


RESEARCH ARTICLE

How individual, social, and ecological conditions influence dispersal decisions in male vervet monkeys

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Abstract

Dispersal between social groups reduces the risk of inbreeding and can improve individuals' reproductive opportunities. However, this movement has costs, such as increased risk of predation and starvation, loss of allies and kin support, and increased aggression associated with entering the new group. Dispersal strategies, such as the timing of movement and decisions on whether to transfer alone or in parallel with a peer, involve different costs and benefits. We used demographic, behavioral, hormonal, and ecological data to examine the causes and consequences of 36 dispersal events from 29 male vervet monkeys (*Chlorocebus pygerythrus*) at Lake Nabugabo, Uganda. Adult males' secondary dispersal coincided with the conception season in females, and males improved their potential access to females by moving to groups with higher female-to-male sex ratios and/or by increasing their dominance rank. Males that dispersed with a peer had lower fecal glucocorticoid and androgen metabolite levels than lone dispersers. Subadult males were not more likely to engage in parallel dispersals compared to adult males. Dispersal was also used as a mechanism to avoid inbreeding, but changes in hormone levels did not seem to be a trigger of dispersal in our population. Our findings illustrate the complex individual strategies used during dispersal, how many factors can influence movement decisions, as well as the value of dominance and hormone analyses for understanding these strategies.

KEYWORDS

androgens, behavioral endocrinology, dispersal strategies, dominance, glucocorticoids, primates, proximate mechanisms, seasonality

Abbreviations: fARM, fecal glucocorticoid metabolites and fecal androgen metabolites respectively; fGCM, fecal glucocorticoid metabolites.

1 | INTRODUCTION

Dispersal has important consequences for individual fitness because it limits the risks of inbreeding (Packer, 1979; Perrin & Goudet, 2001) and may enable an individual to improve their reproductive success via increased mating opportunities (Pusey, 1987; Teichroeb et al., 2011). Successful dispersal is a three-step process involving (1) emigration from the natal or residential group, (2) movement between groups and home ranges, followed by (3) immigration into a new target social group (Bowler & Benton, 2005; Wolff, 1994). Male-biased dispersal with female philopatry is the most common pattern in group-living mammals, including Asian and African cercopithecine primates (Greenwood, 1980).

Animals typically disperse at least once (from their natal group), and some species may disperse again after their initial transfer (i.e., secondary or breeding dispersal) (Jack, 2003; Pusey, 1987). For primates, male natal dispersal typically occurs around the age of sexual maturity (Akinyi et al., 2017; Cheney & Seyfarth, 1983; Jack & Fedigan, 2004a). Generally, in species living in multimale groups, natal dispersers have not yet reached their full body size and may therefore not be able to compete with full-grown adult males when joining a new group; thus, they are more likely to immigrate peacefully at the bottom of the dominance hierarchy, despite fewer reproductive benefits (Jack & Fedigan, 2004a; Pusey & Packer, 1987a). Secondary dispersals are hypothesized to be attempts to increase a male's reproductive success through improved access to mates. This access may be achieved by a male increasing his dominance rank (Majolo et al., 2012) or by immigrating into groups with more favorable sex ratios (Cowlshaw & Dunbar, 1991). Secondary dispersals have been observed in several species including lions (*Panthera leo*: Pusey & Packer, 1987b), white-faced capuchins (*Cebus imitator*: Jack & Fedigan, 2004b), ursine colobus monkeys (*Colobus vellerosus*: Teichroeb et al., 2011), yellow baboons (*Papio cynocephalus*: Alberts & Altmann, 1995), and vervet monkeys (*Chlorocebus pygerythrus*: Cheney, 1983).

Both natal and secondary dispersals can be initiated voluntarily by males seeking better mating opportunities (Cheney & Seyfarth, 1983; Jack et al., 2011). Voluntary dispersals may be preceded by males "visiting" or "prospecting" other groups for up to several days prior to their emigration (Cheney & Seyfarth, 1983). For example, natal males may be attracted to nonresident conspecifics (i.e., individuals living outside of the focal individual's current group) and disperse voluntarily, thereby avoiding mating with female relatives in their birth group. Male tenure length in their non-natal group may play a role when they choose to disperse for a second time (Jack, 2003). For example, high-ranking male white-faced capuchin monkeys may disperse voluntarily before their daughters reach sexual maturity, a strategy that reduces the risk of inbreeding (Jack & Fedigan, 2004b). However, dispersal can also be forced on some males (Cheney & Seyfarth, 1983; Teichroeb et al., 2011). Maturing natal males may be evicted by resident males who perceive them as potential competitors, and they may also be evicted following the immigration of a new male or a takeover by a coalition

of immigrating males (Ekernas & Cords, 2007; Teichroeb et al., 2011). Individuals who initiate dispersal voluntarily may receive benefits that are not available to involuntary dispersers, such as timing their transfer with the mating season or moving into groups with favorable sex ratios (Jack & Fedigan, 2004b; Leimberger & Lewis, 2015).

Despite the benefits of dispersal, there are numerous potential associated costs (Cheney, 1983) that can vary depending on whether they are incurred from the locational or social aspects of dispersal (Isbell & Van Vuren, 1996). Locational dispersal refers to permanently transferring from a familiar to an unfamiliar area and may be associated with higher predation and starvation risks during transfer (Alberts & Altmann, 1995; Brent et al., 2011; Pusey & Packer, 1987a; Ridley, 2012). Social costs involve moving from one social environment to another and are usually related to the loss of familiar social partners, including kin, and/or aggression from conspecifics in the new social group (Alberts & Altmann, 1995; Cheney & Seyfarth, 1983; Jack & Fedigan, 2004b; Schoof et al., 2009). Furthermore, resident males may experience the emigration of coresidents or the immigration of new males as social stressors associated with social instability (Akinyi et al., 2017; Marty et al., 2017). Both locational dispersal and social costs, alongside other environmental stressors, may lead to an elevated stress response (A. J. Young & Monfort, 2009; Emery Thompson, 2017), namely increased glucocorticoid levels—a group of hormones associated with the stress response (Sapolsky, 2002). In the short-term, these hormones are adaptive as they allow energy mobilization to deal with threatening situations and provoke aversion through learning (Dhabhar, 2018). In the long term, however, chronically elevated glucocorticoids can be detrimental by having immunosuppressive effects (Sapolsky et al., 2000). Changes in dominance rank can also affect glucocorticoid levels (Schoof et al., 2011), such that dispersing males experiencing changes in their dominance rank may experience glucocorticoid fluctuations.

Androgens are another group of hormones that may play a role in male dispersal. Androgens like testosterone and dihydrotestosterone are implicated in basic male reproductive functions, the development and maintenance of secondary sexual characteristics, and aggression in a reproductive context (reviewed in Dixson, 2012). In species with male-biased transfers and where natal dispersal generally coincides with the attainment of sexual maturity, an increase in androgens may promote initial dispersal (Bronson, 1989; Duffy & Belthoff, 2001). The Challenge Hypothesis predicts that males will experience elevated testosterone during critical periods of interactions with reproductively active females and competition between males (Goymann, 2009; Wingfield et al., 1990). In some primate species, androgens levels have also been shown to be a predictor of rank (*Papio hamadryas ursinus*; Beehner et al., 2006), to increase following alpha rank attainment, and to decrease following rank loss (*Cebus imitator*: Jack et al., 2014; Schoof et al., 2011). After dispersal, immigrating males may have increased androgen levels as they compete for dominance in a new social group, gain access to receptive females, and generally navigate new social relationships (Alberts et al., 1992; Goymann et al., 2019).

Individuals may mitigate the locational and social costs of dispersal by engaging in parallel dispersal, a type of dispersal that occurs either jointly when individuals travel simultaneously with familiar individuals or kin into a new social group, or sequentially when an individual transfers alone but joins a group containing familiar individuals or kin (van Hooff, 2000). Parallel dispersal has been documented in various species, including carnivores (e.g., lions, Pusey & Packer, 1987b), birds (e.g., Arabian babblers, *Turdoides squamiceps*: Ridley, 2012), and numerous primates (Schoof et al., 2009). Males who engage in parallel dispersal may mitigate the costs of locational dispersal by providing shared vigilance against predators (Baldellou & Henzi, 1992; Isbell et al., 1993), and may also reduce the costs of social dispersal by providing the opportunity to receive coalitionary support (Cheney & Seyfarth, 1983; Isbell & Van Vuren, 1996; Schoof et al., 2009; van Hooff, 2000).

The aims of our study were twofold. Firstly, we hypothesized that wild male vervet monkeys (*Chlorocebus pygerythrus*) base their dispersal mode and timing on conditions that would increase their likelihood of mating with unrelated females (i.e., avoid inbreeding). Specifically, we predicted that young males would be more likely to engage in parallel dispersal and adult males in lone dispersal. We also predicted that subadult males would engage in natal dispersal at or before reaching sexual maturity (i.e., 60 months of age) to avoid inbreeding and would exhibit increased androgen levels, while adult males would disperse at or before their tenure length exceeds age at first conception of their potential daughters (i.e., 42.4 months of age). We further predicted that males would be more likely to disperse during the conception season and that changes in male dominance rank would initiate emigrations. Second, we hypothesized that the dispersing male would benefit from dispersal and that both dispersing and resident males would incur costs related to competition. We predicted that males would immigrate into groups that increase their access to females through an increase in dominance rank and/or more favorable sex ratios. Finally, we predicted that both dispersing males and nondispersing males would experience elevated glucocorticoid and androgen levels following changes in male group membership.

2 | METHODS

2.1 | Study area and subjects

We focused on adult and subadult males in three neighboring vervet monkey groups on the shores of Lake Nabugabo, Uganda (0°22'–12°S and 31°54'E). The area surrounding Lake Nabugabo is a human-modified landscape composed of grasslands, patches of forests, swamps, and human settlements (Chapman et al., 2016). Habituation of the vervet study groups began in 2011 for M group, and in 2016 for KS and HC groups. Using known birth dates, we defined subadult males as those between 4 and 5 years of age, and adult males as >5 years of age (Schmitt et al., 2018) or following emigration from their natal group. Subadult males were defined as

older than 4 years because around 4 years, males are comparable in size to adult females (Błaszczuk, 2017; Turner et al., 2018) and they have reached maturity based on tooth eruption (Bolter, 2011). Females are considered to be adults earlier than males, usually around their first conceptions (i.e., 4 years of age: Bolter & Zihlman, 2006). Our study relied on a long-term data set which includes behavioral scans, *ad libitum*, and demographic data (M: 2012–2019; KS & HC: 2016–2019), as well as hormone data from fecal sample collection on all subadult and adult males (M: 2014–2019; KS & HC: 2016–2019). From 2012 to 2016, we followed M group for 6 days per week for 3 consecutive weeks, followed by 1 week without data collection. From 2016 onwards, we monitored two groups per week, rotating between groups, and thus collecting a total of 12 days of data per group per month.

Vervet monkeys engage in nonrandom dispersal, which can be initiated several times in an individual's lifetime, whereby intergroup movement is affected by several factors (Cheney & Seyfarth, 1983). Vervets live in multimale–multifemale groups characterized by female philopatry and male-biased dispersal (Isbell et al., 1991; Struhsaker, 1967). Males engage in natal dispersal around sexual maturity (~5 years of age) and often disperse subsequently, and they may do so alone or in parallel (joint or sequential dispersal) (Cheney & Seyfarth, 1983). Although vervet monkeys are typically characterized by highly seasonal reproductive patterns (i.e., >67% of births within 3 months: *sensu* van Schaik et al., 1999), the vervets at Lake Nabugabo exhibit moderately seasonal reproductive patterns across years (33%–67% of births in 3 months; Schwegel et al., [In press](#)).

2.2 | Operational definitions

We defined confirmed dispersal events as those in which a disappeared male was spotted in a new social group. Presumed dispersal events were those in which a disappeared male was suspected to have emigrated rather than died based on the observation of “roaming” or “visiting” neighboring groups, male age, and/or tenure length. We defined emigration as an individual disappearing from its resident group for at least 30 days, presumably in search of a new target social group to join. We used 30 days as a minimum as some individuals may roam or visit other groups then come back to their original group after a few days. We defined natal emigration as departure from the birth group, while secondary emigrations occurred when males left a group into which they had previously immigrated (Jack & Fedigan, 2004b). Emigrations were considered “voluntary” if they occurred during socially stable periods (i.e., no new male immigration within 3 months preceding emigration). In contrast, “involuntary” emigrations occur when a resident male transfers out of the group within 3 months of the immigration of/takeover by another male (Jack & Fedigan, 2004b; Teichroeb et al., 2011). Immigration was considered successful if a male remained with his new target social group for a minimum of 30 consecutive days. We defined joint parallel dispersal as two or more individuals moving from the same

residential group to the same target group within 7 days of each other, while sequential parallel dispersal was defined as two or more individuals moving from the same residential group to the same target group more than 7 days, but not exceeding 90 days, apart. "Complete" dispersal events are those where males dispersed among our study groups and for which we had behavioral and hormone data before and after dispersal. In cases where a male emigrated from one of the study groups to a group we do not follow, data collection on that male ended, such that no post-dispersal data were available. Similarly, if a male immigrated from an unknown group into a study group, no pre-dispersal data were available.

2.3 | Behavioral and demographic data

We collected scan data at 30 min intervals (2012–2016) and 15 min intervals (2016–present) to record the activity and nearest neighbor information of five randomly selected, noninteracting (i.e., >3 m apart) juveniles, subadults, or adults of either sex in each group, of which we only used male data. We supplemented these scan data with *ad libitum* data of agonistic and sociosexual interactions for males. These data were supplemented with focal animal sampling of all subadult and adult males by K. Snyder from January to June 2019 and by S. L'Allier from July to December 2019. We have recorded demographic changes in the study groups since 2011, including all births, injuries, immigrations, disappearances, and causes of disappearances (i.e., death, emigration, unknown).

2.4 | Hormone data

We collected fresh fecal samples from all subadult and adult males before noon, within 10 min of defecation. We placed a portion of fecal matter that was uncontaminated by urine or soil in a 15 ml tube and stored it in a cooler with ice packs until we could freeze the samples at the end of the day. We opportunistically collected a minimum of one sample per male in each group per month. For preliminary field hormone extraction, we thawed, homogenized, and added 10 ml of 50:50 ethanol:water to 0.5 g of feces. We vortexed feces for 10 min and centrifuged for 20 min to separate the hormone-containing supernatant from the fecal pellet. Thereafter, we pushed 2 ml of supernatant through a solid phase extraction cartridge (SPure Ltd; Maxi-Clean 300 mg Preveil C-18; SP-5122335), followed by a 2 ml wash with deionized water; we sealed the cartridges and stored them in a cool dark space until transport to York University, Canada. To elute the hormones, we washed each cartridge with 1 ml of 5% methanol and eluted with 2 ml of 100% methanol using an Alltech vacuum manifold. We conducted enzyme immunoassays at the Toronto Zoo's Reproductive Endocrinology Lab with modifications to methods described in Terwissen et al. (2014) for fecal glucocorticoid (fGCM) and Majchrzak et al. (2015) for fecal androgen metabolites (fARM). For samples collected before July 2016, eluted hormones

were concentrated 3x for fGCM analysis and 2x for fARM analyses, and samples collected since 2016 have been diluted 4x in EIA buffer. We used a 50 μ l aliquot of the sample or standard in EIA, and ran all samples and standards in duplicate. ACTH challenge in captive vervets demonstrates the biological validity of fGCM (C. Young et al., 2017), while parallelism, inter-assay, and intra-assay coefficients of variation validate the respective enzyme immunoassays (Greenberg et al., 2022).

2.5 | Statistical analyses

We conducted circular statistics in Oriana 4.02 (Kovach, 2011), and all other statistical analyses in R 3.6.2 (R Core Team, 2013) with the significance level set to $\alpha \leq 0.05$.

2.6 | Inbreeding avoidance: age and tenure length

To investigate whether males timed their transfers to reduce risks of inbreeding, we compared each subadult male's known age at natal dispersal to the mean male age at sexual maturity (i.e., 60 months; Bolter & Zihlman, 2006). For adult males and secondary dispersals, we compared male tenure length to females' mean age at first conception (i.e., 42.4 months; Harvey & Clutton-Brock, 1985). For both, we used Wilcoxon one-sample one-tailed tests.

2.7 | Dominance and sex ratio

To ensure sufficient data were available to quantify male dominance rank, we defined the pre- and post-dispersal periods as 90 days prior to and 90 days after the day of dispersal, respectively. We calculated Elo-ratings using the R package "EloRating," wherein the outcomes of consecutive male–male agonistic interactions are used to assess the probability that an individual will win their next agonistic interaction and assign them a score based on these outcomes and probability (Neumann et al., 2011). For this calculation, we used agonistic bouts involving subadult and/or adult males, defined as all agonistic interactions occurring between two individuals within 15 min (i.e., the length of focal follows), from which we determined the winner and loser of the bout, or a draw if both individuals directed and received aggression. We calculated an optimized *k*-value for the male dominance hierarchy in each group by exploring a range of possible *k*-values between 5 and 200 with a resolution of 5000 (Newton-Fisher, 2017). The *k*-value is a constant which informs how much the Elo-rating will change following an agonistic interaction, while the resolution determines how many *k*-values within our range were tested. We then compared the log-likelihoods associated with each *k*-value across groups and determined that *k* = 76.75 was the best fit across all three study groups.

For complete dispersal events, we converted Elo-ratings to ordinal ranks (Levy et al., 2020). We calculated dispersing male ranks

in their residential group before departure (i.e., one day before the date of transfer) and their rank 90 days following immigration in the target group. We considered males to have changed their rank if they either increased or decreased by at least one position. We used a paired-samples Wilcoxon test to examine changes in a male's ordinal rank or group sex ratio pre- and post-dispersal. We further evaluated the potential improvement in each male's access to females after dispersal by comparing the log response ratio for the change in (1) dominance rank and (2) sex ratio when moving from the residential to the target group. To do this, we divided the post-dispersal values (either rank or sex ratio) by the pre-dispersal values, and log-transformed the results. For the rank values, we added a correction by multiplying by -1 to adjust the negative values that represented an increase in rank, for easier comparison. We considered changes to a male's relative competitive ability (i.e., compared to male coresident competitors) to be relative to his own rank before and after dispersal (Marty et al., 2016), so a male who increased his rank following dispersal was considered to have increased in competitive ability. We defined sex ratios as the number of adult females per adult male in a group, regardless of female reproductive status and excluding the male who dispersed between both groups.

2.8 | Hormone analyses

In contrast to the dominance rank analysis, for hormones we opted for a 60-day pre- and post-dispersal window. We chose this timeframe to account for the relatively small number of monthly samples for certain males but did not want to exceed 60 days since hormone levels seem to only vary within the first month of immigration (Bergman et al., 2005; Marty et al., 2017). For each male in a group (i.e., dispersing and resident males), we calculated mean fGCM and fARM levels for the pre- and post-dispersal period and calculated baseline levels for each male within a 180-day interval before and after the dispersal period, respectively (i.e., if dispersal is day 0, post-dispersal baseline is 61–240 days). All fecal hormone metabolite levels were log-transformed to meet assumptions of normality. We used paired t -tests to examine hormone differences during the dispersal period versus the baseline. We calculated Z-scores to compare hormone levels between dispersing males and nondispersing resident males. We used Wilcoxon tests to examine the potential effects of age category and dispersal mode on hormone levels and used Spearman's rank correlation to test for rank effects on hormone levels.

2.9 | Seasonality of conceptions and dispersals

We estimated conception date by subtracting the mean vervet gestation length of 163 days (Johnson et al., 1973) from birth dates. To calculate conception and dispersal seasonality, we calculated the total number of these events in each month across all years. We tested for the nonuniformity of the distribution of conceptions and

dispersals using a Rayleigh Z test and used a Spearman's rank correlation (r_{sp}) to test for a relationship between conception and dispersal distributions. We compared conceptions and dispersals to each other between July 2012 and June 2019, although some dispersals prior to this period were used for other analyses (see above).

3 | RESULTS

3.1 | Dispersal mode

We recorded 36 dispersal events from 29 males between January 2012 and December 2019; 26 of these were confirmed dispersal events, while 10 were presumed events. All emigrations were voluntary as there were no male take-overs in the 3 months prior to any male's emigration. We identified 21 lone dispersals (58%) and 15 parallel dispersals (42%), of which 10 were considered joint parallel dispersals and 5 were sequential parallel dispersals (Table 1). Using the 36-event data set, subadult males were not significantly more likely to engage in parallel dispersal than adult males (Chi-square test: $\chi^2 = 0.785$, $p = 0.376$). However, when we included only confirmed dispersals (i.e., 26 events), subadult males were the only ones to be involved in sequential dispersals. There was no evidence that mode of dispersal was influenced by the individual's rank prior to emigration (ANOVA: $F = 0.008$, $DF = 1$, $p = 0.928$). Furthermore, the mode of dispersal did not significantly influence the degree of rank improvement after dispersal (Wilcoxon rank-sum test: $W = 5$, $p = 0.705$).

3.2 | Inbreeding avoidance: age and tenure length

Mean age at confirmed natal dispersals for males of known age was 55.1 ± 12.3 months (mean \pm SD, median = 58.5, range 36–69 months, $N = 8$), which was not later than the typical age of sexual maturity of 60 months (Wilcoxon one-sample one-tailed test: $V = 13$, $p = 0.273$). Mean adult male tenure length was 35 ± 17 months (mean \pm SD, median = 27, range = 17–59 months, $N = 7$), which was not significantly later than the typical female age at first conception of 42.4 months (Wilcoxon one-sample one-tailed test: $V = 9$, $p = 0.223$).

TABLE 1 Frequency of each mode of dispersal for each male age class (confirmed events)

Mode of dispersal	Subadult	Adult	Unknown	Total
Lone dispersal	10 (6)	7 (4)	4	21 (14)
Joint parallel	4	4 (3)	2	10 (9)
Sequential parallel	3	2 (0)	0	5 (3)
Total	17 (13)	13 (7)	6	36 (26)

3.3 | Dominance and sex ratio

Approximately half of dispersing males (4 out of 7) increased their ordinal rank by at least one position following dispersal, but this was not significant (Paired samples Wilcoxon test: $V = 14$, $N = 7$, $p = 0.534$). Eight of 11 (72%) males for whom we had pre- and post-dispersal group sex ratio data moved to a group with a more favorable female-to-male sex ratio, but this change was not significant ($V = 18.5$, $N = 11$, $p = 0.213$). We found no correlation between sex ratio improvement and ordinal rank improvement ($r_{sp} = 52.917$, $R = 0.055$, $p = 0.91$) in the seven males for whom we had complete dispersal data; however, none of the males moved into groups with both lower sex ratios and lower dominance rank (Figure 1). The type of dispersal (i.e., natal vs. secondary) did not significantly affect the degree of rank improvement after dispersal (Wilcoxon rank-sum test: $W = 8$, $p = 0.162$).

3.4 | Variation in fGCM and androgen metabolite levels

We collected 1119 fecal samples since 2014. Because some subjects dispersed or disappeared, the total number of fecal samples collected per male varied (range 5–62, mean = 20 ± 17.4 SD). Across all samples, fGCM levels ranged from 0.32 to 2.26 ng/g (mean = 1.40 ± 0.33 SD) and fARM levels ranged from 0.57 to 2.87 ng/g (mean = 1.86 ± 0.29 SD).

Dispersing males did not have significantly higher fGCM (Tables 2 and 4) or fARM (Tables 3 and 4) levels in the 60-day pre-

emigration period when compared to their baseline period. In the 60 days following immigration into a new target group, dispersing males had lower fGCM but not fARM levels compared to their baseline. In the 60 days prior to dispersal, there was no significant difference in fGCM or fARM levels between natal and secondary dispersers. There was also no statistically significant difference in fGCM or fARM levels between lone and parallel dispersers in the 60 days following immigration. Nondispersing males in the resident group had hormone levels comparable to their baseline prior to the emigration of a male coresident. However, male immigration was associated with a significant decrease in both fGCM and fARM levels for males of the new target group compared to their baseline. Natal ($n = 9$) and secondary dispersers ($n = 5$) did not differ in either fGCM ($W = 22$, $p = 0.527$) or fARM ($W = 11$, $p = 0.937$) levels. Lone dispersers ($n = 6$) had higher fGCM ($W = 24$, $p = 0.050$) and fARM ($W = 26$, $p = 0.022$) than parallel dispersers ($n = 5$). Male dominance rank was positively correlated with fARM ($r_{sp} = -0.411$, $S = 2856$, $p = 0.051$), but not fGCM ($r_{sp} = 0.019$, $S = 1984.5$, $p = 0.929$).

3.5 | Seasonality of conceptions and dispersals

Between July 2012 and June 2019, conceptions ($N = 119$) were moderately seasonal (Rayleigh test: $Z = 41.538$, $p < 0.001$), with 62% of events occurring between April and June (mean date = May 28, $\mu = 146.7^\circ$, $R = 0.591$, Figure 2a). The timing of confirmed dispersal events ($N = 25$) was also moderately seasonal (Rayleigh test: $Z = 4.787$, $p = 0.007$), with 56% of transfers occurring between April

TABLE 2 Results of paired *t*-tests for each prediction on the variation of mean male fGCM levels during the pre-emigration and post-immigration periods

Dispersal period	fGCM comparison (n)	t	DF	p
Pre-emigration (60 days prior)	Dispersers levels versus their baseline (14)	-0.817	13	0.428
	Non-dispersers levels versus their baseline (83)	-1.019	82	0.311
Post-immigration (60 days after)	Dispersers levels versus their baseline (11)	-2.772	10	0.020*
	Non-dispersers levels versus their baseline (75)	3.477	74	0.001*

Note: (n) represents the sample size of males included in each comparison.

Abbreviation: fGCM, fecal glucocorticoid metabolites.

*Indicate statistical significance.

TABLE 3 Results of paired *t*-tests for each prediction on the variation of mean male fARM levels during the pre-emigration and post-immigration periods

Dispersal period	fARM comparison (n)	t	DF	p
Pre-emigration (60 days prior)	Dispersers levels versus their baseline (14)	0.228	13	0.823
	Non-dispersers levels versus their baseline (83)	-1.763	82	0.082
Post-immigration (60 days after)	Dispersers levels versus their baseline (11)	0.866	10	0.407
	Non-dispersers levels versus their baseline (75)	3.254	74	0.002*

Note: (n) represents the sample size of males included in each comparison.

Abbreviation: fARM, fecal androgen metabolites.

*Indicate statistical significance.

TABLE 4 Summary of descriptive statistics modes and types of dispersal for both fGCM and fARM

Dispersal period	Dispersal group (n)	Mean fGCM \pm SD	Mean fARM \pm SD
Pre-baseline (180 days prior)	Emigrating males (14)	1.32 \pm 0.21	1.82 \pm 0.23
	Resident males (83)	1.39 \pm 0.24	1.79 \pm 0.18
Pre-emigration (60 days prior)	Emigrating males (14)	1.39 \pm 0.30	1.80 \pm 0.25
	Resident males (83)	1.43 \pm 0.19	1.85 \pm 0.24
	Natal dispersers (9)	1.397 \pm 0.23	1.731 \pm 0.24
	Secondary dispersers (5)	1.391 \pm 0.44	1.936 \pm 0.24
Post-immigration (60 days after)	Immigrating males (11)	1.29 \pm 0.13	1.78 \pm 0.23
	Resident males (75)	1.31 \pm 0.22	1.76 \pm 0.24
	Lone dispersers (6)	1.339 \pm 0.05	1.898 \pm 0.22
	Parallel dispersers (5)	1.252 \pm 0.18	1.643 \pm 0.17
Post-baseline (180 days after)	Immigrating males (11)	1.42 \pm 0.15	1.86 \pm 0.21
	Resident males (75)	1.43 \pm 0.22	1.88 \pm 0.19

Note: (n) represents the sample size of males included in each comparison.

Abbreviations: fARM, fecal androgen metabolites; fGCM, fecal glucocorticoid metabolites.

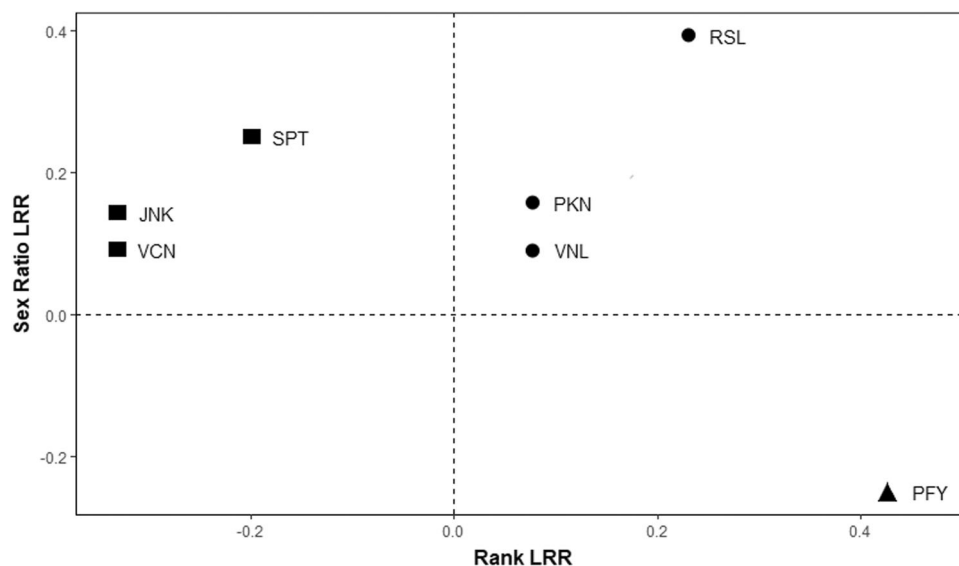


FIGURE 1 Log response ratios (LRR) score interactions between sex ratio and rank changes following dispersal. Squares indicate males who decreased in rank but moved to a group with a more favorable sex ratio. The triangle indicates a male who increased in rank but decreased in number of females available per male. Circles indicate males who have increased both their ordinal rank and sex ratio compared to pre-dispersal settings. No male dispersal involved a decrease in both rank or AF:AM sex ratio.

and June (mean date = May 25, $\mu = 143.5^\circ$, $R = 0.428$, Figure 2b). When we included both confirmed and presumed dispersals ($N = 33$), 45% of which occurred between April and June (mean date = June 3, $\mu = 152.8^\circ$, $R = 0.284$), there was a trend toward nonuniform distribution of male transfers (Rayleigh test: $Z = 2.666$, $p = 0.069$). Despite the difference in mean dates of conception and confirmed dispersal being only 3 days, the correlation between conceptions and confirmed dispersals was not significant ($r_{sp} = 158.14$, $R = 0.45$,

$p = 0.145$). When we examined both confirmed and presumed natal ($N = 17$) and secondary dispersals ($N = 13$), the correlation between the timing of conceptions and dispersals was significant for secondary dispersal events (Figure 2c, $r_{sp} = 111.71$, $R = 0.61$, $p = 0.035$). However, natal dispersals did not coincide with conceptions ($r_{sp} = 368.13$, $R = -0.29$, $p = 0.366$), despite there being a trend toward a seasonal distribution in natal dispersals (mean date = June 2, $\mu = 151.8^\circ$, $R = 0.466$; Rayleigh test: $Z = 2.822$, $p = 0.057$).

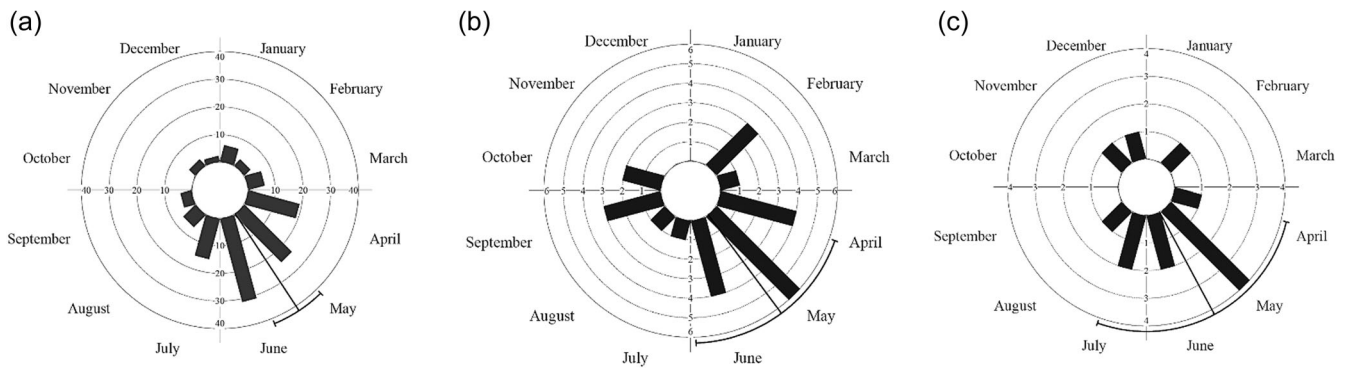


FIGURE 2 Seasonality of (a) conceptions ($N = 119$), (b) confirmed dispersals ($N = 25$), and (c) secondary dispersals ($N = 13$) that occurred between July 2012 and June 2019. Axes identify the number of events for each month, and the bold line represents the mean vector and 95% confidence interval.

4 | DISCUSSION

Individual and socioecological conditions were related to dispersal in male vervet monkeys. Males appeared to avoid potentially mating with related females since (1) natal males dispersed around the age at sexual maturity and (2) adult male tenure length was similar to female age at first conception. Males engaging in secondary, but not natal, dispersal timed their movement to coincide with female conception seasonality. Furthermore, dispersing males increased either in rank, immigrated to groups with more favorable sex ratios, or both. These results are consistent with the hypothesis that males transfer to maximize their reproductive success. Our findings indicate that dispersing males did not have elevated fGCM or fARM levels before dispersal. For resident males, however, immigrations of new male in their group were associated with both elevated fGCM and fARM levels.

Although age did not independently influence dispersal significantly, our results suggest that inbreeding avoidance does. We predicted that subadults would disperse at or before 60 months of age, the approximate age at which vervet males reach sexual maturity. Both the mean (55.1 months) and median (58.5 months) age at dispersal for our eight males are consistent with the hypothesis that males time their first transfer from their natal group as a mechanism to avoid inbreeding. As predicted, neither the mean (35 months) nor median (27 months) adult male tenure length exceeded the typical female age at first conception (42.4 months), suggesting that males time their secondary dispersals to avoid inbreeding. C. Young et al. (2019) reported similar results in vervet monkeys and suggested that while emigration may be a mechanism to avoid mating with mature daughters, other proximate mechanisms, such as phenotype matching (Alberts, 1999) and the Westermarck effect (i.e., development of sexual aversion through familiarity between related individuals; Paul & Kuester, 2004), may also reduce the risk of inbreeding while avoiding the potential costs of dispersal for those males whose tenure is longer than predicted. Furthermore, these alternative mechanisms may be used by females as well, as costs of

inbreeding may be higher for them than for males (Lehmann & Perrin, 2003; Widdig et al., 2017). These mechanisms may thus explain how these monkeys avoided inbreeding despite a small portion of our males ($N = 10$) remaining in their groups after reaching sexual maturity or after their putative daughters reached the average age of first conception.

We also predicted that males would potentially increase their access to females following dispersal via an increase in dominance rank or by immigrating into a group with an improved female-to-male sex ratio. A male who increased both his dominance rank and moved to a group with a more favorable sex ratio would have the highest increase in reproductive potential among the dispersing males. While there was no overall significant increase in male rank or improvement in group sex ratio following dispersal, it is interesting to note that no males simultaneously experienced a decrease in both rank and female-to-male sex ratio. These results suggest that most males may have experienced a trade-off between rank and sex-ratio following dispersal, with only one male increasing his overall potential access to females through both mechanisms. That said, it is difficult to provide a holistic view of the benefits each male incurred from dispersal. In the future it would be relevant to look at the degree of reproductive success of dispersing males using paternity data and compare it to their respective log response ratio scores.

Adult males engaging in secondary dispersal timed their movement with the conception season in females, and there was a trend for subadult natal males to also engage in seasonal dispersal. Other studies have found similar relationships between the timing of dispersals and mating peaks (*Verreaux's sifakas*, *Propithecus verreauxi*: Brockman et al., 2001; Leimberger & Lewis, 2015; Hanuman langurs, *Presbytis entellus*: Borries, 2000), including in a highly seasonally breeding population of vervets in South Africa (C. Young et al., 2019). In the highly seasonally breeding primate, *Verreaux's sifaka*, Leimberger and Lewis (2015) found the rate of successful immigration by both subadult and adult males to be much higher during the pre-mating season than during the mating (or conception) season. Regardless, timing their transfer with the conception season and

moving to a group with a more favorable sex ratio may be an alternative used by most males to increase their mating and reproductive opportunities when rank improvements following dispersal are not possible due to competition.

Contrary to our predictions, there was no evidence of change in fGCM nor fARM in dispersing males before their emigration. Dispersing individuals spend time outside of their group before emigration, which is thought to be stressful due to a lack of protection from predators and social support (Kawazoe & Sosa, 2019; Leimberger & Lewis, 2015). An increase in fGCM levels during dispersal was observed in meerkats (A. J. Young & Monfort, 2009), but not in some primates (yellow baboons, *Papio cynocephalus*: Akinyi et al., 2017; anubis baboons, *Papio hamadryas*: Bergman et al., 2005; crested macaques: Marty et al., 2017). We also predicted that if natal dispersers emigrate at or around the age of sexual maturity, the dispersal event could be triggered by increased androgen levels associated with reproductive maturation. However, we did not find evidence that dispersing males experienced any increase in fARM levels prior to dispersal. This is in contrast to findings by Brockman et al. (2001) for *Verreaux's sifakas* and Holekamp and Smale (1998) for hyenas (*Crocuta crocuta*). Our findings that fGCM and fARM were not elevated from baseline in dispersing males could be because our males did not prospect to other groups long enough for it to be reflected in fecal hormones. Alternatively, it could be that because all our dispersals appear to be voluntary rather than involuntary (i.e., evictions), dispersing males may not have received increased aggression within the group before emigrating.

Dispersal events has led to demographic changes in both the groups from which males emigrated and the groups into which they immigrated, resulting in a need for group individuals to navigate new social relationships. This is likely especially true for dispersing males, as well as males already present in the new target social group following an immigration event, such that forming new social relationships with unfamiliar individuals could be stressful and the presence of new males could represent an increase in male–male competition. As such, we predicted that both dispersing and resident males would have increased fGCM and fARM levels following an immigration event. Contrary to our prediction, dispersing males in our study population actually had lower fGCM levels after immigration compared to baseline, while fARM levels remained stable. The lower fGCM levels prior to emigration were likely not a result of changes in diet nor weather since natural food availability is consistent year-round at Lake Nabugabo, and conceptions (which overlap with the dispersal season) were not significantly associated with weather in the previous month (i.e., maximum temperature, humidity, rainfall) (Schwegel et al., *In press*). We also found that resident males in the target group have higher fGCM and fARM levels within the first 2 months of receiving a new immigrant compared to their baseline. This result is consistent with what Alberts et al. (1992) found in male yellow baboons, and likely reflect shifting social dynamics associated with the arrival of a new male.

Finally, contrary to our expectations, we did not find any difference in hormone levels between natal and secondary dispersers

but found that lone dispersers had higher fGCM and fARM levels than parallel dispersers. Immigrating alone may expose the individual to higher risks of predation and having to navigate new social relationships without support from a familiar individual may prove stressful for the dispersing males. Thus, the mutual support of parallel dispersers may explain their lower fGCM levels (Cheney & Seyfarth, 1983; Isbell et al., 1993). This same lack of social support may also mean the immigrants engage in more frequent aggressive encounters, which would explain the higher fARM levels in lone dispersers. However, we were not able to confirm this with behavioral data.

Studying animal dispersal poses a significant challenge, especially in primates, because it is a behavior that occurs rarely throughout a study period. To obtain a larger sample size, studies would have to span several decades. Besides, long-term study projects may not focus solely on dispersal, as it would require a lot of resources to follow specific individuals for long enough to get sufficient data for analyses (Jack & Isbell, 2009). In the case of this study, we identified a total of 36 dispersal events over 7 years (2012–2019), which is within the range of similar studies of primate dispersal (e.g., Cheney & Seyfarth, 1983; 28 dispersals in vervets; Onyango et al., 2013; 113 natal dispersals in yellow baboons; Teichroeb et al., 2011; ≥ 24 emigrations and 55 immigrations in ursine colobus; Jack & Fedigan, 2004b; ≥ 26 emigrations and 34 immigrations in white-faced capuchins; Leimberger & Lewis, 2015; 18 immigrations in *Verreaux's sifaka*; Marty et al., 2017; 14 emigrations and 14 immigrations in crested macaques). However, the questions raised in this paper required the separation of these events into separate categories (type of dispersal, mode of dispersal, movements between known or unknown groups, etc.). The nature of the research questions led to small sample sizes in some analyses; therefore, the lack of support for some of our predictions may simply be a reflection of low statistical power.

5 | CONCLUSION

We found partial support for the first hypothesis stating that male dispersal would be triggered by specific individual and socioecological factors. Only a few explanations, such as timing with female conception seasonality and inbreeding avoidance, were supported by our data. The second hypothesis, that males would disperse in a way to minimize the costs and maximize the benefits of dispersal as much as possible, was mostly unsupported, despite a few exceptions. Overall, males are likely unable to influence individual, social, and ecological factors that affect their transfer. This in turn could mean that they may be very limited in their ability to optimize the success of dispersal. Our findings emphasize how important it is to consider the individual and its context when evaluating dispersal strategies.

AUTHOR CONTRIBUTIONS

Simon L'Allier: conceptualization (lead); data curation (equal); formal analysis (lead); funding acquisition (supporting); investigation (equal); methodology (equal); writing—original draft (lead).

Megan A. Schwegel: data curation (equal); formal analysis (supporting); software (supporting); writing—review & editing (equal). **Alessandro Filazzola:** formal analysis (equal); methodology (equal); software (equal). **Gabriela Mastromonaco:** formal analysis (equal); methodology (equal). **Colin A. Chapman:** funding acquisition (supporting); project administration (supporting); resources (supporting); validation (supporting). **Valérie A. M. Schoof:** Conceptualization (supporting); funding acquisition (lead); methodology (equal); resources (lead); supervision (lead); writing—original draft (equal).

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at <https://figshare.com/s/82aa17a07226ecf7d449>.

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