Behavioral Endocrinology of Male Dispersal in Vervet Monkeys at Lake Nabugabo, Uganda

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Abstract

Dispersal between social groups reduces risks of inbreeding and may provide individuals with reproductive opportunities. However, this movement may come with socio-ecological costs, such as risks of predation and starvation, loss of allies, kin support, and increased conspecific aggression. Dispersal strategies, such as the timing of movement and decisions on whether to transfer alone or in parallel with a peer may be associated with different costs and benefits between individuals. This research uses long-term demographic, behavioral, hormone, and ecological data to examine the triggers and consequences of 36 dispersal events from 29 male vervet monkeys (*Chlorocebus pygerythrus*) at Lake Nabugabo, Uganda. Dispersing adult males timed their transfer with the conception seasonality and improved their potential access to females by moving to a group with higher female-to-male sex ratio or by increasing their dominance rank. However, we argue that each transfer is unique to each individual and their own socio-ecological context.

Keywords

Dispersal strategies, proximate mechanisms, primates, behavior, endocrinology, reproduction

Dedication

This work is dedicated to the people I have met throughout my progress for this research who have taught me how to focus on the moment, to be present in my own life, and have changed the perception I have of myself and others.

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1 | Introduction

1.1 | Dispersal: functions and benefits

Dispersal of individuals through the habitat has important consequences for individual fitness. Dispersal is a behavior that helps maintain genetic diversity through gene flow (Alberts & Altmann, 1995; Cheney & Seyfarth, 1983; Lawson Handley & Perrin, 2007) and limits inbreeding depression by reducing the possibility that individuals will reproduce with close relatives (Packer, 1979; Perrin & Goudet, 2001). Inbreeding avoidance is crucial for long-term viability of animal populations. However, dispersal patterns may be altered for species living in human-modified or fragmented habitats (Brady et al., 2011; Cornelius et al., 2017). Mammals living outside protected areas may be disproportionately affected, because anthropogenic habitat modifications may influence matrix permeability (e.g., deforestation affect arboreal primates' movement) and the success of dispersal strategies (Castellón & Sieving, 2006).

Inbreeding may be avoided through various mechanisms. One such example is the Westermarck effect, a mechanism thought to be used in kin recognition which relies on familiarity among related individuals and may play a role in sex-biased dispersal (Paul & Kuester, 2004). In primates, familiarity is mostly developed through a preferential relationship with the mother, as offspring of the same female may interact more with each other than with non-maternal kin (Chapais, 2008). The Westermarck effect hypothesizes that this familiarity results in sexual aversion between kin, thereby reducing inbreeding. This aversion is thought to be most strongly expressed in females because they incur greater costs than males from having offspring that possess deleterious alleles, since females invest most in the production and care of offspring (Trivers, 1972). This cost is especially prominent in primates where females gestate and nurse offspring over a long period of time (Lehmann & Perrin, 2003).

Another common mechanism observed in many group-living animals, possibly derived from the Westermarck effect (Paul & Kuester, 2004), is the dispersal of individuals from one social group to another. Dispersal is a three-step process involving 1) emigration from the natal or residential group, 2) movement across the habitat (i.e., locational transfer) between social groups, followed by 3) immigration into a new social group (i.e., social transfer) (Bowler & Benton, 2005; Ridley, 2012; Wolff, 1994). Among birds and mammals, sex-biased dispersal is widespread, with dispersal being undertaken primarily by individuals of one sex dispersing, although exceptions may

occur (Greenwood, 1980; Isbell & Van Vuren, 1996). Male-biased dispersal with female philopatry is the most common pattern observed in group-living mammals, including Asian and African monkeys (Cercopithecines) (Greenwood, 1980). This pattern involves males changing groups while females stay in their natal group throughout their lives (Greenwood, 1980; Wrangham, 1980). This strategy helps both sexes to reduce the risk of inbreeding. Males may improve their reproductive success due to greater sexual receptivity of females in new social groups, through an increase in mating opportunities by acquiring a higher dominance rank following dispersal, and/or through a more favorable sex ratio in a new social group (Pusey, 1987; Teichroeb et al., 2011). On the other hand, females remaining with relatives in a familiar habitat and cooperating together against females from other groups gain inclusive fitness benefits through a rise in competitive ability in the defense of shared resources (Sterck et al., 1997).

Males may disperse from both the birth group (i.e., primary or natal dispersal), and in some species, they may disperse again after their initial transfer (i.e., secondary or breeding dispersals) (Jack, 2003; Pusey, 1987). Male natal dispersal typically occurs around the attainment of sexual maturity (Akinyi et al., 2017; Cheney & Seyfarth, 1983; Jack & Fedigan, 2004a). However, natal dispersers are generally not at their full body size yet and may therefore not be able to compete with full-grown adult males when they join 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 by males to improve their access to mates and potentially increasing their reproductive success by 1) increasing their dominance rank (see Box 1) and/or 2) immigrating into groups with more favorable sex ratios, especially in seasonally breeding species (Cowlishaw & Dunbar, 1991). Secondary dispersals have been observed in several species (e.g., lions, *Panthera leo*: Pusey & Packer, 1987b; white-faced capuchins, *Cebus capucinus*: Jack & Fedigan, 2004b; vervet monkeys, *Chlorocebus aethiops*: Cheney, 1983). Male tenure length in their non-natal group may also play a role in the timing of secondary dispersal (Jack, 2003). For example, dominant 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).

Box 1: Dominance rank and its influence on reproductive success in primates

Evolutionary theories typically refer to a clear relationship between agonistic interactions and reproductive success. However, in a social group, these dynamics may be more complex (Fedigan, 1983). In primates, the high mating success of a dominant male may not necessarily mean high reproductive success (Alberts et al., 2006). Subordinate males may engage in counter-strategies to reproduce with females (Berard et al., 1994). However, despite a few exceptions, there are several benefits of high dominance rank on reproductive success, especially for males (reviewed in Majolo et al., 2012). These benefits include higher win-rates in direct competition with subordinate males, female mate choice, and mate guarding during conceptive cycles. But the degree of benefits a high dominance rank can provide may vary between species with differing life history traits (e.g., longer lifespan and slower development) (Altmann & Alberts, 2003).

The explanations for both natal and secondary dispersals are linked to inbreeding avoidance and both intra- and inter-sexual selection (Jack & Fedigan, 2004b; Pusey, 1987; Teichroeb *et al.*, 2011). Both natal and secondary dispersals can be initiated voluntarily by males seeking better mating opportunities and attracted to extragroup members (Cheney & Seyfarth, 1983; Jack *et al.*, 2011). On the other hand, dispersal can also be forced on some males (Teichroeb et al., 2011). Natal males who attain sexual maturity in a group become potential mates to females, and hence competitors to resident males (Ekernas & Cords, 2007). Such mature natal males may thus be evicted by more dominant males (Cheney & Seyfarth, 1983). They may also be evicted following the immigration of a new male in the group or through complete takeover and replacement of all group males by a coalition of immigrating males (Teichroeb *et al.*, 2011). Individuals who initiate dispersal voluntarily may receive benefits that are not available to involuntary dispersers, such as being able to time their transfer with the mating season or moving into groups with favorable sex ratios that may result in additional mating opportunities (Jack & Fedigan, 2004b; Leimberger & Lewis, 2015).

1.2 | Potential costs and condition-dependent dispersal

Despite the benefits of dispersal in terms of inbreeding avoidance and a possible increase in reproductive opportunities, there are numerous potential costs associated with this behavior (Cheney, 1983). The costs 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. Locational costs may include higher predation and starvation risks during transfer, as well as higher stress levels, as the individual moves to an area without knowledge of food and predator locations (Alberts & Altmann, 1995; Brent et al., 2011; Pusey & Packer, 1987a; Ridley, 2012). Social dispersal refers to moving from one social environment to another. Social costs are related to aggression from conspecifics in the new social group and the loss of familiar social partners (Alberts & Altmann, 1995; Cheney & Seyfarth, 1983; Jack & Fedigan, 2004b; Schoof et al., 2009). Unfamiliar individuals may be perceived as potential competitors, and therefore tend to be more aggressive with each other than familiar individuals (Ydenberg et al., 1988). Dispersing individuals may also be observed roaming at the periphery of a new group for a certain period of time which may reduce aggression from unfamiliar members when attempting to join the group (Isbell et al., 1991).

For most primates, the dispersal opportunities available to each individual are highly variable (Jack & Isbell, 2009). Primates are characterized by condition-dependent dispersal (Bowler & Benton, 2005), where numerous factors may influence dispersal decisions. These conditions may include ecological factors such as seasonality and habitat fragmentation (Ekernas & Cords, 2007), social factors such as dominance rank, group stability, and breeding season (Jack *et al.*, 2011), and individual factors such as age and developmental stage (Jack et al., 2014). For instance, habitat modification through land conversion and fragmentation is of growing concern and poses a serious threat to many species, including primates (Marsh, 2013). Fragmentation may limit dispersal opportunities, as it creates greater travel distances between suitable habitats (Linder & Palkovitz, 2016). Seasonal variation in food availability or diet quality can cause nutritional stress due to changes in energy intake, which might affect behavior (Emery Thompson, 2017). In addition, males with lower dominance ranks might initiate dispersal in an attempt to improve their dominance rank by moving to neighboring groups, while high ranking males may do so to avoid mating with potential daughters who have reached reproductive age (Jack & Fedigan, 2004b). Group size, social instability (e.g., rank reversals, recurrent takeovers, short tenure lengths of

dominant males), and sex-ratios can promote dispersal or affect the timing of the event (Jack *et al.*, 2011). Dispersal success might also be affected in seasonally breeding species, as resident males may defend their group membership more actively to maintain access to females during this critical reproductive period (Leimberger & Lewis, 2015). Individual variation in physical and physiological characteristics may impact their ability to compete with other individuals in the group. Younger, smaller males (i.e., subadults) and older males may be more affected by the risks of locational and social dispersal than larger adult males in their prime. Conversely, prime-age males with bigger body mass and stronger competitive ability may not experience as much of these costs. Physical differences between subadult, prime-aged, and older males may be associated with variation in hormone levels (Jack et al., 2014), which in turn may have an effect on behavior (Higham, 2016).

Various environmental and social stressors may increase glucocorticoid (GC) 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 throughout the body to deal with threatening situations and provoke aversion through learning (Dhabhar, 2018). In the long term, however, they can be detrimental to the individual by having immuno-suppressive effects (Sapolsky et al., 2000). Higher GC levels could be a result of the potential costs of locational dispersal, such as nutritional stress or hypervigilance to predators (Emery Thompson, 2017), or social costs of dispersal, such as aggression from conspecifics. Dispersals are rare events that can occur over relatively long periods, and can be very stressful not only to the dispersing individual but also to residents of the immigrating group since changes in male membership may lead to social instability (Akinyi et al., 2017; Marty et al., 2017). Dominance rank can also greatly affect GC levels depending on an individual's position in the hierarchy. Several social characteristics, including rank stability and conflict avoidance, may affect whether low-ranking or high-ranking individuals tend to have higher GC levels (Sapolsky, 2005).

In addition, androgens (ARs) are hormones implicated in basic male reproductive functions, the development and maintenance of secondary sexual characteristics, and aggression in a reproductive context (Dixson, 2012). The Challenge Hypothesis predicts that males will show elevated testosterone, one specific type of AR, during critical periods of interactions with reproductively active females and competition between males compared to non-reproductive

baseline levels (Wingfield et al., 1990; Beehner et al., 2006; Goymann, 2009). Androgens, including testosterone, have also been shown to be a predictor of rank in a group of wild chacma baboons (*Papio hamadryas ursinus:* Beehner *et al.*, 2006), while they increased only following alpha rank attainment in white-faced capuchins (Schoof et al., 2011). In species with male-biased transfers and where natal dispersal generally coincides with attainment of sexual maturity (Cheney & Seyfarth, 1983), an increase in ARs may promote initial dispersal (Bronson, 1989; Duffy & Belthoff, 2001). After dispersal, immigrating males may have increased AR levels as they compete for dominance in a new social group (intra-sexual interactions) or gain access to receptive females (inter-sexual interactions) (Alberts et al., 1992; Goymann et al., 2019). Such hormones, when released into the bloodstream following internal or external stimuli, may change the likelihood of occurrence of a particular behavior within the appropriate social or environmental context (Neave, 2008; Nelson, 2011). Thus, studying hormone levels over long periods can shed light on the proximate mechanisms of dispersal (e.g., timing of transfer, voluntariness of dispersal, social conditions of individuals).

One way to mitigate the locational and social costs of dispersal is to engage in parallel dispersal (van Hooff, 2000). Parallel dispersal can occur 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. Parallel dispersal has been documented in various species, including carnivores (e.g., lions: Pusey & Packer, 1987b), birds (e.g., Arabian babbler, *Turdoides squamiceps*: Ridley, 2012), and numerous primates (reviewed in Schoof et al., 2009). Interestingly, many of the species known to disperse more than once in a lifetime are also frequently documented to disperse in parallel (e.g., lions: Pusey & Packer, 1987b; Japanese macaques, *Macaca fuscata*: Sprague et al., 1998; vervets: Cheney, 1983). Males who disperse in parallel may mitigate the costs of locational dispersal by providing shared vigilance against predators (Baldellou & Henzi, 1992; Isbell et al., 1993). Parallel dispersal may also reduce the costs of social dispersal by providing the opportunity to receive coalitionary support from peers or related individuals against aggression from unfamiliar individuals (Cheney & Seyfarth, 1983; Isbell & Van Vuren, 1996; Schoof et al., 2009). Males who engage in parallel dispersal may also have lower GC levels than lone dispersers if this strategy mitigates the costs of dispersal (Table 1). Parallel dispersal may provide other benefits by maintaining relatedness

between dispersing males, enabling coalitionary support from a familiar individual, and/or improving inclusive fitness (Schoof et al., 2009; van Hooff, 2000).

1.3 | Context of dispersal and decision-making

Variation in the ecological, social, and individual contexts of dispersal may create cost and benefit asymmetries between the dispersing individuals. Specific dispersal conditions may negatively or positively affect each individual differently depending on their own status. For instance, subadult males (SAMs) might be better off engaging in parallel dispersal if transferring alongside another male reduces associated costs and increases competitive ability (Kuester *et al.*, 1995). In contrast, prime adult males (AMs) might not experience the costs of locational and social dispersal as much, and transferring in parallel might reduce the benefits of dispersal if they must then compete against an additional coresident male in their new group.

Dispersal is considered to be a risky and potentially very costly behavior, so in cases where it is initiated voluntarily, we expect the individual to benefit substantially from this intergroup movement. The evolutionary explanations for dispersal are well-understood, however the underlying proximate causes of individual dispersal decisions are still poorly understood (Jack & Fedigan, 2004b; Young & Monfort, 2009). Potential causes include behavioral mechanisms triggered by socio-ecological stimuli, as well as changes associated with individual development, ontogeny, genetics, and physiology that lead to variation in behavior (Tinbergen, 1963). Exploring these proximate causes of dispersal, and how the context of individual dispersal affects its success in transferring individuals, is critical in understanding group dynamics and changes in composition and structure in species with sex-biased philopatry.

The aims of this research were twofold. Firstly, we tested the hypothesis that specific factors trigger male dispersal in wild vervet monkeys (*Chlorocebus pygerythrus*). Specifically, we examined the potential impact of individual, social, and ecological factors (hereafter "general context of dispersal") on each individual's decision-making as to when, where, and how they disperse to other social groups (i.e., timing of transfer, moving to a group with favorable sex ratio, and mode of dispersal respectively), as this may affect a male's ability to attain a high dominance rank upon immigration (see Table 2). Secondly, we hypothesized that males, according to the context of their own dispersal, will make movement decisions that minimize the costs of movement and maximize its reproductive benefits following immigration (see Table 3).

Vervet monkeys engage in non-random dispersal, meaning that the inter-group movement decisions of individuals is affected by several factors (Cheney & Seyfarth, 1983). Compared to many mammalian species, vervets – like most primates – are long-lived animals with relatively slow development and a long life-history (Jack & Isbell, 2009). However, vervets are an ideal primate species for this study as they typically reach maturity faster and disperse earlier than other primates, offering the potential to document more dispersal events (Isbell & Jaffe, 2013). They live in multimale-multifemale groups characterized by female philopatry and male-biased dispersal (Isbell et al., 1991; Struhsaker, 1967). Both resident males and females can be involved in aggressive home range defense (Isbell et al., 1993). 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). Cheney et al. (1988) found there was no positive correlation between male rank and mating success. However, as mentioned earlier, mating success may not be directly related to reproductive success (i.e., fecundity). Genetic studies of paternity in vervet monkeys have yet to be conducted. 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 population of vervets at Lake Nabugabo appear to exhibit moderate seasonal reproductive patterns (33-67% of births in 3 months), possibly as a result of increased access to high-quality human foods available in the human-modified habitat (Schoof *et al.*, 2015). Females attain sexual maturity at around 4 years of age (Cheney et al., 1988) and do not present any visual signs of ovulation during the conception cycle (Andelman, 1987).

Table 1
Modes of dispersal and their relative potential costs an individual would experience

		Social costs	
		Low	High
Locational costs	Low	Joint dispersal (parallel)	---
	High	Sequential dispersal (parallel)	Lone dispersal

Table 2
Hypothesis 1 - Male dispersal is triggered by individual (i), social (s) and ecological (e) factors

Predictions		Predictor	Response
1(s)	Males will time their movement with the conceptive seasonality of females.	Conceptive season	Timing of dispersal
2(e)	Dispersals will occur more frequently during periods of higher food availability to reduce risks of locational dispersal.	Fruit availability	Timing of dispersal
3(i)	a. SAMs will disperse once they reach sexual maturity to avoid inbreeding.	Age	Timing of dispersal
	b. AMs will disperse before their daughters become sexually mature to avoid inbreeding.	Tenure length	Timing of dispersal
4(s)	a. SAMs will disperse once they begin challenging resident males and increase their competitive ability.	Elo-trajectories	Timing of dispersal
	b. AMs will disperse as they are decreasing in competitive ability to increase their rank and access to females.	Elo-trajectories	Timing of dispersal
5(s)	Social instability will trigger involuntary dispersal.	Male immigration	Dispersal (yes/no)
6(i)	Natal dispersers will have increased AR levels prior to dispersal as compared to baseline because of increases in reproductive competition as they reach sexual maturity.	AR levels	Dispersal (yes/no)
7(i)	GC levels in dispersing males will be higher than baseline during the prospecting of other groups.	Dispersal	GC levels

Table 3
Hypothesis 2 - Males will transfer in a way to minimize the locational and social costs (c) and maximize the benefits (b) of dispersal

Prediction		Predictor variable	Response variable
1(b)	a. If dispersal serves to maximize reproductive opportunities, dispersing males will increase their ordinal rank after dispersal.	Dispersal	Dominance rank
	b. The degree of rank increase may be dependent on whether dispersal is natal or secondary (i.e., possible interaction).	Type of dispersal	Dominance rank
2(b)	Males will disperse to a group with favorable sex ratios, with more females per male than in their residential group.	Sex ratio	Dispersal
3(b)	Parallel dispersal will be more common in SAMs than in AMs due to the benefits of improved competitive ability against other males in the target group.	Age category	Mode of dispersal
4(c)	If psychosocial and energetic demands are higher following dispersal, GC levels will be higher in dispersers than in non-dispersers.	Dispersal	GC levels
5(c)	Lone dispersers will exhibit higher GC levels than parallel dispersers as they will be more affected by the costs of dispersal.	Mode of dispersal	GC levels
6(b)	After dispersal, immigrating males may have increased AR levels as they compete for dominance in a new social group or gain access to potential mates.	Dispersal	AR levels

2 | Materials and methods

2.1 | Study area and subject

This study was conducted at Lake Nabugabo, located in Masaka District in central Uganda (0°22′-12°S and 31°54′E). The area surrounding Lake Nabugabo is a human-modified, yet diverse, landscape composed of grasslands, patches of forests, swamps, and human settlements (Chapman et al., 2016). There has been deforestation to make space for agricultural crops and buildings in and around the village of Bbaale. Two wet seasons occur from March to May and from November to December, interspersed with two dry seasons from December to February and May to October (Chapman et al., 2016).

Habituation of the three vervet study groups on the shores of Lake Nabugabo began in 2011 for Matovu (M) group, and early 2016 for Kasozi (KS) and Holiday Center (HC) groups. All three social groups were included in the analyses, and their composition changed extensively since the beginning of the study period due to births, dispersals, disappearances (unknown causes), and deaths by predators such as snakes, birds, dogs, and humans. This study focused on subadult males and adult males, and any dispersal events and disappearances for which we had sufficient information were of interest.

2.2. | Operational definitions

For this study, we defined emigration as an individual leaving the resident group, presumably in search of a new social group to join. Natal emigration was defined as a departure from the natal group, which can only be determined when the male's birth group is known. Secondary (or breeding) emigrations occurred when males left a group into which they previously immigrated (Jack & Fedigan, 2004b). We were able to confirm dispersals when males were observed later in one of our three study groups or to neighboring groups. On the other hand, dispersals were presumed when males disappeared from a study group and were suspected to have emigrated rather than died. This was determined if typical roaming behavior was observed in the individual, while also considering age or tenure length in the resident group. Emigrations were considered 'voluntary' if they occurred without any significant increase in aggression towards the dispersing individuals, whereas 'involuntary' emigrations occurred following a male immigration within 3 months prior to emigration (Jack & Fedigan, 2004b; Teichroeb et al., 2011). Immigration

was defined as an individual that has been a resident of his new social group for a minimum of 30 consecutive days without leaving the group. Before immigration, some individuals may be found roaming (i.e., staying at the periphery of the target social group for a certain period), but such males may not be considered immigrants yet. Joint parallel dispersal was defined as groups of two or more individuals moving from the same residential group to the same target group within a maximum of 7 days of each other's movement. Sequential dispersal was defined in a similar way as joint parallel dispersal, but with temporal parameters in which dispersal of the individuals occurred more than 7 days and not exceeding 90 days apart. Resident males were distinguished from dispersing males as being observed in the same group during the whole dispersal period (within $\pm$90 days of a confirmed dispersal date, for 180 days total) while dispersing males were individuals observed moving between groups during the same period (derived from Kawazoe & Sosa, 2019).

There is still no consensus as to when male vervet monkeys shift from subadulthood to adulthood (Bolter & Zihlman, 2006), with some authors using age (6-7 years old) as a proxy but without any morphological or physiological changes (Bolter & Zihlman, 2006; Cheney et al., 1988). Unfortunately, age was only available for a small number of our subadult males (primarily those in M group since this group has been followed for a longer time) and could not be used to determine changes in age classes for most individuals. In the vervet population at Lake Nabugabo, we considered males to be SAMs between 4 and 5 years of age, and they became adults when they emigrated from their natal group (i.e., after first transfer). Changes to a male's relative competitive ability (i.e., compared to male co-residents competitors) was considered 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 (AF) per adult male (AM) in a group, regardless of female reproductive status and excluding the male who dispersed between both groups.

2.3 | Data collection

My study relied on a long-term dataset 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 SAMs and AMs (M: 2014-2019; KS & HC: 2016-2019). From 2012-2016, M group was followed for 6 days per week for three consecutive weeks, followed by one week

without data collection. From 2016 onwards, all three groups were monitored on a weekly rotation between M, KS, and HC for three weeks, with two groups followed simultaneously by different members of the field research team, followed by one week without data collection. Complete dispersal events for our research occurred when males dispersed between our three known groups (e.g., from M to KS) because we could collect behavioral and hormone data for the immediate periods both before and after dispersal. In cases where a male emigrated from one of the study groups to an unknown group (i.e., group we do not follow), data collection on that male ended, such that no post-dispersal data were available. Similarly, when a male from an unknown group immigrated into one of our study groups, no pre-dispersal data were available for this individual.

2.3.1 | Behavioral observations

For each study day, the field research team collected scan data of five individuals (Altmann, 1974) at 30-minute intervals (2012-2016) and 15-minute intervals (2016-present) to record the general activity (e.g., resting, foraging, moving, grooming, etc.) of five individuals in each group, as well as the presence of a nearest-neighbor. This was paired with opportunistic *ad libitum* data collection of all agonistic and sociosexual interactions for males in the study groups. Continuous focal animal sampling (Altmann, 1974) of all SAMs and AMs was conducted by MSc student Karin Snyder from January to June 2019 and by myself from July to December 2019. State behaviors (e.g., resting, foraging, grooming), as well as events including agonism (e.g., chase, supplant, cower, fear grimace), and sociosexual interactions (e.g., mount, present, inspect, mating refusal) were recorded both during scans and focal follows. Sampling effort did not differ between transferring males and other individuals throughout the study.

2.3.2 | Demography and dispersal events

Demographic changes in the three study groups have been recorded since 2011, including all births, deaths, disappearances, emigrations, and immigrations. We also recorded injuries and dates and causes of disappearance (i.e., death, dispersal, unknown). If a male disappeared from their social group and was located in another study group or observed in a non-study group during an intergroup encounter, the disappearance was labeled as “confirmed dispersal”. In cases where we suspected a dispersal rather than a death based on age, tenure length, and recent antecedents of disappearances and returns, but without knowledge of the direction of the transfer (i.e., to which group the individual moved to), we identified the event as a “presumed dispersal”. We considered

dispersal events to be “complete” when we have for both before and after the transfer, meaning when a male moved between two known groups we followed at the time (e.g., from M to KS in 2017). Thus, all dispersal events that occurred before 2016 are incomplete, since the only social group we followed was M group. Still, these events are useful for some analyses.

2.3.3 | Plant phenology

Since June 2011, temporal variation in food availability at Lake Nabugabo was evaluated by attributing monthly young leaf, mature leaf, flowers, unripe fruit, and ripe fruit scores between 0 and 4 (0 = 0%, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, 4 = 76–100%) for 27 plant species known to be consumed by vervet monkeys in the area (Chapman et al., 2016), with several species only added in more recent years for a total of 41 species. Between 1 and 5 individuals per species were selected, depending on the rarity of the species, and a maximum total of 70 individuals monitored across all species. Given that 77% of the Nabugabo vervet diet is comprised of fruit (Chapman et al., 2016), we limited our food seasonality analyses to unripe and ripe fruit. A sum of both unripe and ripe fruit scores was calculated for each plant and an average for each species as well as for all species was calculated for each month across all study years (following Chapman et al., 2005).

2.3.4 | Fecal samples and hormone assays

Fresh fecal samples were collected before noon from each SAM and AM within 10 minutes of defecation, a portion uncontaminated by urine or soil collected in a 15mL tube, and placed in an ice pack while in the field. Samples were frozen on the same day of collection until thawed for hormone extraction in the field lab. After thawing at room temperature, samples were homogenized with a spatula and 10 ml of 50:50 ethanol:water was added to 0.5g of feces. Samples were then vortexed for 10 minutes to extract hormones and centrifuged for 20 minutes to separate the hormone-containing supernatant from the fecal pellet. Thereafter, 2 mL of the supernatant was inserted in a solid phase extraction (SPE) cartridge (SPure Ltd, Maxi-Clean 300mg Prevail C-18, SP-5122335), followed by a 2 mL wash with deionized water. These cartridges were then sealed and stored in a dark and cool space until transport to the Glendon Primate Behavioral Endocrinology Lab at York University, Canada. Each cartridge was washed with 1 mL of 5% methanol and eluted with 2 mL of 100% methanol using an Alltech vacuum manifold. The extracted hormone metabolites were then taken to the Toronto Zoo’s Reproductive Endocrinology

Lab for analyses of fecal glucocorticoid metabolite (fGCM) and fecal androgen metabolite (fARM) levels using enzyme immunoassay (EIA) methods developed by Majchrzak et al. (2015).

For reconstitution of GC metabolites, 450 μL of the eluted hormone solution was dried then reconstituted in 150 μL of enzyme immunoassay (EIA) buffer solution, while 75 μL of the eluted AR solution was dried and reconstituted in 150 μL of the same EIA buffer (Terwissen et al., 2014). For both metabolites, 50 μL of the reconstituted solution was aliquoted into microtiter plates using an in-house EIA. The GC plates were coated with 0.25 μg of polyclonal goat anti-rabbit IgG (GARG), followed by a coating buffer. After overnight incubation at room temperature, plates were washed, then blocked with 250 μL of EIA buffer. Then, 100 μL horseradish peroxidase was then applied on each plate, and 100 μL of cortisol antiserum (polyclonal R4866) was added for GCs and a testosterone specific antibody (R156/R157) for ARs. Following a second overnight incubation, GC plates were washed and a 200 μL substrate solution was added, while AR plates only had a two-hour incubation. Absorbance was measured using spectrophotometry (Terwissen et al., 2013). Each sample was run in duplicate and the concentration for both fGCM and fARM levels was calculated, which is expressed in ng/g.

Biological validation of fGCM levels has previously been done using an adrenocorticotropic hormone (ACTH) challenge in captive vervet monkeys (see Young et al., 2017). To test for parallelism, serial dilutions in EIA buffer of vervet hormone extracts were compared to a 5-point standard curve (GC standard: Sigma H0135, 78-20,000 pg/mL; AR standard: Steraloids Inc., A6950, 48-12,5000 pg/mL). Linear regression indicates a high degree of parallelism between the standard curves and the serially diluted samples for both GC ($R = 0.996$, $P < 0.001$) and AR ($R = 0.966$, $P < 0.01$). For GC, the inter-assay coefficients of variation (CV) were 6.4% (high pool) and 9.7% (low pool), and the intra-assay CV was 7.4%. For androgens, inter-assay CV's were 11.0% (high pool) and 15.7% (low pool), and intra-assay CV was 6.0%.

2.4 | Statistical analyses

The majority of statistical analyses were conducted using the statistical programming software R (version 3.6.2) (R Core Team, 2013) with the significance level set to $\alpha \leq 0.05$.

2.4.1 | Seasonality of conceptions, fruit availability, and dispersals

We evaluated conception seasonality by using the birth dates of all infants and subtracted the mean gestation length of 163 days in vervets (Johnson et al., 1973). We recorded a total of 119 births and 25 confirmed dispersals (33 total) between July 2012 and June 2019 for all three groups. The total number of conceptions and dispersals were calculated separately, grouped by month of the year, and were compared to investigate degrees of seasonality. Circular statistical analyses for seasonality of conceptions, fruit availability, and dispersals were conducted using Oriana (version 4.02) (Kovach, 2011). A Rayleigh test was conducted to evaluate non-uniformity of the data for both conceptions and dispersals, while Moore's modified Rayleigh test was used for food seasonality. A Spearman's rank correlation rho was used to calculate the correlation between conception and dispersal distributions.

2.4.2 | Inbreeding avoidance

To determine if males timed their transfers to reduce risks of inbreeding, we compared each SAM's age at natal dispersal to the maximum age at which they reach sexual maturity, as this is when they are expected to attempt mating with females the most (i.e., 60 months: Bolter & Zihlman, 2006). For AMs and secondary dispersals, we compared male tenure length to females' mean age at first conception (i.e., 42.4 months), based on data from wild populations and supplemented with data from captive populations (see Harvey & Clutton-Brock, 1985). We respectively used Wilcoxon one-sample one-tailed tests in both cases.

2.4.3 | Dominance and sex ratio

For dominance analyses, we calculated Elo-ratings using the R package "EloRating" (Neumann *et al*., 2011). Elo-ratings represent values that can either increase or decrease depending on the outcome of an agonistic interaction between two individuals. The "winner" of that interaction will win points and the "loser" will lose an equivalent number of points. The formula also considers the likelihood of winning for both individuals and will assign points accordingly. The number of points that can be won or lost from an interaction is set by the *k*-value, as well as the probability of winning and losing in and between specific dyads. The value of *k* can be set arbitrarily based on species-specific information about the importance of agonistic interactions (Neumann et al., 2011; Newton-Fisher, 2017). Alternatively, an optimized *k*-value can be

calculated using a likelihood approach based on the best fit for the species (Foerster et al., 2016). For this study, we calculated an optimized *k*-value for each study group by exploring a range of possible k-values between 5 and 200 with a resolution of 5000 (Newton-Fisher, 2017). The best *k*-value obtained for each group was then associated with its log-likelihood and compared to the values for the other two groups. We opted to use a *k*-value of 76.75, which was the common best fit for all three groups based on a graphical representation of each log-likelihood for each group. Agonistic interactions occurring between two same individuals within 15 minutes (i.e., the length of focal follows) were considered as the same bout, i.e. merged as one interaction with one outcome.

We used male Elo-trajectories for all pre-dispersal periods to evaluate the trend of a male's competitive ability as dispersing males may be roaming and visiting other groups to eventually transfer to. Using Elo-ratings, we estimated all residents and dispersing males' Elo-trajectories for 90-day periods before each confirmed dispersal date. To determine if the direction of the trajectory was significantly different from zero, we calculated Z scores for each male for each dispersal event.

For complete dispersal events (i.e. where we had data for both before and after transfer), we used ordinal rank metrics as it better predicts males' access to females for reproduction, which is the main driver of intra-sexual competition in males (see Levy et al., 2020). We calculated their ranks in their residential group before departure (i.e., one day before the confirmed date of transfer) and their rank 90 days following immigration in the target group. We decided to use 90 days for each pre-dispersal period to increase sample size for agonistic interactions used in our analyses. Males were considered to have changed their rank if they either increased or decreased by at least one position (e.g., from 3rd ranking to 2nd ranking). We evaluated changes in ordinal rank and AF:AM sex ratio using a paired-samples Wilcoxon test. To evaluate the degree of potential improvement in each male's access to females after dispersal, we compared 1) the change in dominance rank from group A to group B and 2) the change in sex ratio when moving from A to B. We used a log response ratio (LRR) for each variable and compared their values to one another. To do so, 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. Using LRR for rank and sex ratio changes allows us to measure the increase (or decrease) of a male's potential

access to females following immigration. A male who would increase both his dominance rank and move to a group with a more favorable sex ratio would have the highest increase in reproductive potential among the dispersing males.

2.4.4 | Hormone analyses

All fecal hormone metabolite levels were log-transformed to meet assumptions of a normal distribution. For each dispersal event for which hormone data were available, we selected all samples within 60-day periods before and after the confirmed dispersal date. For this analysis, these 60-day periods will hereafter be referred to as "dispersal periods" (before or after). We chose this timeframe to account for the relatively small number of monthly samples for certain males, but we did not want to exceed 60-days as other authors have found hormone levels to vary only within the first month of immigration (Bergman et al., 2005; Marty et al., 2017). Mean fGCM and fARM levels were calculated for each dispersal period for all males that were present in the group during this interval. We compared the mean values of these periods to the baseline hormone levels, which was calculated using a mean of all samples collected in 180-day periods either before or after the dispersal period (e.g., if dispersal is day 0, post-dispersal baseline is 61-240 days). We calculated Z-scores to compare hormone levels between dispersing and non-dispersing males. We used a paired samples t-test to determine if there was a difference between a male's hormone values during the dispersal period and that of his baseline levels. We also tested for potential effects of age category, rank before dispersal, and mode of dispersal on hormone levels using an analysis of variance (ANOVA).

3 | Results

3.1 | Seasonality of conceptions, fruit availability, and dispersals

A total of 36 dispersal events from 29 separate males were recorded. We were able to confirm male transfers for 26 of these events and presumed dispersal for the remaining 10 events. We considered all emigrations to be initiated voluntarily, as we did not observe any male take-overs three months prior to the males' transfers. Fruits were uniformly available throughout the year (Moore's modified Rayleigh test: $R = 0.535$, $0.5 > p > 0.1$); therefore, we did not pursue further analyses on the timing of fruits and dispersal. 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 28th, μ=146.7^{o}, $R = 0.591$, Figure 1a). Timing of confirmed dispersal (N = 25) events were also moderately seasonal (Rayleigh test: $Z = 4.787$, $p = 0.007$), with 56% of transfers occurring between April and June (mean date = May 25th, μ= 143.5^{o}, $R = 0.428$, Figure 1b). The difference in mean dates of conception and confirmed dispersal was three days; however, the trend in the correlation between conception seasonality and the timing of confirmed dispersals was not statistically significant (Spearman's rank correlation rho: $S = 158.14$, $R = 0.45$, $p = 0.145$). When we included all dispersal events (confirmed plus presumed dispersals, N = 33), 45% of which occurred between April and June (mean date = June 3rd, $R = 0.284$, $\mu = 152.8°$), the timing of male transfers did not differ significantly from a uniform distribution (Rayleigh test: $Z = 2.666$, $p = 0.069$). When we examined all natal (N = 17) and secondary dispersals (N = 13) separately, the correlation between the timing of conceptions and dispersals was significant for secondary dispersal events (Figure 1c, Spearman's rank correlation rho: $S = 111.71$, $R = 0.61$, $p = 0.035$) but not for natal dispersals ($S = 368.13$, $R = -0.29$, $p = 0.366$).

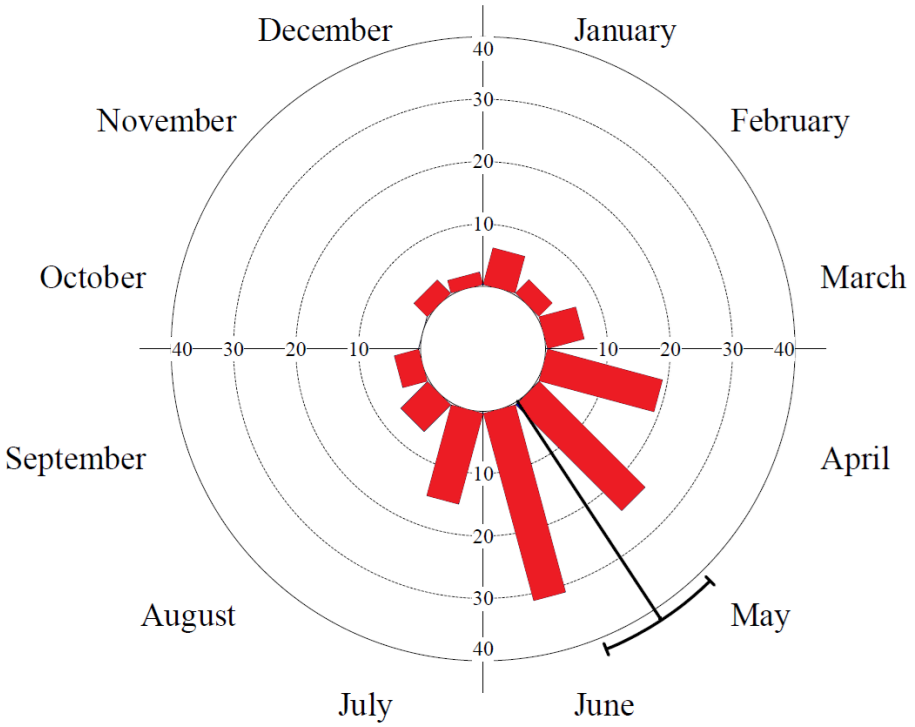

Figure 1a. Offspring **conception** seasonality grouped by month of the year for all adult females between July 2012 and June 2019. There is a total of 119 conceptions, with the axes identifying the number of conceptions for each month, and the bold line representing the mean vector and 95% confidence interval.

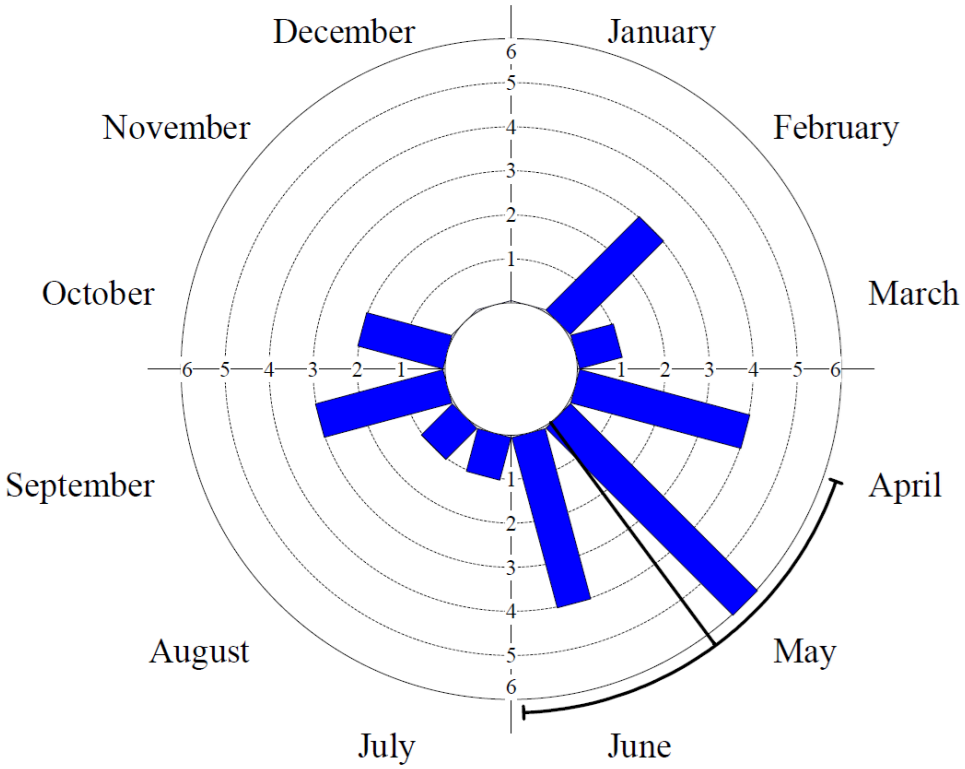

Figure 1b. Timing of **confirmed** dispersals grouped by month of the year for all focal males between July 2012 and June 2019. There is a total of 25 events, with the axes identifying the number of events for each month, and the bold line representing the mean vector and 95% confidence interval.

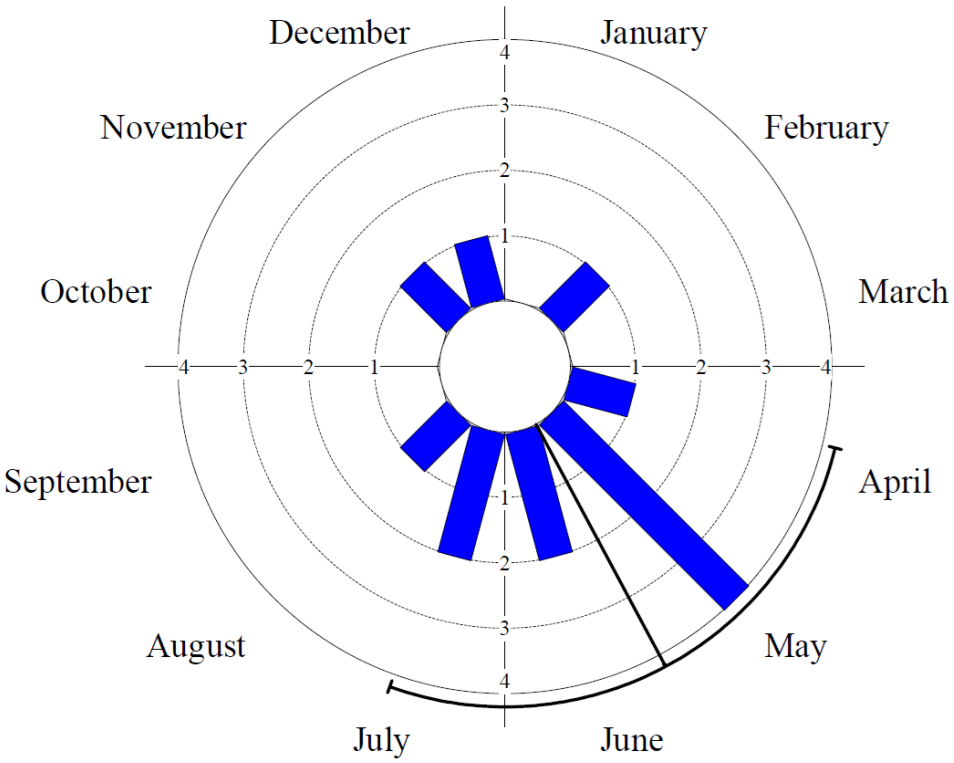

Figure 1c. Timing of **secondary** dispersals grouped by month of the year for all focal males between July 2012 and June 2019. There is a total of 13 events, with the axes identifying the number of events for each month, and the bold line representing the mean vector and 95% confidence interval.

3.2 | Inbreeding avoidance

Known natal male age at dispersal in our study groups ranged from 36 to 69 months (mean = 55.1±12.25 SD, median = 58.5, N = 8). Male vervet monkeys typically reach sexual maturity at around 60 months of age (Cheney et al., 1988) and males of known age in our study population did not transfer earlier than this (Wilcoxon one-sample one-tailed test: V = 13, p = 0.273). Tenure length of AMs in our focal groups ranged from 17 to 59 months (mean = 35±16.98 SD months, median = 27, N = 7). To determine whether males would leave their social group before potentially mating with their daughters, we compared the mean tenure length of males at Nabugabo to the mean age at first conception in female vervet monkeys, which is 42.4 months (Harvey & Clutton-Brock, 1985). On average, males transferred did not transfer before their potential daughters would reach sexual maturity (Wilcoxon one-sample one-tailed test: V = 9, p = 0.223).

3.3 | Dominance and sex ratio

Only one SAM and one AM significantly improved their competitive ability in their resident group prior to dispersal, shown by an increase in Elo-trajectory (see Table A1 in Appendix for all results). However, all other dispersing males (89%) did not show any significant change in Elo-trajectories.

Although 72% (8 of 11) of our focal males moved to a group with a more favorable female-to-male sex ratio, the overall change in the number of females per male was not significant (Paired samples Wilcoxon test: $V = 18.5$, N = 11, $p = 0.213$; Figure 2). Also, while 57% of our males (4 out of 7) increased their ordinal rank by at least one position following dispersal, the overall increase was not statistically significant ($V = 14$, N = 7, $p = 0.534$). Figure 3 illustrates the log response ratio (LRR) interactions between sex ratio and ordinal rank change after immigration into a new group. Having a positive LRR for either sex ratio or rank means that the individuals have improved their potential access to females. Thus, a male who moved to a group with a more favorable sex ratio while also increasing his ordinal rank will have the highest benefits from dispersing to a new group. Of the seven males for whom we had sufficient data, only three moved to a group with a more favorable female-to-male sex ratio while also increasing their ordinal rank (Figure 3: upper-right quadrant). However, there was no correlation between sex ratio improvement and ordinal rank improvement (Spearman's rank correlation rho: $S = 52.917$, $R = 0.055$, $p = 0.91$). The type of dispersal (i.e., natal vs. secondary) did not affect the degree of rank improvement after dispersal, even though all males who improved in rank were subadult males engaging in natal dispersal (Wilcoxon rank-sum test: $W = 8$, $p = 0.162$).

Across our study period, we identified 21 lone dispersals and 15 parallel dispersals, 10 of which were considered joint parallel dispersals and five that were sequential parallel dispersals (summarized in Table 4). Parallel dispersals accounted for 41% of all events, but SAMs were not more likely to engage in parallel dispersal than AMs (Chi-square test: $\chi^2 = 0.785$, $p = 0.376$). Parallel dispersals were evenly distributed between SAMs and AMs, although when we included only confirmed dispersals, SAMs were the only ones to be involved in sequential dispersals. Similar to dispersal type, the mode of dispersal did not have a significant influence on the degree of rank improvement (Wilcoxon rank-sum test: $W = 5$, $p = 0.705$). Mode of dispersal was not influenced by the individual's rank prior to emigration (ANOVA: $F = 0.008$, DF = 1, $p = 0.928$).

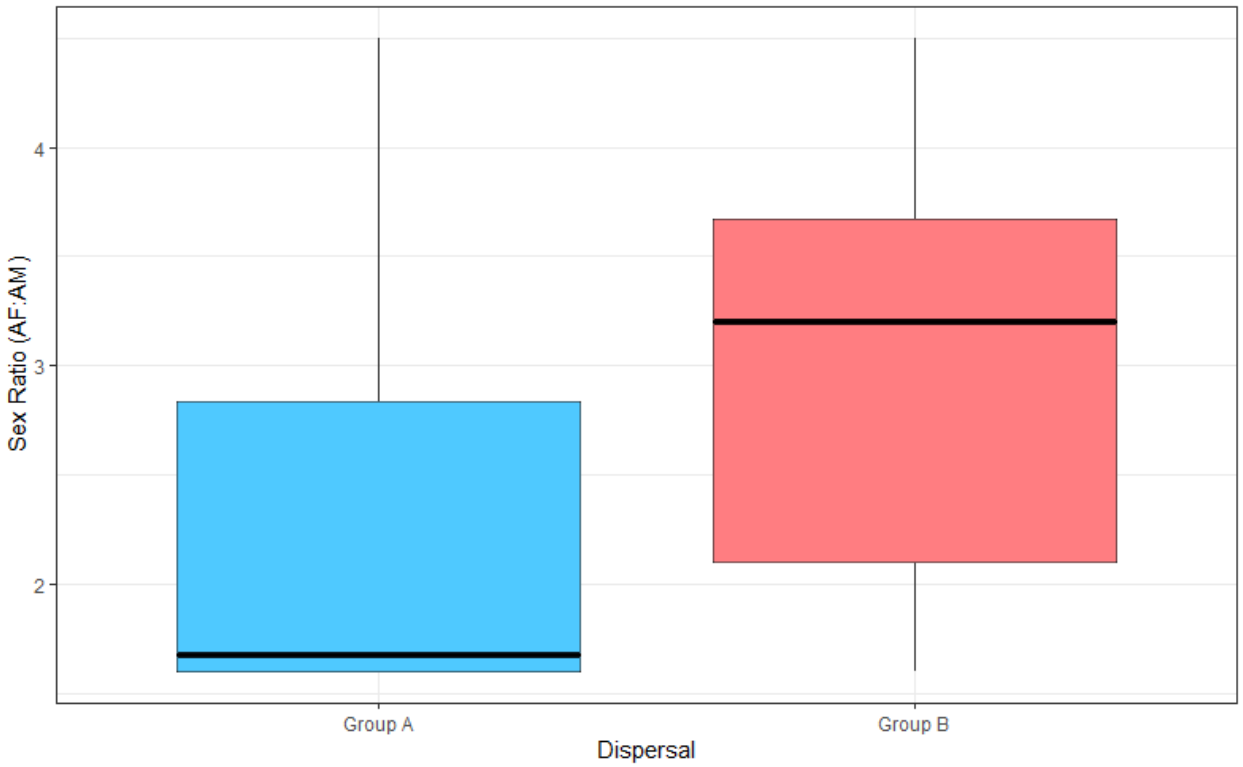

Figure 2. Boxplot of number of adult females per adult male (AF:AM) sex ratio changes (N=11) by dispersing from the residential group (Group A) to the target group (Group B).

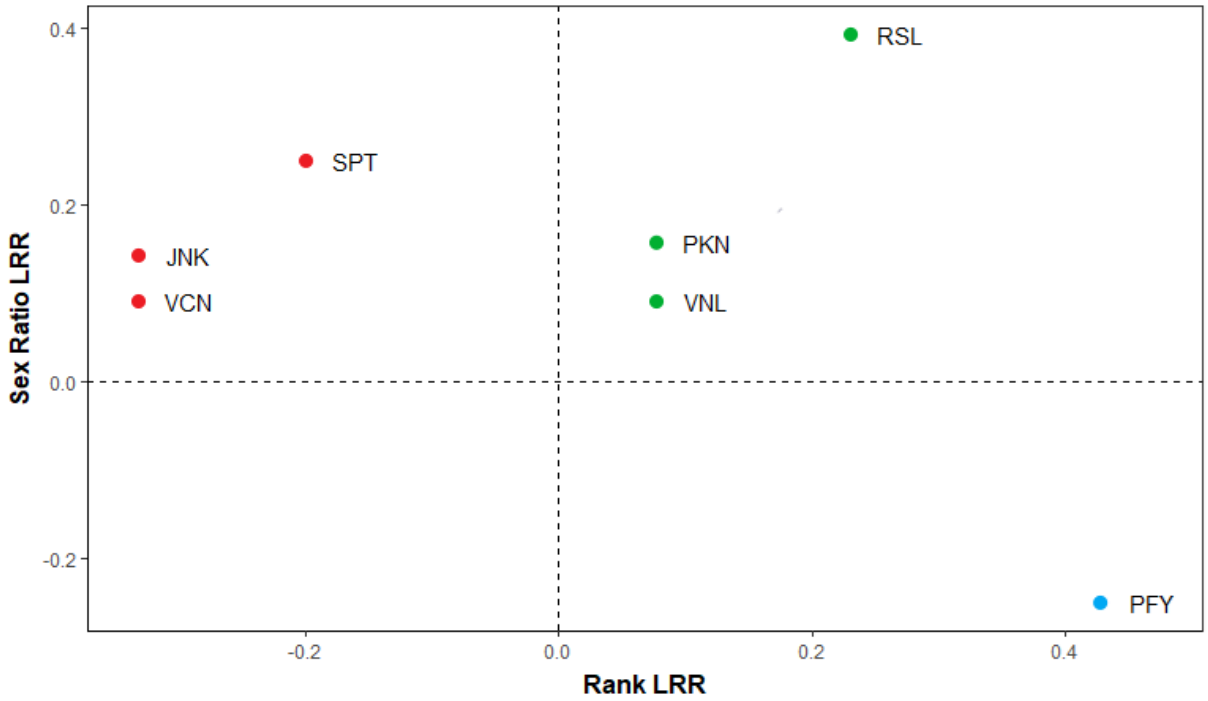

Figure 3. LRR score interactions between sex ratio and rank changes following dispersal. Green data points indicate males who have increased both their ordinal rank and sex ratio compared to pre-dispersal settings. Red points indicate males who decreased in rank but moved to a group with a more favorable sex ratio. The blue point indicates a male who increased his rank but decreased in number of females available per male. No male dispersal involved a decrease in both rank or AF:AM sex ratio.

3.4 | Variation in fecal glucocorticoid and androgen metabolite levels

A total of 1119 fecal samples were collected from males since 2014. Because some of the study subjects dispersed or disappeared throughout the study period, the total number of fecal samples collected per male varies (range 5-62, mean = 20±17.4 SD). Across all samples, fGCM levels ranged from -0.446 to 1.843 ng/g (mean = 0.822±0.387 SD) and fARM levels ranged from 0.215 to 2.573 ng/g (mean = 1.367±0.335 SD).

Dispersing males did not have significantly higher fGCM levels in the 60 days prior to emigration when compared to their fGCM baseline (Table 5). This was also true for all other males in the group (non-dispersing males) during this same period. In the 60 days prior to emigration, natal dispersers did not have higher fGCM levels compared to males engaging in secondary dispersals. Following dispersal (i.e., within 60 days after immigration), newly immigrated males did not have significantly higher fGCM levels compared to their fGCM baseline. However, male immigration was associated with a small but statistically significant increase in fGCM levels for male residents of the new group, compared to the pre-immigration period (mean increase of 0.092 ng/g). Lone dispersers did not have higher fGCM levels following dispersal compared to parallel dispersers.

Dispersing males also did not have significantly higher fARM levels in the 60 days prior to emigration when compared to their baseline (Table 6). However, in contrast to findings for fGCM levels, non-dispersing males had small but significantly higher fARM levels in the 60 days prior to the dispersal of a male co-resident when compared to their own baseline (mean increase of 0.086 ng/g). Natal dispersers did not have higher fARM levels than secondary dispersers prior to dispersal. After immigration, similarly to fGCM levels, dispersing males did not have increased fARM compared to their baseline levels. Non-dispersing males also did not have any significant increase in fARM levels. We did not find lone dispersers to have significantly higher fARM levels compared to parallel dispersers following immigration. Neither fGCM nor fARM levels were found to be influenced by the mode of dispersal (lone or parallel), the rank of the individual before emigration, or age category (SAM or AM) (ANOVA, $P > 0.05$, see Table A2 and A3 in Appendix for all results).

Table 4
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)

Table 5
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	Testing	*T*	DF	*P*
Pre-emigration (60 days prior)	Dispersers levels vs. their baseline	0.779	13	0.449
	Non-dispersers levels vs. their baseline	1.482	81	0.142
	Natal dispersers vs. secondary dispersers levels	0.154	4	0.885
Post-immigration (60 days after)	Dispersers levels vs. their baseline	1.731	9	0.117
	Non-dispersers levels vs. their baseline	2.515	73	0.014*
	Lone dispersers vs. parallel dispersers levels	1.681	3	0.191

Table 6
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	Prediction	*T*	DF	*P*
Pre-emigration (60 days prior)	Dispersers levels vs. their baseline	0.239	13	0.815
	Non-dispersers levels vs. their baseline	2.307	81	0.024*
	Natal dispersers vs. secondary dispersers levels	1.414	4	0.230
Post-immigration (60 days after)	Dispersers levels vs. their baseline	0.981	9	0.352
	Non-dispersers levels vs. their baseline	1.498	73	0.138
	Lone dispersers vs. parallel dispersers levels	1.524	3	0.225

4 | Discussion

The timing of intergroup movement may be very important for a male to optimize his access to mating and reproduction, as males transferring too young or too early may experience more of the costs of dispersal. We found that some individual and social conditions, but not ecological ones, trigger dispersal in male vervet monkeys (Hypothesis 1). Males engaging in secondary dispersal timed their movement to coincide with female conception seasonality, but this pattern was not significant for males engaging in natal transfers. Neither natal nor non-natal males dispersed in time to avoid potentially mating with related females. Furthermore, males have increased either in rank, immigrated to groups with more favorable sex ratios, or both. This supports the hypothesis that males would transfer in a way to minimize the locational and social costs and maximize the benefits of dispersal (Hypothesis 2). Our findings did not show that dispersing males had increases in either hormones, but resident males had elevated fGCM levels after an immigration and elevated fARM levels before an emigration occurred. However, this effect in resident males but not in dispersers may be due to a small sample size of fecal samples for dispersing males.

Adult males engaging in secondary dispersal timed their movement with the conception season in females, while subadult natal males transferring for their first time did not. Other primate 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 (Young et al., 2019). Although adult vervet males in our study appeared to time their secondary dispersal with female conceptions, we did not examine whether this was associated with increased access to females and increased paternity in the group. Furthermore, males engaging in natal dispersal may not yet have the competitive ability to directly move into a group during the conception season, which is likely a period of increased intrasexual competition between males for access to mating. Social costs of dispersal when entering a new group may be higher for subadult males during this mating period, which may be why they would transfer at other, potentially sub-optimal periods. In the highly seasonally breeding primate Verreaux's sifaka, Leimberger & 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. This difference may be due to the degree of breeding seasonality: while species in the

above-named studies have a high degree of breeding seasonality, our vervet study population has moderate breeding seasonality, with conceptions occurring throughout the year despite a more concentrated period between April and June. In contrast to our predictions, our results show that there is no variation in fruit availability at Lake Nabugabo, but our methods may not reflect reality adequately. The method used for this paper treated all trees equally. It did not take into consideration trees that would have higher fruiting potential. For instance, a score of 3 for ripe fruits on a *Maesopsis* and a score of 3 on a *Ficus* may not mean the same amount of fruit available for one tree because of the difference in the size of these trees (Peters et al., 1988). Also, we could not use tree diameter at breast height (DBH), which accounts for the size of each tree for which we assign a fruiting score, due to data gaps (see Chapman et al., 2005).

We also hypothesized that inbreeding avoidance may trigger individuals to disperse. Contrary to our prediction, subadult and adult male vervets did not disperse before the attainment of sexual maturity and age at first conception of potential daughters, respectively; however, they did disperse around these ages (i.e., the means did not significantly differ). These results differ from other primate studies that looked at inbreeding avoidance as a trigger of dispersal (Jack & Fedigan, 2004b; Lehmann & Perrin, 2003; Melnick et al., 1984), but are similar to results found in a South African population of vervets (Young et al., 2019). However, Young et al. (2019) suggest alternative mechanisms may be used for inbreeding avoidance in primates. The authors' propose 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 (Paul & Kuester, 2004), may reduce the risk of inbreeding while avoiding the potential costs of dispersal (Young et al., 2019). 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 also explain why two of our males remained for much longer in their group, both dispersing after 59 months of tenure.

Our prediction that a recent change in dominance rank (increase in subadult and decrease in adult males) may trigger dispersal was not supported. We did not find that Elo-trajectory, or a recent change in dominance before dispersal, was associated with dispersal for either subadult or adult males. Only two dispersing males had significantly increasing Elo-trajectories and increased

their ordinal rank by at least one position before dispersal, while no significant decrease in Elo-trajectories was found in other dispersers.

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. While eight of 11 males moved into groups with more favorable sex ratios, these improvements were not statistically significant. We found similar results for ordinal rank improvement, where four out of seven males improved by at least one position. Despite the degree of increase in rank not being statistically significant, improving rank by one position may still be biologically significant for a male to improve his mating success (Levy et al., 2020). These results are however different from several studies in other primates (white-face capuchins: Jack & Fedigan, 2004b; ursine colobus monkeys (*Colobus vellerosus*): Teichroeb et al., 2011; crested macaques (*Macaca nigra*): Marty et al., 2016), where all dispersing males would at least retain or improve their rank upon immigration. Considering males compete for access to females, those who dropped in rank following immigration are considered to have experience higher costs of dispersal than benefits. Looking at sex ratios is another way to evaluate a male's potential access to females. If there is a higher ratio of females per male in their new group, it may increase the chances of a male to mate with one or more females. This may be especially true for males who are coming in as an unfamiliar individual to the females (i.e., non-troop males, see Takahashi, 2001). Unlike Jack & Fedigan (2004b) who looked at rank and sex ratio change separately, we used log response ratios (Figure 3) to determine which males had the highest benefits from dispersal. Interestingly, no males simultaneously experienced a decrease in both rank and female-to-male sex ratio. Moving to a group with more favorable sex ratio may not provide the same reproductive benefits as maintaining a high rank. However, it is difficult to have a holistic view of the costs each male incurred from the dispersal event. For instance, as we did not follow these males for an extended period immediately following their immigration, we were not able to determine which males would benefit most from these changes. It would be interesting to look at the degree of reproductive success (using male mating access or paternity data from genetics) in dispersing males and compare it to their respective log response ratio scores. Regardless, timing their transfer with the conception season and moving to a group with a more favorable sex ratio may be the alternative used by most males to increase their mating and reproductive opportunities when improving in rank is not possible due to competition.

Contrary to our expectations, there was no significant change in fecal glucocorticoid metabolite (fGCM) levels in transferring males before they emigrated. Dispersing individuals have been documented to spend time outside of their group before emigration, prospecting to other groups, which is thought to be stressful as they do not benefit from group living during this period (e.g., protection from predators, social support: Kawazoe & Sosa, 2019; Leimberger & Lewis, 2015). An increase in fGCM levels during prospecting was observed in meerkats (Young & Monfort, 2009), but some researchers have not found support for this in some primate species (yellow baboons, *Papio cynocephalus*: Akinyi et al., 2017; anubis baboons, *Papio hamadryas*: Bergman et al., 2005; crested macaques: Marty et al., 2017). In our dispersing vervet males, fGCM may have remained stable before dispersal due to their stable access to fruits throughout the year, while also having access to human sources of food (Chapman et al., 2016). This could suggest that unsuccessful foraging is the main driver of elevated fGCM during dispersal (Lodge et al., 2013). Alternatively, this could be because some males in our sample did not prospect to other groups for sufficiently long periods of time for it to be reflected in fecal hormones. It could also be that because all our dispersals appear to be voluntary rather than involuntary (i.e., evictions), dispersing males did not receive increased aggression within the group before emigrating.

We also predicted that males immigrating to a new group and having to navigate new social relationships with unfamiliar individuals, in an unfamiliar area, would have increased fecal glucocorticoid metabolite (fGCM) levels due to the stress of a new socio-ecological environment. Contrary to findings in other species (Bergman et al., 2005; Marty et al., 2017), dispersing males in our population did not have higher fGCM levels after dispersal. However, we did find males in the target group to have higher fGCM levels within the first two months of receiving a new immigrant compared to their baseline before that event. This result is consistent with what Alberts *et al*. (1992) found in male yellow baboons. The fGCM increase may be due to shifting social dynamics during the immigration process of a new male. For instance, female primates rely on strong social bonds to cope with stress (Cheney & Seyfarth, 2009). This may also be true for males who compete with each other for access to females and rely on alliances with both other males and females to maintain their dominance status (Chapais, 1995; Watanabe, 1979).

We did not find evidence to support that males in our vervet population experienced any significant increase in fecal androgen metabolite (fARM) levels prior to or following dispersal.

This is in contrast to findings by Brockman et al. (2001) found in Verreaux's sifakas and Holekamp & Smale (1998) in hyenas (*Crocuta crocuta*). That said, we did find that fARM levels were higher in non-dispersing males before an emigration occurred compared to their baseline. A possible explanation could be that resident males experience elevated intrasexual competition with males that are about to engage in dispersal; this may be especially true if subadult males reaching sexual maturity are increasing copulation attempts with females during the period preceding emigration. Resident males may thus face increased competition for access to females, which would increase their fARM levels (Wingfield et al., 1990). However, in such a case, we would expect the dispersers to experience an increase in fARM levels as well, which they did not. Such an increase in non-dispersers but not in dispersers has never been observed in other populations or species, although Brockman et al. (2001) found resident alpha males to produce higher fARM responses when an unfamiliar male was visiting the group (before immigration). Finally, we did not find any difference between lone and parallel dispersers' fARM levels. This is in contrast with our prediction that lone dispersers would engage in higher rates of aggressive competition than parallel dispersers due to the lack of social partners upon immigration. However, most of our parallel dispersers were subadult males, meaning the difference between lone and parallel dispersers' fARM levels may simply be due to a difference in age (Onyango et al., 2013).

Collecting fecal samples on dispersing males proved to be quite a challenge. While our minimum goal at the Nabugabo Research Site was to collect two monthly fecal samples for each male, dispersing males often disappear from the group several days or weeks before emigration and are not always easily observed within the first days following immigration. For this reason, several of our subjects had only a few (or no) samples collected during the dispersing period (within $\pm$60 days of the dispersal date). Certain field conditions may also render the collection of such samples more challenging (e.g., wet season) (Higham, 2016). Marty et al. (2017), for instance, found in crested macaques that fGCM levels varied significantly within the first seven days of immigration, but stabilized right after. If this were the case in our vervet population, we would not have been able to detect this with the small number of fecal samples obtained.

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 seven 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, while we did not find support for some of our predictions, this may simply be a reflection of low statistical power.

When trying to evaluate how successful the males are following immigration, we ideally need to have extensive behavioral data on each male to determine how well they are doing in the group. Continuous focal samples are usually ideal for this because they allow us to determine how much focal males were involved in reproductive behaviors, and with how many females (i.e., mating success). Genetic data would also be quite useful, as we would be able to tell which male sired which offspring, giving us a good idea of their reproductive success compared to other males. While genetic samples are available, paternity analyses have not yet been conducted. Therefore, we were only able to speculate that those who increased in rank and moved to a group with a favorable sex ratio would *potentially* improve their reproductive success, and whether this was a result of their specific dispersal decision.

Another limitation comes from the field site at Lake Nabugabo being relatively young, having been established in 2011 for one study group, and 2016 for the remaining two study groups. This means we do not have exact birth dates or even birth groups for most individuals. The best we could do was to infer the age category (subadult, adult) of each individual and whether they were born in this group or not based on their age. For several of the early dispersal events from our dataset, we inferred the age-class of the males who transferred from observed behavior and the presence/absence of scars. Another problem is that we were only following one group between 2012 and 2016. This means any male coming from KS and HC groups to M group were of unknown

age. As such, we had a small sample sizes for our analyses on inbreeding avoidance and the timing of dispersal. In addition, subadult- and adulthood in primates are usually determined by age (e.g., Jack & Fedigan, 2004a; Leimberger & Lewis, 2015; Teichroeb et al., 2011) following methods for determining life-history stages using skeletal growth, dental eruption and wear, and physiology (Bolter & Zihlman, 2006; Harvey & Clutton-Brock, 1985; Turner et al., 1997). This poses a problem for us at the Nabugabo Research Site, due to the lack of known birthdates for several males. We have so far defined males as reaching adulthood once they emigrate from their natal group. This is a somewhat arbitrary definition that may affect our results significantly. For comparison, Jack & Fedigan (2004b) found subadult males to engage in secondary transfers at their field site with white-faced capuchins. By definition, only adult males could be considered to engage in secondary transfers at Nabugabo. Continued long-term research at the site will allow us to refine our definitions for different age classes.

5 | Conclusion

In the Nabugabo Research Site vervet monkey population, we found limited support for the first hypothesis stating that male dispersal will be triggered by specific individual, social and ecological factors. Only a few factors, such as timing with female conception seasonality and inbreeding avoidance, were supported by our data. The second hypothesis followed a similar pattern. We hypothesized that males would disperse in a way to minimize the costs and maximize its benefits as much as possible. Despite a few exceptions, most factors did not support this hypothesis. Overall, this study fails to reject the null hypothesis, and 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.

Dispersal is a behavior that is argued to provide significant reproductive benefits to transferring individuals (Bowler & Benton, 2005; Greenwood, 1980; Isbell & Van Vuren, 1996). It increases individual fitness through inbreeding avoidance and increase in reproductive opportunities. However, this may not be true for all individuals. What we attempted to do in this study is to use an individualized approach for analyzing the proximate mechanisms of dispersal in hopes of observing general patterns. But individuals vary significantly in their social relationships, behavior, and physiology. Cost and benefit asymmetries may be caused by the variation in individuals' social, ecological and individual context of dispersal. Studies of animal dispersal are especially complex when we consider the individual and its interaction with its socio-ecological environment. Studying this high inter-individual variation in dispersal is critical in understanding the proximate causes and consequences of dispersal (Jack & Isbell, 2009).

The findings presented in this study underline the importance of the context for each dispersal event. This research emphasizes how important it is to consider the individual, as they all have their unique traits and characteristics that influence how well they do in a social group, and it may very well make every dispersal event unique. Additional research will be needed to evaluate the male's access to females and their reproductive success using long-term continuous behavioral follows of individuals over a much longer period before and after dispersal. Genetic data would also have greatly improved this project to determine whether males who increased in rank and moved to a group with a favorable sex ratio had increased paternity, and to what degree compared to other dispersing males.

6 | References

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Appendix

Table A1
Dispersing males' Elo-trajectories 90 days before dispersal

Male ID	Age class	Transfer date	Elo-trajectory	Number of obs.	*Z* score	*P*-value
VNL	SAM	2018-05-31	27.589	6	6.419	< 0.001
SPT	AM	2018-05-01	12.739	9	2.964	0.003
PFY	SAM	2018-03-24	6.331	6	1.473	0.141
JN2	AM	2018-11-13	4.415	13	1.027	0.304
VP2	AM	2017-06-10	3.706	7	0.862	0.389
DBY	SAM	2019-09-04	3.146	19	0.732	0.464
PAC	SAM	2019-04-15	2.010	11	0.468	0.640
JAM	AM	2018-07-27	1.088	9	0.253	0.800
VCN	SAM	2018-10-15	0.296	69	0.069	0.945
VP3	AM	2019-08-18	0.216	23	0.050	0.960
PYT	AM	2018-07-13	0.079	19	0.018	0.985
RSL	SAM	2019-04-15	-0.041	18	-0.009	0.993
LIM	AM	2018-12-10	-0.084	16	-0.020	0.985
PUM	SAM	2018-07-09	-0.086	53	-0.020	0.984
HRX	AM	2019-05-16	-0.397	16	-0.092	0.927
PKN	SAM	2019-04-23	-0.402	19	-0.093	0.926
LEF	SAM	2018-02-19	-0.723	5	-0.168	0.867
POM	SAM	2017-11-23	-1.777	8	-0.413	0.680

Table A2
Results of the ANOVA testing the influence of mode of dispersal (parallel, lone), rank before emigration, and age category (SAM, AM) on **fGCM** levels.

Model	Sum Sq.	DF	*F*	*P*
(Intercept)	0.57	1	5.568	0.056
Mode	0.603	1	5.892	0.051
Rank	0.116	1	1.129	0.329
Age	0.018	1	0.178	0.688
Mode:Rank	0.601	1	5.871	0.052
Mode:Age	0.087	1	0.853	0.391
Rank:Age	0.019	1	0.195	0.674
Mode:Rank:Age	0.331	1	3.229	0.123
Residuals	0.614	6		

Table A3
Results of the ANOVA testing the influence of mode of dispersal (parallel, lone), rank before emigration and age category (SAM, AM) on **fARM** levels.

Model	Sum Sq.	DF	*F*	*P*
(Intercept)	1.047	1	12.907	0.011
Mode	0.235	1	2.895	0.139
Rank	0.124	1	1.528	0.263
Age	0.019	1	0.234	0.646
Mode:Rank	0.192	1	2.378	0.175
Mode:Age	0.006	1	0.077	0.791
Rank:Age	0.024	1	0.294	0.607
Mode:Rank:Age	0.043	1	0.531	0.494
Residuals	0.487	6		