reproductive skew.

We investigated whether dispersal partner choice among natal males was kin-biased using binomial generalized linear mixed models (GLMMs). Each time a natal male dispersed, we coded whether he dispersed with each of the potential dispersal partners (i.e. co-resident natal males that were at least 19 months old). We created one null model that did not contain any fixed effects and three alternative models that included one or two fixed effects: (1) age difference between the dispersing male and his potential partner, (2) kinship (i.e. maternal kin, paternal half-sibling, or non-kin), and (3) age difference and kinship (Table 7.2). We combined maternal half-siblings and distant maternal kin into one category "maternal kin" due to small samples sizes. Our data set did not include any distant paternal kin. The fixed effects were not collinear based on low variance inflation factors (VIF, 1.07–1.20). Each model included the random effects group and male identities. We included random intercepts but not random slopes because the latter did not improve the models. We determined the support for each model based on Akaike information criterion corrected for small sample sizes (AICc) (Akaike 1974). The models were computed with the packages lme4 (Bates et al. 2014) in R version 3.3.3. Several models received similar support, and we took model selection uncertainty into account by

Table 7.2 Models of parallel dispersal partner choice and each model's fixed effects, AICc, and delta and Akaike's weight, residual degrees of freedom, and *R*-square

Fixed effects	AICc	Delta	Weight	df	<i>R</i> ²
Age difference + kinship	68.49	0.00	0.63	64	73
Age difference	69.58	1.08	0.37	66	95
Kinship	84.97	16.48	0.00	65	45
Null model	96.32	27.83	0.00	67	46

All models contained group and focal identities as random effects

averaging coefficients across models (Burnham and Anderson 2002) using the R package MuMIn (Barton 2013). We also used MuMIn to calculate each model's conditional *R*-square, which takes both random and fixed effects into account. We used the multiple comparison procedure implemented in the R package multcomp (Hothorn et al. 2014) to investigate differences between all kinship categories.

To investigate whether kin or parallel immigrants resided together longer than other males, we used double-decker semipartialing multiple quadratic assignment procedures in UCINET (Borgatti et al. 2002). This procedure controls for autocorrelation in the data and is therefore well suited for analysing social networks (Hanneman and Riddle 2005). Rows and columns were randomly reshuffled, and *R*-square and regression coefficients were calculated after each permutation for a total of 10,000 permutations. These permuted values were used to create a sampling distribution to evaluate whether our observed values were significantly different from random. The significance level was set to $p < 0.05$. This procedure regressed the outcome matrix (i.e. number of months immigrant males spent co-resident) against multiple predictor matrices: *R*-value, parallel immigration status, and whether the dyad included the alpha male. The latter variable was included because immediate inclusive fitness benefits may only be gained by cooperating with a male kin that occupies the alpha position in groups with high reproductive skew. We used *R*-value instead of kinship categories for this analysis because the mothers and sires remained unknown for the majority of immigrant males. However, several recent studies indicate that marker-based methods reflect genetic similarity more accurately than kinship categories determined from shallow pedigrees (Forstmeier et al. 2012; Robinson et al. 2013), and *R*-values show a relatively high correlation with actual relatedness in some study populations (Wikberg et al. 2014b, 2017).

7.3 Results

7.3.1 Paternity Assignments

We obtained genotypes for 121 of 164 offspring born in the groups (the remaining infants died at an early age), 40 of 41 adult females (the remaining female died early during the study), 16 of 18 alpha males, and 29 of 43 subordinate immigrant males (the remaining males dispersed before sample collection began or their samples did

not amplify). We were able to determine paternity for 111 of 121 infants (Wikberg et al. 2017). For seven of the ten remaining infants, a previous study had genotyped all their candidate sires (including the two alpha males that were not genotyped in this study) and determined their paternity (Jack and Fedigan 2006).

7.3.2 *Reproductive Patterns*

Male siring success varied from 0 to 24 offspring (mean = 1.76, SD = 3.42), and it was largely dependent on whether the male was alpha or subordinate. Alpha males sired 84%, and subordinate males sired 16% of the offspring. All 18 alpha males sired offspring, but the total number of offspring they sired as alpha varied from 1 to 19 (mean = 5.71, SD = 4.56). Alpha males that only sired 1 offspring had short alpha tenures, sometimes only 1 month (unpublished data). The male that sired the highest number of offspring as alpha did so during his tenure as alpha in two different groups. He transferred voluntarily to a study group with a higher number of females, a process that has been observed a number of times in our study population (e.g. Jack and Fedigan 2004b). Only 10 of 32 subordinate males sired offspring (including subordinate males that were not genotyped but present in the group when all infants were assigned to the alpha male) (mean = 0.42, SD = 1.23). In half of the cases when a subordinate male sired offspring (12/24 offspring), the mother of the offspring was the alpha male's daughter and the subordinate male was not kin with the alpha male or the mother. The other cases when a subordinate male sired offspring occurred when the alpha was past prime age (i.e. >16 years), the alpha had recently gained his position, the alpha was wounded, the alpha ranged in the periphery of the group, or when the mother ranged in the periphery of the group. It is possible that the alpha male failed to monopolize reproduction due to these circumstances. The most successful male, Legolas, sired 24 offspring. He sired seven offspring during his 3 years as a subordinate male in the group, which was the highest number of offspring produced by any subordinate male. After the old alpha male left the group, Legolas inherited the alpha position (also see Jack and Fedigan (2018), Chap. 6 in this volume) and sired 17 offspring during the following 5 years. His tenure as alpha has not yet ended (currently >10 years), and he is likely to have an even higher total reproductive success.

Alpha male monopolization of reproduction decreased sharply after 5 years, which corresponds to the age when their daughters approach sexual maturity (Fig. 7.1). For example, Nose completely monopolized reproduction as a new alpha male, while at the end of his 15-year-long tenure, the subordinate male Legolas sired the majority of offspring that were born to Nose's mature daughters. The proportion of infants sired by the alpha male varied depending on group type and alpha male tenure. Alpha males in uni-male groups sired 100% of the offspring (Fig. 7.2). In multi-male groups, alpha males with relatively short tenures (<5 years) monopolized reproduction, while this was not always the case for alpha males with tenures lasting over 5 years (Fig. 7.2).

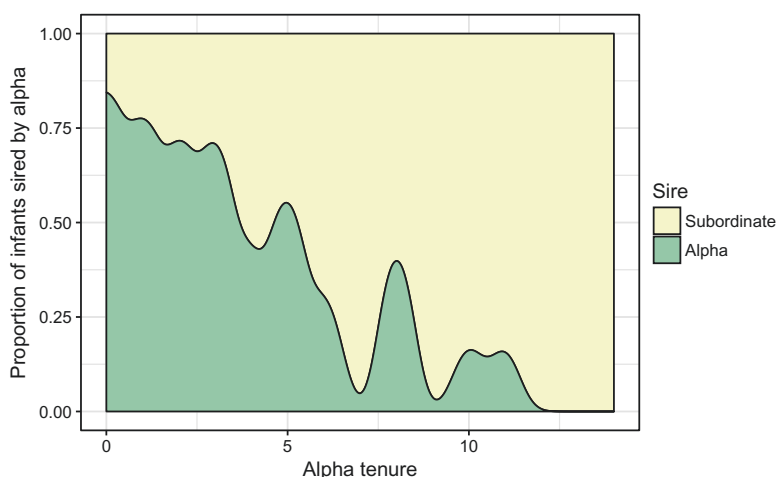


Fig. 7.1 The proportion of infants sired by the alpha male versus the subordinate male(s) during each year of his tenure

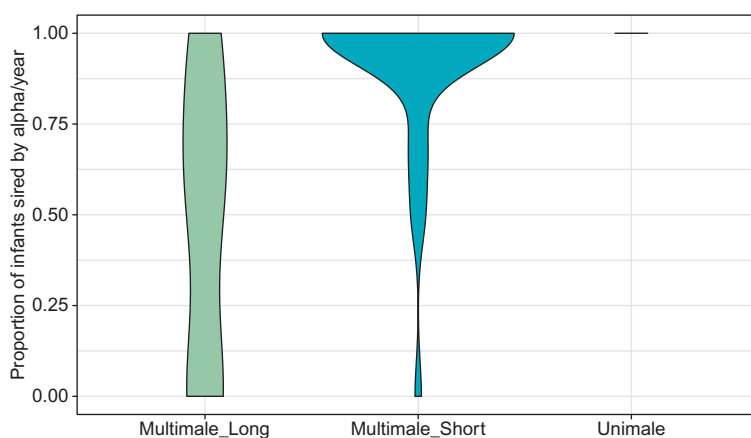


Fig. 7.2 The proportion of infants sired by the alpha male in uni-male groups, multi-male groups with short alpha tenures (<5 years), and multi-male groups with long alpha tenure (>5 years). The length of the violin plot shows the range of values, and the width shows the probability density estimates of values

Alpha males sired all of the infants born during 36 of 54 group-years (Table 7.1). A subordinate male, unrelated to the alpha male Nose, sired all the offspring during 4 of 15 years of the alpha male's tenure (Table 7.1). Six of seven infants born during these 4 years were conceived by the alpha male's mature daughters. Based on Nonacs' B index, reproduction was significantly skewed in 1 of 14 group-years during which the alpha and subordinate males both sired offspring (Table 7.1). Thus, 1 male dominated reproduction during 41 of 54 group-years.

7.3.3 Natal Dispersal Patterns

Of the natal males that dispersed during the study period, 13 dispersed together with other natal males, while 2 dispersed without a partner. However, one of the males that dispersed alone joined a group that contained an unrelated male with whom he had co-resided in his natal group. This dispersal case was therefore classified as delayed parallel dispersal. Most of the dispersing natal males resided with at least one close kin (Fig. 7.3). At the point in time when 1 or more of the 15 natal males dispersed, about half of their potential dispersal partners were close or distant kin ($N = 34$), while the other half were non-kin ($N = 36$). Of these potential dispersal partners, 2/5 maternal half-siblings and 8/12 distant maternal kin, 14/17 paternal half-siblings, and 8/36 non-kin dispersed together. Thus, the category of males that most frequently dispersed together was paternal half-siblings. Our data set did not contain any full siblings or distant paternal kin.

The models that best predicted dispersal partner choice among natal males contained age difference with or without kinship and explained up to 95% of the observed variation, while the null model with only the random effects explained 46% (Table 7.2). The likelihood of parallel dispersal decreased with age difference (Fig. 7.4). Males were more likely to disperse in parallel with paternal kin than with non-kin (Fig. 7.4), while there was no difference between maternal kin and non-kin (Fig. 7.4). The likelihood of dispersing in parallel did not differ between maternal and paternal kin (coefficient = -1.34 , 95% CI 4.85 – 2.15 ; based on multiple comparison procedures and not visualized in Fig. 7.4 that only shows the effect of the two kinship categories in relation to the baseline level non-kin).

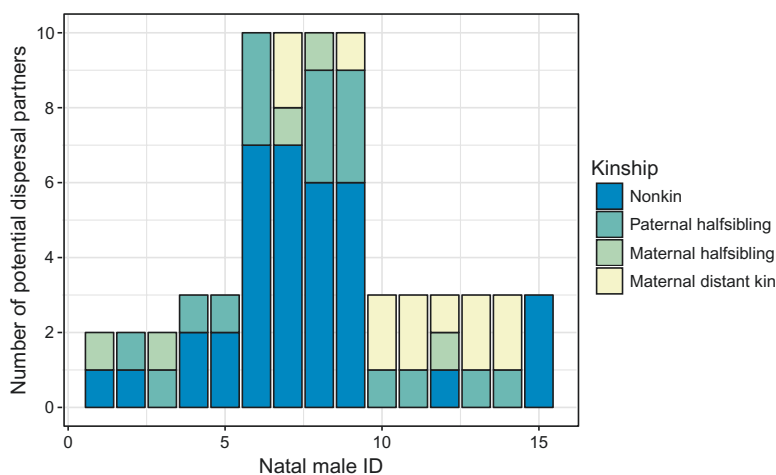


Fig. 7.3 The number of potential dispersal partners of different kinship categories each dispersing natal male had access to

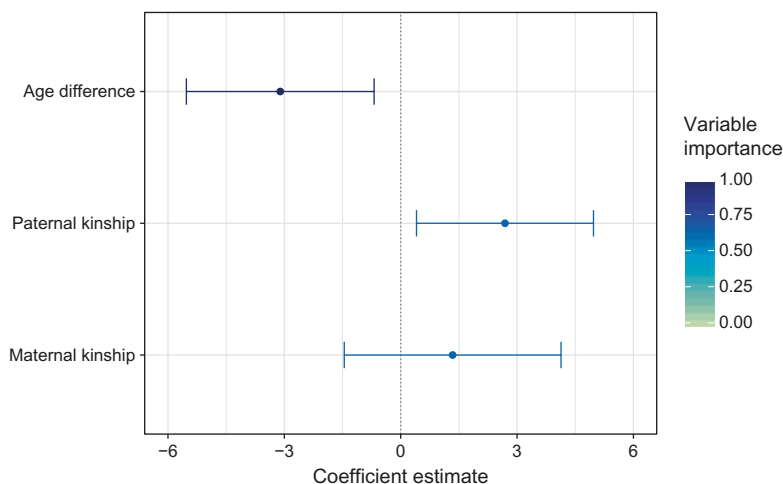


Fig. 7.4 Coefficient estimates and 95% confidence intervals based on averaging across models of parallel dispersal partner choice (see Table 7.2). Coefficient estimates with confidence intervals that do not overlap zero indicate that the variable has a positive or negative effect on the likelihood of parallel dispersal partner choice. Kinship is an ordinal variable with three levels: paternal half-siblings, maternal kin (includes half-siblings and more distant kin), and non-kin (which is the baseline level and not shown in the figure). Age difference is a continuous variable. The variable importance (i.e. the sum of normalized model likelihood over all models that contained the fixed effect) is indicated by colour

7.3.4 Secondary Dispersal Patterns

Of all the cases of secondary dispersal (a.k.a. breeding dispersal) from the study groups when all resident males were genotyped, 11 cases were classified as single emigration or immigration, while 4 cases were classified as parallel emigration. One case of secondary parallel emigration included the alpha male Nose and his two natal sons and one other unrelated natal male. Each of the other three cases consisted of two males that had immigrated in parallel to the study group and had a higher R -value with each other (R : 0.14; 0.45; 0.61) than with the other co-resident immigrant males (R , 0; 0–0.14; 0–0.50).

7.3.5 Co-Residency Times

The groups showed different patterns regarding the time immigrant males spent in co-residency. In LV group, time spent co-resident was predicted by parallel immigration status and R -value (Table 7.3). Males that immigrated in parallel and had lower R -values resided together for longer periods than other males. In GN group, males resided longer with parallel immigrant partners and with the alpha male (Table 7.3). In CP group, males resided longer with the alpha male that had an unusually long tenure (Table 7.3). A small sample size precluded statistical testing in EX group.

Table 7.3 Models of co-residency times between immigrant males

Group	Model		R-value		Parallel immigrant		Alpha	
	R ²	p	Coefficient	p	Coefficient	P	Coefficient	p
CP	0.138	0.026	−0.100	0.343	−0.108	0.168	0.407	0.039
GN	0.319	0.003	0.180	0.107	0.389	0.036	0.274	0.027
LV	0.743	0.034	−0.329	0.042	0.938	0.021	0.051	0.292

R-square and *p*-values are reported for the overall model, while regression coefficients and their *p*-values are reported for each of the predictor variables: *R*-value, parallel immigration partnership, and whether the dyad included the alpha male

7.4 Discussion

These findings show the importance of combining longitudinal demographic and genetic data to fully understand how dispersal and reproductive patterns shape the kin composition of groups and the occurrence of kin cooperation. High male reproductive skew leads to cohorts consisting of paternal siblings, and many natal males dispersed in parallel with their paternal brothers. Surprisingly, kinship did not always have a positive impact on the time immigrant males spent co-resident. It is likely that the costs and benefits of residing with male kin vary with life history stages.

Alpha males with long tenures do not monopolize reproduction to the same degree as relatively new alpha males in white-faced capuchins (Jack and Fedigan 2006; Muniz et al. 2006, 2010; Godoy et al. 2016; Perry 2012; Wikberg et al. 2017), and paternal brothers sired by long-term alpha males may be of dissimilar rather than similar ages. However, most alpha males have relatively short tenures and sire the majority of infants (Jack and Fedigan 2006; Muniz et al. 2006, 2010; Godoy et al. 2016; Perry 2012; Wikberg et al. 2017). This pattern of high reproductive skew leads to most natal animals residing with similar-aged paternal siblings. Our findings indicate that age compatibility and paternal sibship increased the likelihood of parallel dispersal among natal males. Maternal kinship did not have a positive effect on dispersal partner choice even when controlling for age difference, possibly due to this category including both maternal half-siblings and more distant maternal kin. A larger sample size of co-residing maternal brothers is necessary to directly investigate whether males prefer to disperse with their maternal brothers over non-kin.

Parallel secondary dispersal (regardless of kinship) was not common during this study period, but the males that did immigrate in parallel were more closely related to each other than to the other males in the group. Thus, kinship shaped dispersal coalitions both among natal and immigrant males, similar to findings from rhesus macaques (*Macaca mulatta*) (Meikle and Vessey 1981) and long-tailed tits (*Aegithalos caudatus*) (Sharp et al. 2008).

The length of time immigrant males spent co-resident in their breeding group was predicted by parallel immigration status in two of three groups. The reason why the third group did not show a similar pattern may be because it only contained two parallel immigrant males, one of which we believe died during his first year in the

study group. In two groups, subordinate males resided longer with the alpha male than with each other. This finding may simply be a by-product of the alpha males having longer tenures than subordinate males (Jack and Fedigan 2004b). However, it may also be a successful strategy for subordinate males to remain with a long-term alpha past the point when the alpha's daughters start to reproduce. Because alpha males and their daughters avoid inbreeding, a subordinate male can gain direct fitness benefits from supporting an alpha male (Muniz et al. 2006; Godoy et al. 2016; Wikberg et al. 2017). Surprisingly, relatedness only predicted time spent co-resident in one of three groups. Although males often immigrate in parallel with their male kin, they do not necessarily reside together for longer time periods than do male non-kin.

These findings beg the question as to whether kinship is a poor predictor of the maintenance of male coalitions because kin co-residency is associated with high costs and few benefits. Males that disperse in parallel are more likely to succeed in immigrating to a new group (Fedigan and Jack 2004). Once they entered a new group, they all benefit from residing in a social group, via reduced predation risk and increased access to food. In this study, the majority of parallel dispersing males were immature natal males. These young males are not able to gain the alpha position and are not in direct competition against each other for reproductive opportunities. Thus, young males incur relatively low fitness costs from supporting an alpha male while biding their time in a subordinate role (van Noordwijk and van Schaik 2001). Because the alpha male benefits in terms of increased reproductive success from having up to two adult or subadult immigrant males in the group (Wikberg et al. 2017), the subordinate male may gain increased inclusive fitness if he is supporting a related alpha male.

In contrast to immature males, adult co-dispersing males will be in direct competition over the alpha position and a monopoly of reproduction once they gain access to a social group. This can take the form of escalated fighting, some of which result in lethal injuries to the fighting males (Gros-Louis et al. 2003; Fedigan and Jack 2004) or infants (Schoof et al. 2015; Brasington et al. 2017). Thus, the benefits of gaining access to a social group is no longer shared equally among adult males, and the benefits of cooperating with kin may not always outweigh the costs incurred from competing with them. For example, it may not be beneficial for two high-quality male kin to co-reside as alpha and beta males, if the alpha male monopolizes reproduction and would do equally well if supported by a male non-kin, and the beta male is likely to become a successful alpha male in another group. As mentioned above, it is particularly beneficial for a subordinate male to cooperate with an alpha male that has resided in the group long enough for his daughters to mature. Mate choice and inbreeding avoidance between the alpha male and his mature daughters give the subordinate male an opportunity to reproduce (Muniz et al. 2006; Godoy et al. 2016; Wikberg et al. 2017). If the alpha and beta males are close kin, females may also avoid breeding with the beta male if they are able to recognize him as paternal kin and they have

access to unrelated mates. In all cases where a subordinate male bred with the alpha male's mature daughters in this study, the males were unrelated. Thus, inbreeding avoidance may have favoured the evolution of non-kin rather than kin co-residency among male capuchins. The potential costs coupled with few fitness benefits of kin co-residency between adult male kin can perhaps explain why a greater proportion of secondary dispersers than natal dispersers transferred alone. Alternatively, this pattern may simply be due to secondary dispersers having more limited access to male kin that are compatible dispersal partners.

To fully understand the evolution of male sociality, it is necessary to quantify the direct and indirect fitness consequences of male cooperation and competition. Unfortunately, this is extremely difficult to do in wild populations of dispersing, long-lived animals (Silk et al. 2009). Until this can be done, we propose that immature immigrant males are likely to experience a low cost to high benefit ratio of cooperating with same-sex kin, while this may not be the case for adult males.

The traditional models predicting the evolution of primate social structure highlight the importance of dispersal patterns shaping the kin composition of groups and therefore the occurrence of cooperation. Fedigan (1993) pointed out that white-faced capuchins do not conform to this pattern, and her study has been followed by similar reports from other primate species (Schuelke et al. 2010; Wikberg et al. 2012; Teichroeb et al. 2014; Diaz-Munoz and Ribeiro 2014). Findings from the current study suggest that high reproductive skew coupled with parallel dispersal and female mate choice for unrelated mates may be an overlooked factor that has the potential to affect the evolution of kin and non-kin cooperation (also see Widdig 2013). Furthermore, males are likely to experience different cost-benefit ratios of cooperating versus competing with kin depending on their age and other individual traits. Thus, future modelling efforts will benefit from taking into account how dispersal patterns *and* reproductive patterns shape the composition of groups as well as the fitness outcomes of kin cooperation *and* kin competition during different life history stages.

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References

- Akaike H (1974) A new look at the statistical model identification. *IEEE Trans Autom Control* 19:716–723. <https://doi.org/10.1109/TAC.1974.1100705>
- Altmann J (1974) Observational study of behavior: sampling methods. *Behaviour* 49:227–267
- Barton K (2013) MuMIn: Multi-model inference. R package version 1.9.5. <http://CRAN.R-project.org/package=MuMIn>. Accessed 1 May 2017
- Bates D, Maechler M, Bolker B, Walker S, Bojesen Christensen RH, Singman H (2014) lme4: linear mixed-effects models using Eigen and S4. <http://lme4.r-forge.r-project.org/>. Accessed 1 June 2014
- Borgatti S, Everett M, Freeman L (2002) Ucinet for windows: software for social network analysis. Analytic Technologies, Harvard
- Brasington LF, Wikberg EC, Kawamura S, Fedigan LM, Jack KM (2017) Infant mortality in white-faced capuchins: the impact of alpha male replacements. *Am J Primatol* 79:e22725. <https://doi.org/10.1002/ajp.22725>
- Burnham KP, Anderson DR (2002) Model selection and multi-model inference: a practical information-theoretic approach. Springer, New York
- Chapais B (2001) Primate nepotism: what is the explanatory value of kin selection? *Int J Primatol* 22:203–229. <https://doi.org/10.1023/A:1005619430744>
- Diaz-Munoz SL, Ribeiro AM (2014) No sex-biased dispersal in a primate with an uncommon social system-cooperative polyandry. *PeerJ* 2:UNSP e640. <https://doi.org/10.7717/peerj.640>
- Fedigan LM (1993) Sex differences and intersexual relations in adult white-faced capuchins (*Cebus capucinus*). *Int J Primatol* 14:853–877. <https://doi.org/10.1007/BF02220256>
- Fedigan LM, Jack KM (2004) The demographic and reproductive context of male replacements in *Cebus capucinus*. *Behaviour* 141:755–775. <https://doi.org/10.1163/1568539042245178>
- Fedigan LM, Jack KM (2011) Two girls for every boy: the effects of group size and composition on the reproductive success of male and female white-faced capuchins. *Am J Phys Anthropol* 144:317–326. <https://doi.org/10.1002/ajpa.21414>
- Fedigan LM, Jack KM (2012) Tracking neotropical monkeys in Santa Rosa: lessons from a regenerating Costa Rican dry forest. In: Kappeler PM, Watts D (eds) Long-term field studies of primates. Springer, Dordrecht, pp 165–184
- Forstmeier W, Schielzeth H, Mueller JC, Ellegren H, Kempnaers B (2012) Heterozygosity-fitness correlations in zebra finches: microsatellite markers can be better than their reputation. *Mol Ecol* 21:3237–3249. <https://doi.org/10.1111/j.1365-294X.2012.05593.x>
- Godoy I, Vigilant L, Perry S (2016) Inbreeding risk, avoidance and costs in a group-living primate, *Cebus capucinus*. *Behav Ecol Sociobiol* 70:1601–1611. <https://doi.org/10.1007/s00265-016-2168-1>
- Greenwood P (1980) Mating systems, philopatry and dispersal in birds and mammals. *Anim Behav* 28:1140–1162. [https://doi.org/10.1016/S0003-3472\(80\)80103-5](https://doi.org/10.1016/S0003-3472(80)80103-5)
- Griffin AS, West SA (2002) Kin selection: fact and fiction. *Trends Ecol Evol* 17:15–21. [https://doi.org/10.1016/S0169-5347\(01\)02355-2](https://doi.org/10.1016/S0169-5347(01)02355-2)
- Gros-Louis J, Perry SE, Manson JH (2003) Violent coalitionary attacks and intraspecific killing in wild white-faced capuchin monkeys (*Cebus capucinus*). *Primates* 44:341–346. <https://doi.org/10.1007/s10329-003-0050-z>
- Hamilton WD (1964a) The genetical evolution of social behaviour. *J Theor Biol* 7:1–52. [https://doi.org/10.1016/0022-5193\(64\)90038-4](https://doi.org/10.1016/0022-5193(64)90038-4)
- Hamilton WD (1964b) The genetical evolution of social behaviour. II. *J Theor Biol* 7:17–52
- Hanneman RA, Riddle M (2005) Introduction to social network methods. University of California, Riverside
- Hothorn T, Bretz F, Westfall P, Heiberger RM, Scheutenmeister A (2014) Simultaneous Inference in General Parametric Models. <http://lme4.r-forge.r-project.org/>. Accessed 1 May 2017
- Jack KM (2003) Explaining variation in affiliative relationships among male white-faced capuchins (*Cebus capucinus*). *Folia Primatol* 74:1–16. <https://doi.org/10.1159/000068390>

- Jack KM, Fedigan LM (2004a) Male dispersal patterns in white-faced capuchins, *Cebus capucinus* part 2: patterns and causes of secondary dispersal. *Anim Behav* 67:771–782. <https://doi.org/10.1016/j.anbehav.2003.06.015>
- Jack KM, Fedigan LM (2004b) Male dispersal patterns in white-faced capuchins, *Cebus capucinus* part 1: patterns and causes of natal emigration. *Anim Behav* 67:761–769. <https://doi.org/10.1016/j.anbehav.2003.04.015>
- Jack KM, Fedigan LM (2006) Why be alpha male? Dominance and reproductive success in wild white-faced capuchins (*Cebus capucinus*). In: Estrada A, Garber P, Pavelka MSM, Luecke L (eds) *New perspectives in the study of Mesoamerican primates: distribution, ecology, behavior, and conservation*. Springer, New York, pp 367–386
- Jack KM, Fedigan LM (2009) Female dispersal in a female-philopatric species, *Cebus capucinus*. *Behaviour* 146:471–497. <https://doi.org/10.1163/156853909X404420>
- Jack KM, Fedigan LM (2018, this volume) Alpha male capuchins (*Cebus capucinus imitator*) as keystone individuals. In: Kalbitzer U, Jack KM (eds) *Primate life histories, sex roles, and adaptability - essays in honour of Linda M. Fedigan*. *Developments in primatology: progress and prospects*. Springer, New York, pp 91–109
- Jack KM, Sheller C, Fedigan LM (2012) Social factors influencing natal dispersal in male white-faced capuchins (*Cebus capucinus*). *Am J Primatol* 74:359–365. <https://doi.org/10.1002/ajp.20974>
- Jack KM, Schoof VAM, Sheller CR, Rich CI, Klingelhofer PP, Ziegler TE, Fedigan L (2014) Hormonal correlates of male life history stages in wild white-faced capuchin monkeys (*Cebus capucinus*). *Gen Comp Endocrinol* 195:58–67. <https://doi.org/10.1016/j.ygcn.2013.10.010>
- Kalbitzer U, Bergstrom ML, Carnegie SD, Wikberg EC, Kawamura S, Campos FA, Jack KM, Fedigan LM (2017) Female sociality and sexual conflict shape offspring survival in a Neotropical primate. *Proc Natl Acad Sci U S A* 114:1892–1897. <https://doi.org/10.1073/pnas.1608625114>
- Kalinowski ST, Wagner AP, Taper ML (2006) ML-RELATE: a computer program for maximum likelihood estimation of relatedness and relationship. *Mol Ecol Notes* 6:576–579. <https://doi.org/10.1111/j.1471-8286.2006.01256.x>
- Kalinowski ST, Taper ML, Marshall TC (2007) Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Mol Ecol* 16:1099–1106. <https://doi.org/10.1111/j.1365-294X.2007.03089.x>
- Kulik L, Amici F, Langos D, Widdig A (2015) Sex differences in the development of social relationships in rhesus macaques (*Macaca mulatta*). *Int J Primatol* 36:353–376. <https://doi.org/10.1007/s10764-015-9826-4>
- Marshall TC, Slate J, Kruuk LEB, Pemberton JM (1998) Statistical confidence for likelihood-based paternity inference in natural populations. *Mol Ecol* 7:639–655. <https://doi.org/10.1046/j.1365-294x.1998.00374.x>
- Meikle DB, Vessey SH (1981) Nepotism among rhesus monkey brothers. *Nature* 294:160–161. <https://doi.org/10.1038/294160a0>
- Muniz L, Perry S, Manson JH, Gilkenson H, Gros-Louis J, Vigilant L (2006) Father-daughter inbreeding avoidance in a wild primate population. *Curr Biol* 16:R156–R157. <https://doi.org/10.1016/j.cub.2006.02.055>
- Muniz L, Perry S, Manson JH, Gilkenson H, Gros-Louis J, Vigilant L (2010) Male dominance and reproductive success in wild white-faced capuchins (*Cebus capucinus*) at Lomas Barbudal, Costa Rica. *Am J Primatol* 72:1118–1130. <https://doi.org/10.1002/ajp.20876>
- Murray CM, Lonsdorf EV, Stanton MA, Wellens KR, Miller JA, Goodall J, Pusey AE (2016) Early social exposure in wild chimpanzees: mothers with sons are more gregarious than mothers with daughters. *Proc Natl Acad Sci U S A* 111:18189–18194
- Nonacs P (2000) Measuring and using skew in the study of social behavior and evolution. *Am Nat* 156:577–589. <https://doi.org/10.1086/316995>
- Perry S (1998) Male-male social relationships in wild white-faced capuchins, *Cebus capucinus*. *Behaviour* 135:139–172

- Perry S (2012) The behavior of wild white-faced capuchins: demography, life history, social relationships, and communication. In: Brockmann HJ, Naguib M, Mitani JC, Simmons LW (eds) *Advances in the study of behavior*. Academic, Burlington, pp 135–181
- Robinson SP, Simmons LW, Kennington WJ (2013) Estimating relatedness and inbreeding using molecular markers and pedigrees: the effect of demographic history. *Mol Ecol* 22:5779–5792. <https://doi.org/10.1111/mec.12529>
- Schoof VAM, Jack KM (2014) Male social bonds: strength and quality among co-resident white-faced capuchin monkeys (*Cebus capucinus*). *Behaviour* 151:963–992. <https://doi.org/10.1163/1568539X-00003179>
- Schoof VAM, Wikberg EC, Fedigan LM, Jack KM, Ziegler TE, Kawamura S (2015) Infanticides during periods of social stability: kinship, resumption of ovarian cycling, and mating access in white-faced capuchins (*Cebus capucinus*). *Neotropical Primates* 21:192–196
- Schuelke O, Bhagavatula J, Vigilant L, Ostner J (2010) Social bonds enhance reproductive success in male macaques. *Curr Biol* 20:2207–2210. <https://doi.org/10.1016/j.cub.2010.10.058>
- Sharp SP, Simeoni M, Hatchwell BJ (2008) Dispersal of sibling coalitions promotes helping among immigrants in a cooperatively breeding bird. *Proc R Soc B Biol Sci* 275:2125–2130. <https://doi.org/10.1098/rspb.2008.0398>
- Silk JB, Alberts SC, Altmann J (2003) Social bonds of female baboons enhance infant survival. *Science* 302:1231–1234. <https://doi.org/10.1126/science.1088580>
- Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL (2009) The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proc R Soc B-Biol Sci* 276:3099–3104. <https://doi.org/10.1098/rspb.2009.0681>
- Sterck EHM, Watts DP, van Schaik CP (1997) The evolution of female social relationships in non-human primates. *Behav Ecol Sociobiol* 41:291–309. <https://doi.org/10.1007/s002650050390>
- Teichroeb JA, Wikberg EC, Sicotte P, Ting N (2014) Factors influencing male affiliation and coalitions in a species with male dispersal and intense male-male competition, *Colobus vellerosus*. *Behaviour* 151:1045–1066. <https://doi.org/10.1163/1568539X-00003089>
- van Noordwijk MA, van Schaik CP (2001) Career moves: transfer and rank challenge decisions by male long-tailed macaques. *Behaviour* 138:359–395. <https://doi.org/10.1163/15685390152032505>
- van Schaik CP (1989) Social evolution in primates: the role of ecological factors and male behaviour. *Proc Br Acad* 88:9–31
- West SA, Pen I, Griffin AS (2002) Conflict and cooperation - cooperation and competition between relatives. *Science* 296:72–75. <https://doi.org/10.1126/science.1065507>
- Widdig A (2013) The impact of male reproductive skew on kin structure and sociality in multi-male groups. *Evol Anthropol* 22:239–250
- Widdig A, Langos D, Kulik L (2016) Sex differences in kin bias at maturation: male rhesus macaques prefer paternal kin prior to natal dispersal. *Int J Primatol* 78:78–91
- Wikberg EC, Sicotte P, Campos FA, Ting N (2012) Between-group variation in female dispersal, kin composition of groups, and proximity patterns in a black-and-white *Colobus* monkey (*Colobus vellerosus*). *PLoS One* 7:e48740. <https://doi.org/10.1371/journal.pone.0048740>
- Wikberg EC, Jack KM, Campos FA, Fedigan LM, Sato A, Bergstrom ML, Hiwatashi T, Kawamura S (2014a) The effect of male parallel dispersal on the kin composition of groups in white-faced capuchins. *Anim Behav* 96:9–17. <https://doi.org/10.1016/j.anbehav.2014.07.016>
- Wikberg EC, Ting N, Sicotte P (2014b) Familiarity is more important than phenotypic similarity in shaping social relationships in a facultative female dispersed primate, *Colobus vellerosus*. *Behav Process* 106:27–35. <https://doi.org/10.1016/j.beproc.2014.04.002>
- Wikberg EC, Jack KM, Fedigan LM, Campos FA, Yashima AS, Bergstrom ML, Hiwatashi T, Kawamura S (2017) Inbreeding avoidance and female mate choice shape reproductive skew in capuchin monkeys (*Cebus capucinus imitator*). *Mol Ecol* 26:653–667. <https://doi.org/10.1111/mec.13898>
- Wrangham R (1980) An ecological model of female-bonded primate groups. *Behaviour* 75:262–300. <https://doi.org/10.1163/156853980X00447>