

Partially shared consensus decision making and distributed leadership in vervet monkeys: older females lead the group to forage

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Abstract

Objectives: Group living can be advantageous, but for motile organisms, collective movements become necessary. We are just beginning to understand the many ways that animal groups make movement decisions and maintain cohesion. We examined start attempts and success in leading collective group movements in vervet monkeys (*Chlorocebus pygerythrus*) characterized by matrilineal groups and territoriality.

Materials and methods: We recorded 179 start attempts in a single group of vervets at Lake Nabugabo, Uganda and examined individual success in three situations (departing from sleeping site, moving to forage, returning to sleeping site) relative to dominance rank, age, and sex.

Results: Sex and age were associated with both the number of start attempts and success in leading group movements, but there was no effect of dominance rank. Older females were most successful at leading group movements, especially toward foraging sites, while adult and subadult males almost always led the group out of the sleeping site.

Discussion: Collective group movements in vervet monkeys appear to be based on distributed leadership and partially shared consensus decision making. Older females may be repositories of ecological knowledge, resulting in their success at leading the group to forage. Male motivation to lead the way out of the sleeping site appeared related to accessing human food sources before other group members. Young natal males achieved some success leading group progressions because they were motivated to make many initiations, which may be related to their life-stage. These results give us a better understanding of the processes underlying collective movements in cohesive animal groups.

KEYWORDS

age, cercopithecines, dominance, group progressions, sex

1 | INTRODUCTION

Many animal species live in groups because of the substantial benefits, such as reduction of predation risk (Bertram, 1980; Hamilton, 1971; Pulliam, 1973) and improved foraging opportunities (Bertram, 1978; Cody, 1971; Wrangham, 1980; Ward & Zahavi, 1973). To maintain the advantages of group living, motile animals must coordinate their behavior and come to some consensus on the timing and direction of movements (Conradt & Roper, 2010). Animal groups use many different types of decision-making processes to optimize the benefits of gregari-

ousness (reviewed in: Fichtel, Pyritz, & Kappeler, 2011; Fischer & Zinner, 2011; Kerth, 2010). A variety of insects, birds, and fish utilize simple self-organization rules and coordination patterns to stay together (ants, Beckers, Deneubourg, & Goss, 1993; Couzin & Franks, 2003; Deneubourg, Aron, Goss, & Pasteels, 1990; birds, Ballerini et al., 2008; fish, Couzin, Krause, James, Ruxton, & Franks, 2002; Sumpter, Krause, James, Couzin, & Ward, 2008). For decisions made by consensus, group members must collectively choose between mutually exclusive options to synchronize behaviors (Conradt & List, 2009; Conradt & Roper, 2003). One individual (the leader in that particular situation)

initiates a movement and other group members decide whether or not to follow (Stueckle & Zinner, 2008; Petit et al., 2009). This leader may be quickly overtaken by other group members and may not be the one at the front, outside position as the group moves. Consensus decision-making appears to be a common phenomenon in animal groups (reviewed in: Kerth, 2010; King & Cowlshaw, 2009), however, group decisions may entail “consensus costs” for individuals (Conradt & Roper, 2010; King & Sueur, 2011). Consensus costs are the fitness costs that occur when consensus decisions differ from any individual's preferred decision, thus they may sacrifice their preferred destination to synchronize in time and movement with the other individuals in the group (King & Cowlshaw, 2009).

Leadership within a group may be concentrated in a single individual (“personal” leadership, unshared decision making, or despotism) or it may be distributed among several individuals (distributed leadership, shared decision making, or democracy) (Conradt & Roper, 2005; Leca, Gunst, Thierry, & Petit, 2003). In either case, it may be necessary for a critical mass of individuals to decide to follow the leader before the group will move (King & Sueur, 2011). Personal leadership is relatively rare in the Animal Kingdom (Petit & Bon, 2010), but for species that use it, leaders usually have a particular behavioral or physiological trait that causes them to act first or to be followed by others (King, Johnson, & van Vugt, 2009). Leaders may be dominant individuals in their group (*Papio hamadryas*, Kummer, 1968, 1995; *P. ursinus*, King, Douglas, Huchard, Isaac, & Cowlshaw, 2008; *Gorilla beringei beringei*, Watts, 2000; *Canis lupus*, Peterson, Jacobs, Drummer, Mech, & Smith, 2002), motivated by energetic needs (*Hylobates lar*, Barelli, Boesch, Heistermann, & Reichard, 2008; *Equus burchellii*, Fischhoff et al., 2007; modeled simulations, Rands, Cowlshaw, Pettifor, Rowcliffe, & Johnstone, 2003), or have a bold temperament (*Gasterosteus aculeatus*, Harcourt, Sweetman, Johnstone, & Manica, 2009; *Branta leucopsis*, Kurvers et al., 2009). Leaders may also be followed because they have the most knowledge in the group and thus others improve their survival and reproductive success by following them. For instance, in African elephants (*Loxodonta africana*), the oldest matriarch leads the group, seemingly because they are repositories of social and ecological knowledge (Foley, Pettoelli, & Foley, 2008; McComb, Moss, Durant, Baker, & Sayialel, 2001; McComb et al., 2011). Likewise in killer whales (*Orcinus orca*), post-reproductive resident females are more likely to lead collective group movements in years with poor food availability (Brent et al., 2015). These types of characteristics may also make certain individuals more successful in leading group progressions for species using distributed leadership (Dyer, Johansson, Helbing, Couzin, & Krause, 2009).

When leadership is distributed among several group members and consensus is achieved by others deciding whether or not to follow in each situation, movement decisions are more or less the average behavior of all the individuals in the group (Couzin, Krause, Franks, & Levin, 2005; King & Cowlshaw, 2009; Strandburg-Peshkin, Farine, Couzin, & Crofoot, 2015). Thus, individuals may suffer fewer consensus costs with distributed leadership compared with personal leadership because democratic decisions tend to yield less extreme decisions (Conradt & Roper, 2003). Distributed leadership seems to be more

prevalent among animals than personal leadership (reviewed in: Petit & Bon, 2010). For example, when choosing a new nest site, honeybee (*Apis mellifera*) scouts waggle dance (Seeley & Buhman, 2001; Visscher & Camazine, 1999) and ant workers tandem run to recruit other individuals (Franks, Pratt, Mallon, Britton, & Sumpter, 2002; Pratt, Mallon, Sumpter, & Franks, 2002). Both swans (*Cygnus cygnus*, *C. columbianus*, Black, 1988) and African buffalo (*Syncerus caffer*, Prins, 1996) use visual signals to vote and choose when and where to move after resting. In some primates, individuals initiating group movements will use a variety of vocalizations and behaviors to entice other individuals to follow them (e.g., *Cebus capucinus*, Boinski, 1993; Boinski & Campbell, 1995; Leca et al., 2003; *G. b. beringei*, Stewart & Harcourt, 1994) and baboons have shown evidence of compromise among individuals in the direction of group movements when conflicts occur (*P. anubis*, Strandburg-Peshkin et al., 2015).

In species using distributed leadership, there is variation in the number of leaders that may have success within a group (Conradt & Roper, 2005, 2007). In “equally-shared consensus decision-making,” all individuals in the group initiate collective departures with no significant difference in initiation attempts or success among group members (e.g., *Eulemur fulvus fulvus*, Jacobs, Maumy, & Petit, 2008; *Macaca tonkeana*, Sueur & Petit, 2008). While in “partially-shared consensus decision-making,” some individuals initiate more start attempts or are more successful than others. For instance, in rhesus macaques (*M. mulatta*), dominant and older individuals had more success in leading group movements (Sueur & Petit, 2008), while in geladas (*Theropithecus gelada*) group progressions were initiated by lactating females, but the dominant female and male decided whether or not the group would follow (Dunbar, 1983).

Collective group movements and patterns of leadership have not been studied in a wide range of primates using more recent, precise behavioral definitions, which may be why a lot of variability appears to exist in the order (reviewed in: Fichtel et al., 2011; King & Sueur, 2011). We examined collective movements in vervet monkeys (*Chlorocebus pygerythrus*) at Lake Nabugabo, Uganda to define which group decision-making processes they utilize. We recorded individual initiations of group movements (i.e., start attempts), the success of these attempts, and the sequence of the progression of individuals through movements in a single group of vervets over 40 days. Vervet monkeys are a matrilineal, female philopatric species (Struhsaker, 1967a). They are semi-terrestrial (Rose, 1979) and live in cohesive social groups that move together in a coordinated manner (Struhsaker, 1967a). Vervets often suffer from high rates of predation (Isbell, 1990) and group-living appears to be important to them as a predator avoidance mechanism (Seyfarth, Cheney, & Marler, 1980), as well as for improved range defense against other groups (Isbell, Cheney, & Seyfarth, 1991). We asked whether group movement decisions in vervet monkeys were made by a single individual (personal leadership) or whether these decisions were shared (distributed leadership)? If leadership was distributed within the group, was it equally distributed (equally shared consensus decision making), or were some individuals more successful than others (partially shared consensus decision making)? How do factors such as

TABLE 1 Adult and subadult composition of the vervet monkey study group

ID	Sex	Age	Dominance rank		Success index
			Absolute	Tier ^a	
PY	M	A	1		21.9
NM	M	A	2		20.07
OT	M	OS	3		30.67
CL	M	OS	4		29.21
JK	M	A	5		19.17
GT	F	OA	1	1	41.94
MA	F	A	2	1	17.03
TB	F	A	3	1	0
GR	F	OS	4	2	0
LP	F	A	5	2	22.72
LT	F	OS	6	2	12.78
RM	F	A	7	3	38.33
DT ^b	F	A	8	3	42.59
DG	F	YS	9	3	0
TS	F	OA	10	4	32.86
PT	F	A	11	4	17.03
PG	F	YS	12	4	0

OA = older adult; A = adult; OS = older subadult; YS = younger subadult.

^aAbsolute female ranks were harder to identify with subadults entering the hierarchy, so we decided to assign tier rankings to eliminate error.

^bHad a new infant at the beginning of the study.

rank, age, or sex impact leadership ability? Does the situation (leaving the sleeping site, going to forage, returning to the sleeping site) affect which individual is most likely to initiate a departure and whether they are successful? Finally, we asked whether participation by certain “key” individuals determined whether an initiation would be successful or not (e.g., Modlmeier, Keiser, Watters, Sih, & Pruitt, 2014)? Though a range of decision-making processes have been shown in primates, we predicted that vervets would show distributed leadership as have most of the cercopithecines examined and females were predicted to be more frequent leaders, as has been seen in several female-philopatric species (reviewed in: Fichtel et al., 2011; King & Sueur, 2011).

2 | METHODS

2.1 | Study site and subjects

This study was conducted with one wild group of vervet monkeys (*Chlorocebus pygerythrus*) located at Lake Nabugabo, Masaka District, Central Uganda (0°22'12"S and 31°54'00"E). Lake Nabugabo is a small satellite lake lying to the west of Lake Victoria, at an elevation of 1,136 m. The environment surrounding the lake is primarily wetland with a few forest patches. The west side of Lake Nabugabo includes some human-modified areas, like active farmers' fields, fallow fields, and several buildings. The vervet study group (M group) ranged through a human-modified area along the lakeshore with two primary

sleeping sites and a home range of approximately 5.61 ha (Teichroeb, White, & Chapman, 2015). The group was habituated to observers and comprised 25–28 individuals (3 adult males, 8 adult females, 1–2 subadult males, 4 subadult females, and 9–11 juveniles and infants) during the study (Table 1). All adult and subadult individuals could be recognized and identified by facial and body features, while identification of juveniles was less reliable. Changes in group composition during this study were due to two infant births and one natal subadult male who returned to the group after failing to transfer to a neighboring group.

2.2 | Data collection

The group was followed for 40 days (July–August 2014) for a mean of 7.17 hr per day (range 4.75–8.75 hr, median 7.5 hr) and all occurrences of start attempts (defined below) were collected (Altmann, 1974). Daily follows usually began prior to the monkeys leaving their sleeping site at 6:45 and ended when the monkeys returned to their sleeping site at approximately 17:30. Observers took a 2–3 hr break around noon when the monkeys would forage and rest high in the trees of the forest patches. During this time, the vervets rested or exhibited a “feed-as-you-go” manner of movement (Fichtel et al., 2011) where individuals could not be easily identified due to limited visibility. Indeed, start attempts were hard to discern and the individuals initiating them were difficult to identify whenever the group was moving through forest patches. We only retained data on start attempts when we could be absolutely certain that we had observed one, which usually occurred when the vervets were leaving a forest patch after resting or using open areas ($N = 179$).

Concurrent with data on start attempts, we collected instantaneous samples on individual spatial position and behavior every 15 min, and also noted whether the group as a whole was moving or stationary. Once the group was stationary (meaning that the position of the group did not move for at least one instantaneous scan—range: 15–29 min), we began watching for start attempts (individuals trying to initiate a group movement). An initiator had to move half the diameter of the group spread (approximately 10–15 m) after the stationary scan in a particular direction away from the group edge to give a start attempt. Though it was rare, an individual could initiate a new group movement when the group was already in motion if there was an obvious change in the direction ($>90^\circ$) from the current movement. The first individual consenting to the initiation (i.e., followers) had to travel in the same relative direction, moving behind the initiator within a 45° trajectory (Fichtel et al., 2011) within 15 min (Leca et al., 2003). Once the 15-min window had passed, if no individual(s) followed the initiator, then the start attempt was deemed failed, or unsuccessful. A successful start attempt was defined as a movement of at least 13 individuals, which was half of the group size (Erhart & Overdorff, 1999). This threshold ensured that the entire group would follow, though often quite slowly. Start attempts were also considered unsuccessful if the initiator returned to the original location within the 15-min window or if fewer than 13 individuals followed, meaning a displacement of the whole group did not occur. We followed Leca et al. (2003) in using the 15-min window because previous observations showed that this vervet

group often moved quite slowly from one area to another and we did not want to discard start attempts that would eventually be successful by using too short a time criterion. During sampling of group progressions, we also noted the date, time, location, initiator identity, first follower identity, the time it took for the first individual to follow (first follow latency period), order of subsequent followers, identity of sequential followers, and return time, if applicable. Group movements were further categorized by the purpose for which they occurred. For this study, three non-mutually exclusive situations were identified: departing from the sleeping site in the morning, moving to a new foraging location, and returning to the sleeping site in the evening. These situations were defined for each progression based on the location of the group, the direction of travel, the behavior after the progression, and the time of day that the movement took place. Though foraging could have occurred upon leaving and entering the sleeping site, we analyzed these situations separately because they involved another purpose and thus could have revealed different patterns of leadership. *Ad libitum* data were collected on social behaviors, such as grooming, mating, aggression, displacements, or vocalizations whenever observers were with the group (Altmann, 1974).

For analyses, we classified the age categories of individuals (Table 1) as follows: For males, the age classes were adult (non-natal) and older subadult (natal) based on body size and known place of origin. There were no younger subadult males in the group at the time of the study. For females, the age classes used were older adult, adult, older subadult, and younger subadult (Table 1). Infants and juveniles did not make initiation attempts. The study group has been followed continuously since 2011 (C.A. Chapman, unpubl. data), so we knew the date of birth for some subadult females, and the transition from subadult to adult had been observed for others. However, the relative age of some females had to be estimated. This was done for the "older adult female" category, where two females were placed based on their traits that are characteristic of old individuals (i.e., wrinkled and sagging facial skin, long and pendulous nipples, and stiff limbs leading to slow gaits and limps) (modified for vervets from: Borries, Sommer, & Srivastava, 1991; Strum & Western, 1982).

The dominance relationships of the adult members of M group were assessed during the 40 follow days of this study (average follow: 7 hr) based on agonistic interactions (aggression and/or submission) collected *ad libitum*. These were compared with dominance relationships that had been established in previous years of observation (2012 and 2013) to determine changes due to immigrations, emigrations and the maturation of individuals. Male dominance rankings were obvious due to consistent agonistic interactions. However, the use of coalitions by females meant that changes to their dominance rankings were not always as obvious. Thus, to avoid inaccuracies in analyses of the impact of female dominance rank on success in leading group progressions, we binned females in tiers of dominance ranks (Table 1).

2.3 | Data analysis

To determine if leadership was concentrated in one or a few individuals or if it was distributed among all group members, we used G-tests of

goodness-of-fit. Observed numbers of start attempts and successful instances of leadership were compared with even expected values (the mean of start attempts and mean of successful attempts, respectively) for all adult and subadult members of the group.

We ran a Spearman correlation on the proportion of start attempts and the percentage of successful attempts for individuals to determine if those that made many start attempts achieved success more often (Leca et al., 2003). We used Generalized Estimating Equations (GEEs) to examine influences on success in leading group progressions overall and when the group was moving to forage (Ghisletta & Spini, 2004). GEEs were chosen over linear mixed models because they tend to be more conservative (Walker et al., 2009). For our first GEE, we investigated the factors determining overall success in leading group progressions. The dependent variable in our model was success index for each individual, which was calculated following a measure used by Leca et al. (2003). Due to a large number of start attempts by some individuals and few by others, it was necessary to weight the success rates of all individuals by multiplying by a constant ratio (success rate of all group members).

$$\begin{aligned} \text{Success index} &= \text{Rate}_{\text{Successful attempts per individual}} \\ &\times \text{Rate}_{\text{Successful attempts for group}} \times 100 \\ &= \frac{\text{No. of successful start attempts}}{\text{No. of start attempts}} \\ &\times \frac{\text{Total no. of successful start attempts}}{\text{Total no. of start attempts}} \times 100 \end{aligned}$$

Since success index did not differ from a normal distribution (Shapiro-Wilk test, $p = .182$), a linear distribution was used in the GEE. A power analysis was run to ensure that the sample size of 17 individuals was sufficient for the analyses. The power of the test decreased with an increasing number of independent variables so we minimized these (i.e., addition of one extra independent variable decreased the power of the test by 11% for the same effect size). The independent variables were dominance rank and the interaction between sex and age (because we were interested in the success of different age-sex classes). Individual ID was included in the model as a random factor. The power of the GEE, where larger numbers indicate a low probability of a Type 2 error, was 68% to determine an effect size (minimum deviation from the null hypothesis) of 35%. Post hoc analyses to determine the direction of relationships between age and dominance rank on success indices and the proportion of start attempts were performed with Spearman correlations because these were ordinal variables. For these analyses on dominance rank and success indices, statistics on males and females were run separately because they had sex-specific dominance ranks. Since sex is a categorical variable, post hoc analyses on sex versus the proportion of start attempts and success indices were done using point biserial correlations.

Another GEE was used to examine the influence of age, sex, and dominance rank on the success or failure of each start attempt when the group was moving to forage. The dependent variable was the success or failure of each start attempt, so a binary logistic distribution was used. A power analysis was run to ensure that the sample size of 131 was sufficient for the analyses. A larger sample size meant that more independent variables could be added to the GEE model. The

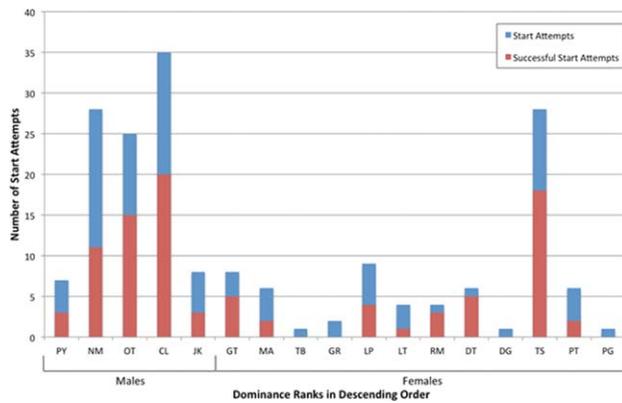


FIGURE 1 The number of start attempts versus the number of successful start attempts for all adult and subadult individuals in the vervet group with individuals plotted in descending order dominance ranks within sex

independent variables used were dominance rank, age, sex, and the interaction between sex and age. The power of the GEE was 97.3% to determine an effect size (minimum deviation from the null hypothesis) of 15%. Individual ID was included as a subject variable in the model to account for repeated observations on the same individuals over time. We calculated the odds ratio for the variable of sex from the parameter estimates of the GEE to determine the odds of a successful female start attempt in a foraging situation versus that of a male. Sex-specific post hoc analyses on dominance rank and success indices (as described above) for each individual in a foraging situation were done using Spearman correlations because dominance hierarchies were sex-specific. For the second and third group movement situations that we identified, returning to the sleeping site and departing from the sleeping site, power analyses showed that the sample sizes were too small to run GEEs, so we provide some descriptive analyses below.

In our final analyses, we used three different metrics to determine if particular individual(s) were “key” to the success of group movements, meaning that the group was unlikely to move if this individual did not join the progression. We compared individuals to first see: (1) whether they were involved in few unsuccessful progressions; and after they joined a progression, (2) the latency of their first follower, and (3) the mean number of followers they had within the first minute. We rationalized that “key individuals” should not be involved in unsuccessful movements often and should have many others quickly follow them when they decided to join a group progression. Analyses were two-tailed with $\alpha = 0.05$ set for significance. G-tests were done with the Handbook of Biological Statistics (McDonald, 2009; <http://www.biostathandbook.com/gtestof.html>), and other tests were performed in SPSS/PASW (IBM Corp, Version 22.0, Armonk, NY) and R 3.2.2 (R Core Team, 2015).

3 | RESULTS

3.1 | Personal or distributed leadership?

A total of 179 discrete start attempts were collected. The number of start attempts per individual was skewed with a range of 1–35 and a

median of 6 start attempts per individual ($\bar{x} = 10.5$, $SD = 11.0$). The G-test of goodness-of-fit examining observed start attempts versus even expected values (10.5 start attempts per individual) was significant ($G = 167.9$, $df = 16$, $p < .0001$), indicating that start attempts were not evenly distributed among individuals (Figure 1).

Of 179 start attempts, 92 were successful (51.4%). The number of successful start attempts per individual was skewed with a median of 3 and range of 0–20 ($\bar{x} = 5.4$, $SD = 6.5$). Successful start attempts were also not evenly distributed among individuals (Figure 1). The G-test of goodness-of-fit comparing the frequency of successful start attempts for each individual to an even number of expected successful attempts (5.4 per individual) was significant ($G = 119.4$, $df = 16$, $p < .0001$). After unsuccessful start attempts ($N = 87$), where initiators had no or few followers, they would generally return to the group or join the group as it moved in another direction ($N = 10$).

3.2 | Patterns of dominance rank, sex and age

For individuals, the proportion of start attempts and the percentage of successful attempts were correlated (Spearman, $N = 17$, $r_s = 0.63$, $p = .006$) indicating that the more an individual attempted to lead group movements the more likely it was that they would be successful. The results of the first GEE showed that individual success index was significantly affected by the interaction of sex and age (Wald $\chi^2 = 37.6$, $df = 1$, $p < .0001$, $\beta = -4.72$, $SE = 0.77$). The negative parameter estimate indicated that the effect of sex on success index was stronger than the effect of age. Post hoc analyses showed that although males had higher proportions of start attempts (Point biserial, $N_{\text{males}} = 5$, $N_{\text{females}} = 12$, $r_{pb} = -0.61$, $p = .009$), they were not more successful than females ($N_{\text{males}} = 5$, $N_{\text{females}} = 12$, $r_{pb} = -0.21$, $p = .409$) (Figures 1 and 2). Age was not correlated with the proportion of start attempts (Spearman, $N = 17$, $r_s = -0.435$, $p = .081$), but older individuals were more successful ($N = 17$, $r_s = -0.557$, $p = .02$) (Figure 2). In terms of age–sex classes, this translated into older adult females showing the highest mean success indices (32.4, $N = 2$) relative to other age–sex classes (adult females: 23.0, $N = 6$; older subadult females: 6.3, $N = 2$; young subadult females: 0, $N = 2$; adult males: 20.4, $N = 3$; older

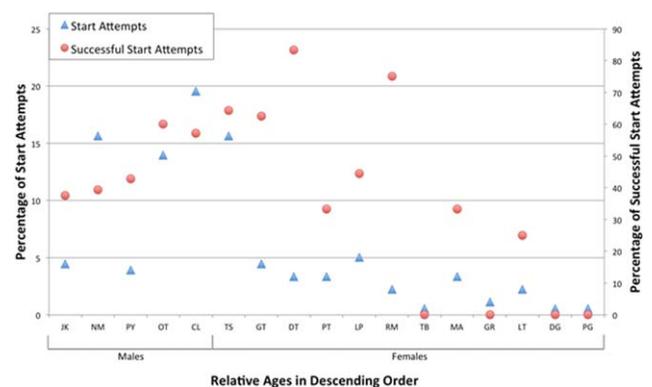


FIGURE 2 The percentage of start attempts for each individual plotted with their percentage of successful start attempts. Individuals are organized in order of age from oldest to youngest, within sex

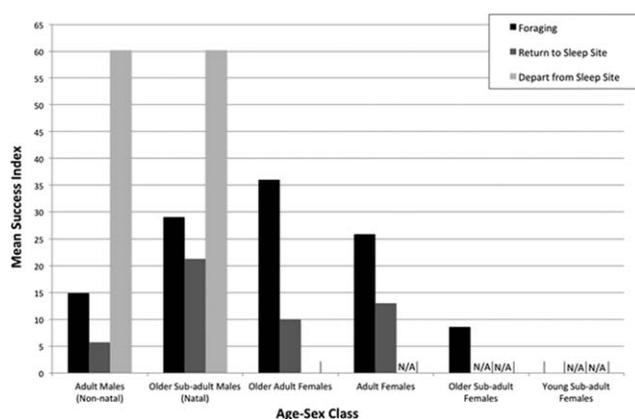


FIGURE 3 The mean success indices for each age–sex class in the three different movement situations. Lack of a bar indicates a true zero (individuals tried to lead in those contexts, but were unsuccessful), while N/A indicates that there were no start attempts for that age–sex class

subadult males: 29.9, $N = 2$) (Table 1 and Figure 2). The GEE showed that overall, individual success indices were not influenced by dominance rank (Wald $\chi^2 = 1.1$, $df = 1$, $p = .288$, $\beta = 2.04$, $SE = 1.92$). Sex-specific post hoc tests on dominance rank showed that it was not correlated with the proportion of start attempts (Spearman, males: $N = 5$, $r_s = 0.3$, $p = .624$, females: $N = 12$, $r_s = -0.011$, $p = .977$) or with success index for either sex (males: $N = 5$, $r_s = -0.2$, $p = .747$, females: $N = 12$, $r_s = 0.143$, $p = .657$) (Figure 2).

3.3 | Influence of situation

Start attempts toward new foraging areas were successful 51.1% of the time ($N = 67/131$). The success of start attempts toward new foraging areas ($N = 131$) was influenced by age with older individuals being more successful (Wald $\chi^2 = 60.2$, $df = 1$, $p < .0001$, $\beta = 2.37$, $SE = 0.31$), as well as sex (Wald $\chi^2 = 81.0$, $df = 1$, $p < .0001$, $\beta = 4.21$, $SE = 0.47$) and the interaction between sex and age (Wald $\chi^2 = 55.8$, $df = 1$, $p < .0001$, $\beta = -1.67$, $SE = 0.22$). The odds ratio calculated from parameter estimates in the GEE showed that the odds of a female start attempt being successful during foraging were 67.2 times greater than for a male. In terms of age–sex classes, the oldest adult females showed the highest mean success indices (40.0, $N = 2$) relative to other age–sex classes (adult females: 23.0, $N = 6$; older subadult females: 0.09, $N = 2$; young subadult females: 0, $N = 2$; adult males: 14.9, $N = 3$; older subadult males: 29.0, $N = 2$) (Figure 3). In the GEE, there was no overall effect of dominance rank on the success of start attempts during foraging (Wald $\chi^2 = 0.6$, $df = 1$, $p = .447$, $\beta = 0.05$, $SE = 0.07$). Sex-specific post hoc analyses revealed that dominance rank did not influence success indices for either males or females in this situation (Spearman, males: $N = 5$, $r_s = 0.5$, $p = .391$, females: $N = 10$, $r_s = 0.283$, $p = .419$).

When the group was returning to their sleeping site in the evening, 40% of start attempts were successful ($N = 12/30$). In this situation, 63.3% (19/30) of start attempts were by males (older subadult: 36.6%, adult: 26.7%), while 36.7% (11/30) of start attempts were by females

(adult: 13.3%, older adult: 23.3%). Older subadult males had the highest average success index of 21.3 ($N = 2$) (Figure 3). Success index in this situation was not correlated with sex (Point serial, $N_{\text{males}} = 4$, $N_{\text{females}} = 5$, $r_{pb} = -0.06$, $p = .884$), dominance rank (Spearman, overall: $N = 9$, $r_s = 0.46$, $p = .213$, males: $N = 4$, $r_s = 0.6$, $p = .4$, females: $N = 5$, $r_s = 0.354$, $p = .559$), or age ($N = 9$, $r_s = 0.303$, $p = .427$).

When the group was leaving their sleeping site in the morning, a higher percentage of start attempts (72.2%, 13/18) were successful. Most start attempts (94.4%, 17/18) were by adult (55.5%) and older subadult (38.9%) males. The one female that attempted departure from sleeping site was unsuccessful, while overall mean male success index in this situation was 60.2 ($N = 4$ males) (Figure 3). Post hoc correlations could not be run on sex due to the small sample size of females. Dominance rank (Spearman, $N = 5$, $r_s = 0.436$, $p = .436$) and age ($N = 5$, $r_s = 0.433$, $p = .467$) showed no correlation with success index when leaving the sleeping site. Sex specific analyses with dominance rank were also not possible due to low sample size.

3.4 | Key individuals

No single individual emerged as key to the success of group progressions. Three females were involved in a very low number of unsuccessful progressions (more than one standard deviation below the mean). These were adult female LP, adult female DT, and her subadult daughter DG. The shortest mean latencies for followers to join an individual in a progression were seen for two other adult females, alpha female GT (1.125 s) and low-ranking adult female PT (1.25 s). The individuals with greatest mean number of followers within 1 min of joining a progression were alpha female GT (2.39) and subadult female DG (2.31).

4 | DISCUSSION

Our results show that group progressions in vervet monkeys at Lake Nabugabo, Uganda are based on distributed leadership (Leca et al., 2003) and partially shared consensus decision making. Group progressions were not led by a single individual nor were only a few individuals successful. Instead, all adult and subadult group members attempted to lead group progressions at least once during the course of the study and many were at least occasionally successful. Partially shared consensus decision making (Conradt & Roper, 2005) has been used to describe circumstances in which unsuccessful initiators would return to the group and unsuccessful start attempts were common (Stueckle & Zinner, 2008), as we observed in vervets. The fact that unsuccessful initiators return to the group implies that a threshold number of group members have to agree to move in order for the start attempt to be successful. This system of distributed leadership and partially shared consensus decision making should mean that consensus costs are not extreme for individual vervets within the study group, even when they are not the leader, because relatively democratic decisions on the timing and direction of group movements should result (Couzin et al., 2005; King & Cowlishaw, 2009).

Juveniles were never seen to make a start attempt and the more other individuals tried, the more likely it was that they would be

successful. This indicates that motivated individuals may have a large influence on group movement decisions in vervet monkeys. Similar results were found for chacma baboons (*Papio ursinus*, Stueckle & Zinner, 2008); however, no relationship between start attempts and success was identified for white-faced capuchins (*Cebus capucinus*, Leca et al., 2003). In general, male vervets attempted group progressions more frequently than females (with the exception of the oldest female). Indeed, we found that all five adult and subadult males led at least one successful movement, while there were four young females who never led a successful progression. Some males may have ended up leading more often than some females because they were persistent in trying. Overall, however, females had fewer unsuccessful attempts in comparison with males, a result that has also been found in some (e.g., *Panthera leo*, Schaller, 1972; *Crocota crocuta*, Holekamp, Boydston, & Smale, 2000; *Cebus capucinus*, Leca et al., 2003; *Propithecus verreauxi*, Trillmich, Fichtel, & Kappeler, 2004; *Eulemur rufifrons*, Pyritz, Kappeler, & Fichtel, 2011; primates reviewed in: Erhart & Overdorff, 1999; Kappeler, 2000), but not all (e.g., *Papio ursinus*, King et al., 2008; Stueckle & Zinner, 2008; *P. anubis*, Strandburg-Peshkin et al., 2015), female philopatric species.

We found that female vervets in our oldest age-class were the most successful in leading the group overall, especially when movements were toward foraging areas. For the females, age was a predictor for how many progressions they attempted and for how many were successful. It is possible that young females begin learning how to lead progressions with foraging situations. Young subadult females only attempted to lead group movements while foraging, and made no attempts to lead when departing and returning to the sleeping site. As age class increased for the females in our dataset, they became more successful at leading group progressions, especially when movements were toward new foraging areas. Similar to elephants and killer whales (*Loxodonta africana*, Foley et al., 2008; *Orcinus orca*, Brent et al., 2015), older female vervets may be repositories for long-term ecological knowledge and experience may play a large role in successfully leading group progressions. Vervet monkeys are female philopatric and at Lake Nabugabo they are quite territorial, defending a small (5.61 ha, Teichroeb et al., 2015) and almost exclusively used range. Therefore, the oldest females in the group should have the longest-term knowledge of the best, safest food sites and seasonal patterns of food availability. An alternative hypothesis here would be that group movements are structured by kinship in vervets and older females have the most relatives in the group and thus generate the most followers when they move (King & Sueur, 2011). Without data on kinship, we are currently unable to test this alternative hypothesis. However, the importance of experience is further supported by our data in that subadult females and non-natal males, who are somewhat lacking in experience, were the least successful in leading group progressions.

Female leadership in some other species has also been suggested to be due to female energetic and nutritional needs (primates: Barelli et al., 2008; Boinski, 1991, 1993; Erhart & Overdorff, 1999; Pyritz et al., 2011; equids: Fischhoff et al., 2007). Females may initiate travel to new food sites because they are limited by food to maximize their

reproductive success (Trivers, 1972) and pregnancy and lactation are energetically costly. When start attempts are successful, females may be able to control the destination (and thus the food source), how long the group travels, and the time they spend at that food source (Erhart & Overdorff, 1999). By this hypothesis, it would be expected that lactating females would be the most motivated to make start attempts because lactation is generally more energetically costly than pregnancy (Butte & King, 2005). We did not explicitly test for the effect of female energetic needs with our data set but the most elderly female in the group, who was not lactating at the time of the study, showed the most start attempts of all the females.

As with females, age was an excellent predictor for how many times males attempted group progressions and for their success, but in the opposite direction as the female pattern. Natal subadult males attempted many group progressions and were more often successful than older, immigrant males. This observation may be explained by the life-stage of these subadult males. This is the age when males often increase their risk-taking and sensation-seeking behaviors (Romer, 2012; Setchell & Lee, 2004) and attempts to get the group to move may be motivated by attraction to other vervet groups on the edge of the range to assess dispersal and future mating opportunities (van Noordwijk & van Schaik, 2004). Alternatively, the observation that subadult males were often successful at leading group progressions could be explained by the fact that they are natal and thus grew up in their current home range. They knew the range relatively well and have also kin in the group, thus these factors could explain subadult natal males having more successful initiation attempts than adult immigrant males, who neither have kin in the group nor long-term range knowledge. In opposition to this hypothesis are the facts that subadult females are also natal and have kin in the group but they had the lowest rates of attempts and success in leading group progressions. Therefore, we propose that the motivation and sometimes success of subadult males was best explained by their life-stage.

Males (both adult and subadult) almost exclusively led the group out of their sleeping site in the morning. Very often, the first visited area by these males was a compost heap used by a local hotel, which was near the main sleeping site. Thus, the motivation for these males to leave the sleeping site appeared to be gaining access to a feeding area with easy to acquire, calorific human food before other group members. The same pattern was noted during feeding experiments on this same group of vervets (Teichroeb & Chapman, 2014). When experiments were set up and baited near the sleeping site, adult and subadult males left the sleeping trees at first light to gain access to the rewards available at experimental sites before others in the group could approach. By being first out of the sleeping site and moving to a new foraging location, these initiations technically involve two of the situations we identified. However, it is notable that initiations out of the sleeping site showed a different pattern of leadership in regards to sex than movements to new foraging areas during the course of the day. Initiations out of the sleeping site had the highest probability of being successful (72.2%), regardless of who initiated them, because on most days, the group would leave the sleeping site at around the same time.

Thus, these initiations may not be as important in showing patterns of leadership for vervets compared with initiations in other situations, where the probability of success was much lower.

Unlike some other species (e.g., *Gorilla beringei beringei*, Schaller, 1963; *Helogale parvula*, Holekamp et al., 2000; *Canis lupus*, Peterson et al., 2002), dominance rank was not related to either the number of start attempts or the rate of successful start attempts for vervets at Nabugabo. The highest-ranking individual in the group, the alpha male, attempted the least number of start attempts compared with all other males and was only moderately successful. In comparison, the highest-ranking female was quite successful at leading group progressions. However, because she was also an older individual, her age and sex may be confounding variables giving her long-term residency and multiple kin. (Note that, due to the matrilineal dominance system in vervets, age and dominance rank were not related overall.) In several other animal species, dominance rank has also been shown to have no effect on leadership success (e.g., *Anser indicus*, Lamprecht, 1992; *Taeniopygia guttata*, Beauchamp, 2000; *Cebus capucinus*, Leca et al., 2003; *P. anubis*, Strandburg-Peshkin et al., 2015)

Our results are almost perfectly in-line with the observations of vervet group progressions published more than 40 years ago by Struhsaker (1967b). He found that some, but not all, individuals made start attempts and achieved success in leading progressions. Juveniles were never seen to make start attempts. Dominance did not predict success and three individuals were more successful than chance, two adult females and one older, peripheral subadult male. Older individuals appeared to attempt progressions and be successful more often than others suggesting the importance of experience.

Though previous research has shown that certain keystone individuals can have a disproportionate effect on group dynamics (reviewed in: Modlmeier et al., 2014), either because they are more informed (e.g., Dyer et al., 2009) or have a certain personality or temperament (e.g., Briard, Dorn, & Petit, 2015; Harcourt et al., 2009; Kurvers et al., 2009), our analysis did not demonstrate that a single individual in our vervet group could be considered vital to the success or failure of a group progression. To qualify as a “key” individual in our study, he or she had to have been involved in few unsuccessful progressions and have a large number of followers within a short amount of time after joining a progression. Although there was no individual that satisfied all of these criteria, it is interesting to note that the individuals who qualified for any of these conditions were all female. This appears to reinforce our earlier conclusion that the natal female core of the group drives group movements to a greater degree than males.

This study and the results of previous research on the same group (Teichroeb et al., 2015) further reiterate that those individuals that initiate successful collective movements (i.e., leaders) may not be the same as those that maintain spatial positions at the front, outside edge of moving groups. Three of the four adult females with the highest success indices in leading group progressions in this study (carried out in 2014) were not those found consistently at the front of the group as it moved in 2012. Two of these females were found in the center of the group and one was found in the rear of the group most frequently (Tei-

chroeb et al., 2015). Thus, these females may often be leading from positions in the center or the rear of the group. Once the group decides to move and follow a specific initiator, other individuals can quickly overcome the group member that started the initiation; an observation also made by Struhsaker (1967b) in his vervet study group. This reinforces the notion that spatial position and the initiation of collective movements must be examined as separate phenomena.

Future research can help us gain a better and more comprehensive understanding of group progressions in vervet monkeys. We did not assess the use of vocal and behavioral signals that may be used in the pre-departure period to coordinate group progressions (reviewed in: Petit & Bon, 2010), however these may be occurring. In addition, although we did not explicitly test this notion, we noted that the success of leaders may be affected by infant status. Female vervets, other than the mother, have intense interest in infants and infant-handle at high rates (Fairbanks, 1990). During this study, two infants were born; one at the beginning of data collection and the other close to the end. The female who gave birth near the beginning of the study (*DT*) had the highest overall success index in the group. For the other female (*TB*), we collected limited data that seemed to show a causal relationship between the presence of an infant and the success of her leadership. *TB* was normally unsuccessful in leading group progressions, but after her infant was born, the number of individuals that followed her within 1 min increased. Future work to evaluate the effect of infant status would need to assess multiple females before and after infant births.

In conclusion, we found that vervet monkey collective group movements follow a pattern of distributed leadership and partially shared consensus decision making. Older female vervets had the greatest success in initiating successful group movements, especially when the group was moving toward new foraging areas. No effect of dominance rank on leadership ability was detected but motivated individuals seemed to be able to gain some success by making repeated start attempts. This study only examined patterns of leadership in a single group that happened to have some older adult females present. It would be informative to examine the determinants of leadership success in other vervet groups with varying age structure to see if this pattern is ubiquitous in this species.

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