

INDIVIDUAL FACTORS PREDICTING THE DISAPPEARANCE AND
REPRODUCTIVE SUCCESS OF VERVET MONKEYS (*CHLOROCEBUS*
PYGERYTHRUS)

MEGAN A. SCHWEGEL

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Abstract

Social network analysis (SNA) is an increasingly popular method of quantifying social interactions and relating these to individual characteristics. However, few studies have considered how demographic events influence social networks and how social position affects fitness among species that live around humans. Using the gambit of the group and proximity data, I performed SNA on vervet monkeys to determine how social centrality predicted which individuals were more likely to disappear and to have infants that survived past one year. Older males with a lower or decrease in social centrality were more likely to disappear, where older males were more likely to emigrate, and individuals who decreased in their eigenvector centrality were more likely to have a human-related death. Females with a greater betweenness tended to have greater infant survival rates. Overall, emigration was influenced by natural history while human-related disappearances and reproductive success were mediated by social position.

Keywords: Dynamic social network analysis, human-modified landscape, primates, dispersal, death

Dedication

I dedicate this thesis to my family and friends whose humour and support allowed me to thrive while working on this paper. I would also like to dedicate this work to the fauna that kept me entertained throughout this process: the vervet monkeys at Lake Nabugabo, whose shenanigans I got to observe in person and through the behavioural data, the neighbourhood fox, coyote, and red-tailed hawk who made the occasional appearance outside the window of my workspace, and most importantly my cat, Smudge, who started this program with me but wasn't around to see the end. You are missed.

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1.0 General Introduction

1.1 Background Information

The survival and reproduction of animals depends on their interactions with conspecifics (e.g., mating, cooperation, competition) (Thompson 2019), other species (e.g., predation, symbiosis, competition), and the biotic and abiotic aspects of their physical environment (e.g., food availability, weather) (Alberts 2019). Consequently, it is critical to understand the interactions between animals and these social and ecological aspects of their environment. Describing social structure and social interactions of species has been a topic of research for several decades (Struhsaker 1967a; Hinde 1976). Recently, more studies have started using social network analysis (SNA) as a tool to quantify these conspecific interactions and perform hypothesis testing (Wey et al. 2008; Croft et al. 2011; Farine and Whitehead 2015). While some studies have started using dynamic SNA to investigate changes in social structure over time (Borgeaud et al. 2017; Farine 2018; Larson et al. 2018), including in response to demographic changes (Shizuka and Johnson 2020), few studies consider wild populations of species that live near humans (e.g., Morrow et al. 2019). Proximity to humans may change social interactions, such as how female bonnet macaques (*Macaca radiata*) tend to direct more aggression to others and have more reciprocal, albeit fewer, affiliative interactions while feeding on tourist handouts and human refuse rather than on natural foods (Ram et al. 2003). Likewise, provisioning may benefit individuals, such as by increasing reproductive success through greater birth rates and lower infant mortality (Takahata et al. 1998), while also potentially generating human-wildlife conflict that may lead to individual harm or death (Chapman, Twinomugisha, et al. 2016). To fill this knowledge gap, I investigated the consequences of social network position on natural and

human-related demographic events and reproductive success in a wild population of vervet monkeys (*Chlorocebus pygerythrus*) living in a human-modified environment.

Social structure is inherently important because it underlies the advantages and disadvantages of sociality, and specifically for group-living. For many species, group-living is an important adaptive strategy to increase the survival and reproductive success (i.e., fitness) of individuals by incurring overall greater benefits relative to potential costs (Alexander 1974; Krause and Ruxton 2002). For group-living individuals, the benefits of associating in groups, which may include improving resource defence through cooperation with other group residents (Wrangham 1980), reducing predation risk (Hamilton 1971; Chapman and Chapman 1996), facilitating finding mating partners, and improving energy conservation (reviewed in Krause and Ruxton 2002), outweigh the costs, such as greater competition among co-residents (Janson and Goldsmith 1995) and increased risk of disease transmission (Freeland 1976; González-Hernández et al. 2014). While all individuals living in a group receive net benefits, not all individuals receive the same benefits or pay the same costs (King et al. 2008).

Sociality can be described using various nested categories. A society (*sensu* Kappeler and van Schaik 2002), social group (*sensu* Struhsaker 1969), or community (*sensu* Whitehead 2008) is defined as an aggregation (Whitehead 2008) of individuals who interact more with one another ($\geq 80\%$ of non-aggressive encounters) than with other conspecifics (Struhsaker 1969; Kappeler and van Schaik 2002). These aggregations are then subdivided into groups based on which individuals interact and associate preferentially within a society (Hinde 1976; Whitehead 2008). These groups describe the society's social structure (Kappeler and van Schaik 2002). Many papers refer to societies as (social) "groups" (e.g., Silk et al. 2003; Borgeaud et al. 2017); however, to distinguish between those animals who move together as a unit and are found in

relative proximity to one another at all times (society) from those individuals who are interacting or associating preferentially at a given time (group), I will be using the term “society” instead of “group” to describe a social group.

1.2 Social Position

Various environmental characteristics, such as the distribution of food, can influence the spatial positioning of individuals and as such affect which individuals have the opportunity to interact (Hinde 1976; Whitehead 2008). Thus, spatial and social networks often overlap and influence one another (Albery et al. 2020), yet they remain distinct. For example, dominance rank is often linked to social centrality. Dominance refers to the outcome of agonistic interactions between individuals with consequences for an individual’s access to resources (Drews 1993). Dominance can be defined at the dyadic and society levels, where dominance status refers to whether an individual is dominant or subordinate within a dyad, while dominance rank indicates an individual’s relative position within the society’s dominance hierarchy (Drews 1993). In primates, high-ranking society members tend to have more associations than low-ranking individuals (Schino 2001; Silk et al. 2003; Sueur, Petit, et al. 2011; Bret et al. 2013; but see Schoof and Jack 2014). While high-ranking individuals may be socially central, their spatial centrality can vary depending on context: high-ranking individuals may be spatially central at times, namely when the society is stationary, or they may be positioned peripherally, such as when foraging at the front of the society (Teichroeb et al. 2015).

Considering the distinction between spatial and social position, I defined “centrality” in reference to social centrality, or the individual’s relative importance (i.e., social position) within the society’s structure (Freeman 1979; Wey et al. 2008). Thus, an individual who is more central has a higher social position, where I use social position and centrality interchangeably and I

discuss dominance rank separately from social position. Social position is dependent on an individual's interactions and associations. Interactions are direct observations of affiliative or agonistic behaviours in which an individual influences the behaviour of another individual (Hinde 1976; Whitehead 2008), whereas associations are defined as social contexts, often quantified by spatial proximity, that usually foster interactions (Whitehead and Dufault 1999; Whitehead 2008). While associations do not involve direct observations of behavioural changes, associations are argued to be indicative of the strength of social ties, and thus a relevant measure of social centrality (Cords 1997).

In addition to spatial position enabling interactions, individuals exhibit preferences for social partners based on individual characteristics, such as dominance rank. High-ranking members tend to have more social partners since they have access to resources (e.g., food, space, social partners: Struhsaker 1967a), and may tolerate and share access with lower-ranking individuals in exchange for grooming or other benefits (Seyfarth 1977; Seyfarth 1980; Kapsalis and Berman 1996; Borgeaud and Bshary 2015). Because of this commodity exchange (based in Biological Market Theory: Noë and Hammerstein 1994), individuals presumably benefit most from social centrality because they gain social partners, and, in turn, indirectly gain access to food and/or space. As a result, social centrality and access to food and/or space are associated via dominance. Furthermore, similarly-ranked individuals may preferentially or more reciprocally associate with one another (i.e., have stronger, higher-quality ties: Seyfarth 1980; Silk, Altmann, et al. 2006; Mitani 2009; Silk et al. 2010a; Kalbitzer et al. 2017; but see Perry et al. 2008), in part because individuals tend to prefer associating with kin who are in turn similarly-ranked (Seyfarth 1980). Theoretically, individuals may prefer to associate with high-ranking conspecifics since those who are high-ranking may provide better coalitionary support (Seyfarth 1977) or allow

access to resources (Borgeaud and Bshary 2015), but there would be more competition to associate with high- than with mid- or low-ranking individuals (Seyfarth 1977).

Aside from rank, individual preferences also extend to kinship and age. Namely, individuals tend to form stronger ties with kin and will form a greater number of strong ties when more kin are present (Silk, Alberts, et al. 2006) because of indirect fitness benefits (Hamilton 1964). Similarly, age cohorts may tend to have stronger ties than unrelated individuals outside the age cohort because same-aged peers may share paternity when alpha males sire the most offspring (Altmann 1979; Alberts et al. 2006; Jack and Fedigan 2006; Muniz et al. 2010; but see: Silk, Altmann, et al. 2006; Minkner et al. 2018).

1.3 Social Network Analysis

Based on the SNA framework (Croft et al. 2011), social integration encompasses various metrics including: 1) degree centrality (i.e., number of social partners), 2) betweenness centrality (i.e., how often an individual acts as the most direct connection between other society members), 3) closeness (i.e., the extent to which an individual is closely connected to all other society members), and, more recently, 4) eigenvector centrality (i.e., the connectedness of an individual based on the number and strength of their own and their direct partners' ties), and 5) local clustering coefficient (i.e., the number of ties between an individual's direct partners) (Freeman 1979; Wasserman and Faust 1994; Wey et al. 2008; Sueur, Jacobs, et al. 2011; Voelkl et al. 2011; Farine and Whitehead 2015; Thompson 2019). In addition, social ties can be characterized by bondedness metrics that quantify how often dyads interact, such as tie strength or weighted degree centrality (Barthélemy et al. 2005; Wey et al. 2008; Thompson 2019). Ultimately, social centrality depends on the number of social partners, type of interaction (i.e., affiliative versus agonistic), and the strength of social ties (Crofoot et al. 2011; McFarland et al. 2017).

1.4 Vervet Monkeys

Vervet monkeys (*Chlorocebus pygerythrus*) live in multimale-multifemale societies and exhibit male-biased dispersal with female philopatry (Struhsaker 1967a; Cheney 1981). The female dominance hierarchy is determined by the matriline (Bramblett et al. 1982), while the male hierarchy is based primarily on competitive ability (McGuire 1982). The male dominance hierarchy has been differentially characterized as dominant (Struhsaker 1967a) or co-dominant to that of females (Lancaster 1971; Young, McFarland, et al. 2017). Given the hierarchies are formed by distinct mechanisms (McGuire 1982), I considered these hierarchies separately. I focused on three societies of vervet monkeys that live around Lake Nabugabo, Uganda in a human-modified environment. The field team has studied the Nabugabo vervets since June 2011, making them a good study population for considering both the differences between natural and human-driven demographic changes and fitness.

1.5 Objectives

In this thesis, I addressed two aspects related to the social networks of vervet monkeys. First, in section 3, I focused on how social centrality can be used to predict demographic changes within a society. Specifically, I compared individual factors, including age-class, sex, society membership, social network position, and dominance rank, among monkeys who remained within their society relative to those monkeys who disappeared by emigration or human-related modes. I also compared these factors between individuals who emigrated relative to those who died. In section 4, I focused on the fitness consequences of social centrality for females, where I explored whether a female's social position influenced the survival of her offspring to one year. The hypotheses and predictions from sections 3 (hypotheses 1-5) and 4 (hypothesis 6) are summarized in Table 1.

Table 1. Summary of hypotheses and predictions regarding sociality, disappearances, and reproductive success in three societies of vervet monkeys at Lake Nabugabo, Uganda. Hypotheses 1-5 are addressed in section 3 and hypothesis 6 in section 4.

Hypothesis	Prediction
1. Sex-specific philopatry and dispersal influence sociality	<ul style="list-style-type: none"> a) Males more likely to disappear from society b) Males less socially central than females, thus c) Individuals disappearing from society are less socially central
2. Male dispersals are voluntary and aimed at avoiding inbreeding	<ul style="list-style-type: none"> a) Older males are more likely to disperse b) Those who emigrate will not differ in rank or static social position from those who remain c) Those who emigrate will not change in rank d) Those who emigrate will decrease in dynamic social centrality versus those who remain e) Those who emigrate will decrease in dynamic social centrality versus those disappearing otherwise f) Those emigrating (male-biased) will have a lower static social centrality on average than those disappearing in other ways (either sex)
3. Human-related disappearances are not related to change in social behaviour	<ul style="list-style-type: none"> a) Human-related disappearances are unpredictable and spontaneous (i.e., no change in rank/dynamic centrality)
4. High-ranking and socially central vervets have priority of access to food	<p>High-ranking/socially central individuals (static) may be more likely to have a human-related death than to</p> <ul style="list-style-type: none"> a) remain in society or b) emigrate
5. (Alternative) Spatially peripheral individuals are at greater risk of predation. Predation is not foreseeable	<ul style="list-style-type: none"> a) Individuals less socially central (static) may be more spatially peripheral and thus more likely to be predated or receive conspecific aggression rather than disappear because of emigration b) The dynamic social position of individuals who disappear by predation will not change from baseline to the month before disappearance
6. Socially central individuals are afforded within society protection and/or access to resources	<p>Socially central mothers are more likely to have infants that survived to one year compared to less central females</p>

2.0 General Methods

2.1 Study Site, Subjects, and Collection

Starting in June 2011 with one society (“M”) and adding two societies in January 2016 (“HC” and “KS”), the field team has been collecting long-term behavioural observations and demographic data on vervet monkeys (*Chlorocebus pygerythrus*) at Lake Nabugabo in southwestern Uganda (0°22’ S 31°54’ E) (Chapman, Twinomugisha, et al. 2016). The field site is a combination of grasslands, areas undergoing natural regeneration of vegetation, forest patches, agricultural land, as well as various buildings (Chapman, Twinomugisha, et al. 2016). The home ranges of the societies are between 0.254 and 0.394 km² (Martins 2022). The field team habituated the societies and was able to recognize all study individuals within six months of commencing the study of each society. Field data were collected six days a week for three weeks, followed by one week without observations, and rotated between the societies such that one society may not be observed for up to 15 consecutive days (Schwegel et al. 2022). The team performed group scan sampling (Altmann 1974) every 30 (2011-2015) or 15 minutes (2016 onward), during which they recorded the behaviour (e.g., resting, feeding, grooming) of five haphazardly selected focal individuals, the identity of their interactant(s), as well as the identity and distance of their nearest neighbour(s). We supplemented scan sampling with *ad libitum* data (Altmann 1974) on same-sex agonistic and sociosexual interactions, as well as demographic information on births, deaths, dispersals, disappearances, and injuries. Continuous focal animal sampling was conducted during three unrelated studies (male focals: January-June 2019, July-December 2019; female focals: May-August 2018), from which same-sex agonistic interactions were extracted to supplement scan and *ad lib* data used to construct the dominance hierarchies.

2.2 Social Network Analysis

2.2.1 *The Gambit of the Group*

I quantified the social networks using nearest neighbour information of all adults (> 4 or 5 years old), subadults (approximately 3 to 4 years), and juveniles (6 months to about 3 years; Struhsaker 1967b) from group scan sampling data. Compared to focal follow data, group scan sampling data better simulate the proximity network of a society because data are available for more individuals per unit of sampling effort (Davis et al. 2018). That said, a study of vervets in South Africa indicated that a combination of *ad lib* and focal follow data (compared to either alone) improved the accuracy of the grooming network, although the networks generated by each data type independently were highly correlated (Canteloup et al. 2020). Furthermore, I used proximity data because associations occur more frequently than affiliative (i.e., grooming) or agonistic (e.g., chasing, supplanting) interactions, which have also been used to quantify social networks (Lehmann et al. 2016; Thompson 2019). Consequently, I was able to maximize the data available even when considering a relatively short timescale (e.g., section 3). Utilizing different behaviours to define a network (i.e., agonistic versus affiliative versus proximity) influences network properties (Lehmann and Ross 2011; Castles et al. 2014; but see Kulahci et al. 2018), such that networks generated by different types of behaviours may not be comparable (Castles et al. 2014; but see Canteloup et al. 2020). To avoid generating a network based on behaviours that may not be comparable (i.e., associations indicate who can interact rather than who does interact; Whitehead 2008), I defined proximity as all individuals occurring within three meters of the focal animal (Tiddi et al. 2011), excluding contact and behavioural interactions (i.e., grooming, play, sociosexual and agonistic behaviours, breastfeeding) (Castles et al. 2014; Schoof and Jack 2014; Canteloup et al. 2020). From the original data set, I excluded any

instances in which there was an obvious error (e.g., focal animal was recorded as interacting with itself, an individual's name was not recognized based on the demographic data, the focal monkey was associating with an individual who had died and for which there was evidence or reasonable suspicion for the death), and where there was an intersociety (“intergroup”) or interspecific interaction or association (i.e., between members of two different societies or between a vervet and another species, such as vocalizing to a dog). I also ensured each individual appeared only once per scan sample (i.e., sampling period) by aggregating entries that occurred on the same date and time in which an individual was observed more than once.

Through combining entries, I invoked the “gambit of the group” to generate an undirected proximity network. The gambit of the group (Aplin et al. 2012; Ilany et al. 2015; Silk et al. 2015) assumes that all individuals who are within a “group” (i.e., are clustered together at a given point in time within a society) may interact with one another (Whitehead and Dufault 1999; Franks et al. 2010; Hoppitt and Farine 2018). In other words, I defined a group as all individuals who were within three meters of at least one other member of the group during a scan sample, such that I assumed an associative relationship where, if A and B are in the same group and B and C are in the same group, then A and C are also in the same group. In accordance, a previous study of vervet monkeys suggested that vervets show triadic closure (i.e., if A and B are friends and B and C are friends, then A and C are friends) (Borgeaud et al. 2016). I chose to use the gambit of the group as a measure of associations for several reasons. First, the associations measured by the gambit of the group are symmetric (i.e., if A is in a group with B, then B is also in a group with A) unlike when studying nearest neighbours, where B may be the closest monkey to A, but A may not be the closest monkey to B (Whitehead 2008). Using a symmetric network for associations is more reasonable than using an asymmetric network because associations

simply represent the opportunity to interact (e.g., being within the range of communication; Whitehead 2008); as such, there is likely little biological significance in A being nearest to B but B not being nearest to A, particularly when you cannot ascertain who is maintaining proximity. Second, some individuals may be less gregarious and/or observed less frequently than others (Franks et al. 2021). By using the gambit of the group, I considered all data related to an individual, even if they were not the nearest neighbour to the focal animal. This decision thus maximized the amount of data available per monkey and did not omit any instances in which the individual was observed. Similarly, when determining tie strength based on association indices (discussed below), all observations of an individual are considered in the calculation, so that associations are standardized across monkeys (i.e., frequency of individual observation is controlled for) (Cairns and Schwager 1986). By using the gambit of the group, I had a better measure of how often each monkey was observed and thus a more accurate calculation of association indices.

2.2.2 Centrality Metrics

Using the gambit of the group data, I calculated four social network metrics, which I broadly refer to as measures of social centrality (cf. Thompson 2019): 1) binary degree centrality (“degree” hereafter), 2) strength (i.e., weighted degree), 3) betweenness centrality, and 4) eigenvector centrality. I chose these metrics for quantifying social centrality (Table 2) because these have previously been associated to varying degrees with individual fitness (e.g., Barocas et al. 2011; Stanton and Mann 2012; Brent et al. 2013; McFarland and Majolo 2013; Nuñez et al. 2015; Cheney et al. 2016; Lehmann et al. 2016; McFarland et al. 2017; reviewed in: Brent 2015; Thompson 2019).

I quantified degree as the number of individuals in the social network with whom the focal animal associated during a specific period. Degree was the only centrality metric that did not depend on how frequently individuals associated.

I calculated strength as the sum of all an individual's dyadic tie strengths (Whitehead 2008; Thompson 2019). In turn, I calculated dyadic tie strength as the half-weight index (HWI), an association index that assumes it is more likely to observe individuals apart than to observe them together (Cairns and Schwager 1986). I made this same assumption because the three societies have many individuals (mean: 35; Schwegel et al. 2022) who may spatially spread out, so that members are not all in proximity at the same time. Among association indices, the HWI is the most commonly used (Cairns and Schwager 1986; Whitehead 2008; Stanton and Mann 2012; Thompson 2019), may be less biased than other indices if present individuals were not recorded (Farine and Whitehead 2015; Hoppitt and Farine 2018), and controls for gregariousness and space-use (Thompson 2019). While the HWI has recently been criticized for arbitrarily assigning half the weight to observations of individuals on their own compared to observations of two individuals during the same sampling period (Hoppitt and Farine 2018), I used the HWI to be comparable with past studies. Furthermore, I did not anticipate there would be a systematic error in which associating individuals were not observed (i.e., group location error; Hoppitt and Farine 2018) because the monkeys are semiterrestrial (so there is generally good visibility of group members) and readily individually identifiable. The HWI is calculated as

$$HWI = \frac{x}{x + y_{AB} + 0.5(y_A + y_B)}$$

where x is the number of times (i.e., sampling periods) that a dyad consisting of monkeys A and B is observed associating within a given period, y_{AB} is the number of times both monkeys were

observed during the sampling period but were not associating/within the same group, and y_A and y_B are the number of times only one of the monkeys was observed during the sampling period (Bejder et al. 1998). Dyadic tie strength ranges from 0 (never associated) to 1 (observed in the same group each time either individual was observed).

Both betweenness and eigenvector centrality were weighted by strength (Newman 2004; Barthélemy et al. 2005) rather than using the presence or absence of ties based on filtered data (i.e., removing interactions that occur infrequently) (Franks et al. 2010), so as to consider weak ties (e.g., Blumstein et al. 2009; McFarland et al. 2017) while reducing the value of interactions that likely happened simply because of general gregariousness (Thompson 2019). I calculated betweenness centrality as the number of shortest path lengths (based on the geodesic distance between individuals according to their strength) on which the focal animal resided (Wey et al. 2008; Farine and Whitehead 2015) and eigenvector centrality as the sum of the strength of the individual and of their direct partners (Table 2).

Table 2. Summary of social network metrics (rationale and calculation) used in the analyses. See Thompson (2019) for other measures of centrality and the costs and benefits of each.

Metric	Rationale/Definition	Calculation	Use in Models
Degree centrality (binary degree)	Used when the number of connections is relevant. Binary degree has been associated with fitness independently of strength (e.g., Lehmann et al. 2016; Senior et al. 2016)	Total number of individuals observed interacting with a focal animal	Given as the proportion of individuals in the network with whom the focal associated (i.e., % of total) – “%degree”
Strength (weighted degree)	The frequency of interactions (i.e., edge weights or tie strength) (Farine and Whitehead 2015). Sum of these frequencies is the weighted degree. Compared to binary degree, weighted degree decreases the importance of chance interactions.	Half weight index (HWI) – most reliable when it is more likely to observe one individual alone vs. two together (Cairns and Schwager 1986)	Given as the z-score calculated within a given network (i.e., each individual’s strength is ranked relative to the others in their network) – “z-strength”
Betweenness centrality	Defines how well an individual connects other members of the society – important for society stability (i.e., the loss of these individuals may have a disproportionate effect on other individuals) (Wey et al. 2008)	Number of shortest path lengths on which the focal animal resides	Given as the z-score calculated within a given network (i.e., ranked relative to the others in their network) – “z-betweenness”
Eigenvector centrality	A good measure of overall centrality of an individual and indicates how important an individual may be as a central figure in the society (Farine and Whitehead 2015)	Sum of an individual’s centralities (strength) and those of their direct partners	Given as the z-score calculated within a given network (i.e., ranked relative to the others in their network) – “z-eigenvector”
Information centrality	Similar to betweenness centrality: measures how often an individual is found on a path between other individuals (Brent 2015)	The average of 1/length of all the paths starting at a node (Amrit and ter Maat 2018) Considers not just the shortest path, but all paths that pass through the node.	Not used: 1. Infrequently used as a social network metric (Brandes and Fleischer 2005) 2. Generates similar results to eigenvector and degree (Amrit and ter Maat 2018)

Local clustering coefficient	Defines how well neighbours associate with one another (i.e., do they form a clique)	Number of ties between direct associates of the focal animal over total number of ties that could exist between these associates (Opsahl and Panzarasa 2009)	Not used: 1. Marginally significant association with fitness 2. Cannot be used on directed networks (Caldarelli 2007; reviewed in Opsahl and Panzarasa 2009)
Closeness (reach)	Indicates how well an individual is connected to all other society members (Wey et al. 2008). Useful when measuring potential speed of information and/or disease spread through a population (Wey et al. 2008; Farine and Whitehead 2015)	Proportion of nodes that can be reached in a given number of steps (away from a focal individual) (Farine and Whitehead 2015)	Not used: connectedness to the entire society (speed of information transfer or disease transmission) is not relevant to my predictions
Reciprocity	Measure of quality of ties: extent to which individuals have a fair exchange of interactions.	$1 - \frac{ (i \text{ grooming } j) - (j \text{ grooming } i) }{i \text{ grooming } j + j \text{ grooming } i}$ (Silk, Alberts, et al. 2006)	Not used: 1. Only relevant to grooming 2. Reciprocity is associated with tie strength, so major information is not being lost (Silk, Alberts, et al. 2006)
Group-level (society-level) metrics: Average path length, diameter, network density	Useful for comparing societies overall. Group-level metrics tend to not vary much across societies, so these measures are less useful (Kasper and Voelkl 2009).	Network density: number of social ties existing within the society divided by the total potential number of social ties	Not used: I am not overtly trying to compare the societies and group-level metrics would be the same between individuals within the same network.

2.2.3 Hypothesis Testing Using SNA

When using SNA to study the social position of individuals in reference to an outcome, such as relative fitness, there are various caveats to consider. Inherently, social network dyadic data are non-independent (Dekker et al. 2007), meaning common statistical tests may be biased because the assumptions underlying these tests are not met (Krackhardt 1988; Croft et al. 2011). To account for this problem, social networks are typically investigated using permutation tests combined with regression analyses (Croft et al. 2011; Farine and Whitehead 2015; Weiss et al. 2021). However, permutation tests have been criticized recently for not testing the correct null hypothesis and may thus lead to high error rates (Weiss et al. 2021). Specifically, pre-network or datastream permutations, wherein the researcher permutes the raw data prior to generating the network (Bejder et al. 1998), test whether the network is differentiated (i.e., individuals show preferences for others) or random (null) rather than whether there is a relationship between network position and the outcome variable of interest (Weiss et al. 2021). Furthermore, permutation tests account for confounds, such as sampling effort and society size, within the social structure alone, but these confounds are not controlled for within the regression model, such that the effect sizes within the model tend to be incorrect when only relying on permutations (Franks et al. 2021). As a result, all statistical significance is placed in the p-value and thus inferences cannot be made based on the models generated (Franks et al. 2021). Similarly, permutations only account for certain types of non-independence (Hart et al. 2022) and are thus incomplete when it comes to social network analyses. Using simulations, Hart et al. (2022) have demonstrated that parametric regression models that specify confounds produce the same p-values as node-label permutations but produce more appropriate effect sizes. Thus, forgoing permutation tests in favour of parametric regression models may be preferable (Hart et al. 2022) and other methods of performing SNA are in the works using a Bayesian approach

(Hart et al. 2021). Given these caveats, I used generalized linear mixed modelling without permutations to perform hypothesis testing (Croft et al. 2011; Hart et al. 2022).

2.3 Dominance Rank

I extracted all dyadic, intrasociety, intrasexual agonistic bouts (i.e., involving only two individuals from the same society and the same sex) throughout the entire study period. I defined a bout as all agonistic interactions that occurred between the same dyad within a 15-minute period, since this is the length of time between scan samples and the length of focal animal samples (Schwegel et al. 2022). For each bout, I recorded the winner and loser, or a draw if both individuals directed aggressive behaviours toward each other during the bout. I considered the male and female dominance hierarchies separately and included individuals within the hierarchy as of their first recorded intrasexual agonistic encounter. The hierarchies thus included juveniles, subadults, and adults. To be included in the hierarchy, the individual had to have been involved in at least five intrasexual agonistic interactions throughout the entire study period (Neumann et al. 2011).

I quantified the male and female dominance hierarchies for each society using Elo scores (Neumann et al. 2011). Initially, I generated each hierarchy using the standard starting value (Elo score = 1000) and k -value ($k = 100$), where k is a parameter that dictates by how much an Elo score will change when an individual wins or loses a bout (Neumann et al. 2011). Once I had the baseline version of the hierarchy for each sex and within each society, I found the optimized k for each hierarchy (using the `optimizek` function in the `EloRating` package; Neumann and Kulik 2014). For the values of k to be tested, I defined the range as $k = 4$ to 200 and the resolution as 491, so that each value of k tested was increased by an increment of 0.4 units (Schwegel et al. 2022). Keeping the sexes separate, I extracted the log-likelihood values associated with each k -

value for each society, subtracted the log-likelihood for a given k from the maximum log-likelihood for that society, and chose the optimized k as the value associated with the lowest standard deviation from the maximum log-likelihood across the societies (Schwegel et al. 2022). I chose one value of k for males and one for females since, presumably, the same agonistic behaviours that occur in each society within a single population would have the same importance in defining how much the individual's dominance rank changed. For females, optimized k was 53.6 and for males, optimized k was 68.8.

In addition to Elo scores, dominance rank can be expressed in other ways, including as ordinal rank – an integer expressing the individual's position within the dominance hierarchy – and proportional rank – a decimal expressing the percentage of society members that an individual dominates (Levy et al. 2020). Ordinal rank better predicts access to social and mating partners among baboons (Levy et al. 2020). However, I instead opted to use proportional rank to standardize dominance rank across societies of different sizes. Thus, once I extracted Elo scores on a particular date (details in the following sections), I determined the proportional rank of the individuals of interest using:

$$\text{proportional rank} = [\text{hierarchy size} - \text{ordinal rank}] / [\text{hierarchy size} - 1].$$

2.4 Data Analysis

To generate the social networks, I wrote code in MATLAB R2020b (The MathWorks Inc. 2020) to extract all entries from the error-checked, long-term dataset that occurred within the period of interest. The period of interest was variably defined as one-month periods before the disappearance of a monkey from their society (section 3), and one-year periods aligning with the reproductive years (section 4). Using a function I generated in MATLAB, I then calculated the

HWI for each individual during that time and organized the results as an adjacency matrix with dyadic tie strength in each cell.

I imported the generated matrices, one per period of interest, into R version 4.1.1 (R Core Team 2021) and used the packages `tnet` (functions: `degree_w`, `betweenness_w`; Opsahl 2020) and `igraph` (functions: `graph_from_adjacency_matrix`, `eigen_centrality`; Csardi and Nepusz 2006) to determine the values of degree, strength, betweenness, and eigenvector centrality. Because the social network metrics depend on society size (Sueur, Petit, et al. 2011; Lehmann et al. 2016; Kulahci et al. 2018), within each network, I calculated the z-scores ($z = \frac{[x_i - \text{mean}(x)]}{sd(x)}$) for each individual and each network metric to standardize these metrics across networks of various sizes (hereafter referred to as “z-strength”, “z-betweenness”, and “z-eigenvector”). As a result, the centrality metrics used in the analyses reflected an individual’s social position relative to the other society members during a specific period, regardless of society size (Blumstein et al. 2009). For degree centrality, there were a few cases in which all individuals had associated with all other individuals within the network, so there was no variability and thus a z-score that was not applicable. Instead, I presented the degree centrality as the percent of all the society members in a given network minus one (to avoid the instance of the individual associating with itself) with whom the individual associated during that time (hereafter, “%degree”).

Because the measures of centrality may be highly correlated, I started each analysis by creating a model with all the fixed effects included and testing for multicollinearity by computing variance inflation factors (VIFs) using the package `performance`, function `check_collinearity` (Lüdtke et al. 2021). I found the highest collinearity ($VIF > 10$; Quinn and Keough 2002) for the z-strength and z-eigenvector (results: Table 4), so I removed z-strength as a predictor (Lehmann et al. 2016). I chose to keep z-eigenvector over z-strength because z-

eigenvector had slightly lower correlations with most other predictor variables (results: Table 4), and eigenvector centrality gauges an individual's potential importance within the network (Farine and Whitehead 2015).

For all of the analyses, I performed automated model selection using the dredge function in the package MuMIn (Bartoń 2020) to choose the best predictors for each outcome. I determined the best model based on the one with the lowest Akaike Information Criterion corrected for small sample size (AICc; further details in section 3.2.3).

3.0 Demographic Changes in Vervet Monkeys

3.1 Introduction

Dynamic social network analysis (SNA) has emerged as a means of observing changes in a social network over time and using these variations to examine dynamic processes, such as the spread of information or disease (reviewed in Farine 2018). Dynamic SNA has also been used to assess the effects of changes in society composition on social structure (Franz et al. 2015; Pfaff et al. 2023). That said, studies differ in the reported impacts of demographic changes on social structure (reviewed in Shizuka and Johnson 2020).

Social factors, including demographic changes, are critical in their influence on social centrality. Demographic changes can involve the addition of society members, through births or immigrations. For example, in many primate species, newborn infants attract female society members – from juveniles as young as six months (Struhsaker 1967b) to adults – who will try to handle the infant, sometimes grooming the mother to be able to do so (Sugiyama 1965; Struhsaker 1967b; Gartlan 1969; Struhsaker 1971). Similarly, male immigrations in a South African population of vervet monkeys tended to increase the eigenvector centrality of resident society members who were present throughout the study (Borgeaud et al. 2017). In turn, the loss of individuals through dispersals, deaths, and disappearances can also shift social centrality. In the same South African vervet population, the disappearance of males decreased the centrality of remaining individuals (Borgeaud et al. 2017). However, the disappearance of males, juveniles, and females increased the dyadic tie strength between those remaining individuals (Borgeaud et al. 2017). The loss of individuals from a society has variously been reported to cause little change in overall interaction and association rates (Franz et al. 2015; Fedurek et al. 2022; Pfaff et

al. 2023), and substantial changes to network stability, with individuals interacting with fewer others and forming smaller, more clustered networks (Flack et al. 2006).

Few studies have investigated changes in, or predictions related to, social network position preceding demographic events. Individuals may become more socially peripheral in anticipation of a demographic event (Shizuka and Johnson 2020), such as by visiting other societies, and thus spending less time in their own society, in preparation for emigration (Cheney and Seyfarth 1983). This pattern was also observed in rhesus macaques (*Macaca mulatta*) before a mass female eviction, where the soon-to-be-evicted females received more aggression from lower-ranked individuals and spent more time grooming one another rather than other members (Larson et al. 2018). Static SNA, in which social centrality is calculated as a whole without considering changes over time (Farine 2018), may also predict participation in a demographic event. For example, among Barbary macaques (*Macaca sylvanus*), those who were part of a strong local cluster in the affiliative network and those who had many agonistic partners were more likely to survive a harsh winter (Lehmann et al. 2016). Similarly, predation risk may depend on individual spatial and social position. In stationary societies, individuals at the periphery have the greatest predation risk (Hamilton 1971), unlike during society movement when those at the leading edge are at greatest risk (Bumann et al. 1997). In turn, spatial positioning may depend on individual characteristics: for instance, high-ranking individuals tend to be spatially central when the society is at rest, but they also tend to forage at the front of the society (Teichroeb et al. 2015). Dominance rank is often associated with social centrality where high-ranking individuals also tend to be more socially central (Schino 2001; Silk et al. 2003; Sueur, Petit, et al. 2011; Bret et al. 2013). As a result, high-ranking, socially central individuals may be at lower risk of predation when the society is at rest, and at higher risk while moving.

Social factors influencing social centrality may also include characteristics of the society itself. Namely, society size may mitigate changes in the social network: larger societies have a greater potential number of social ties since there are more potential partners (Lehmann et al. 2016; Kulahci et al. 2018), and these societies were more resistant to network changes when a central female was removed (Lehmann and Dunbar 2009). However, compared to small societies, larger societies have lower network densities (Kulahci et al. 2018; but see: Lehmann and Boesch 2009; Sueur, Petit, et al. 2011) – that is, they have fewer existing ties relative to total potential ties (Wey et al. 2008; Farine and Whitehead 2015) – and individuals had lower eigenvector centralities (Sueur, Petit, et al. 2011).

Besides social factors, social centrality is subject to individual and environmental factors. To begin, sex may play a role, given that the philopatric sex tends to be more central or engage in more affiliative behaviours than the dispersing sex (e.g., Fedigan 1993; Perry 1996; Borgeaud et al. 2017; but see: Kappeler 1993; Lehmann and Boesch 2009). Likewise, age may contribute to differences in centrality. For instance, older vervet monkeys had a tendency to be more socially central than younger individuals (Borgeaud et al. 2017; but see Canteloup et al. 2021). Alternatively, juveniles may be more socially central than adults, as observed for degree centrality in rhesus macaques (Liao et al. 2018). Moreover, environmental factors, such as food availability and rainfall, also influence the number and/or strength of ties (Henzi et al. 2009; Ilany et al. 2015), in part because social time is limited by animal activity budgets which must also accommodate feeding, resting, and moving (Dunbar et al. 2009).

In considering social, individual, and environmental factors, most studies focus on naturally occurring demographic events in wild populations that live in protected areas and not in proximity to humans. However, human activities may alter these factors since human-wildlife

proximity can entail improved food access via crop foraging, but also greater mortality risk from farmer retaliation attempts (Chapman, Twinomugisha, et al. 2016) or anthroponotic disease transmission (Senghore et al. 2016). To fill this gap, I examined demographic changes in a wild population of vervet monkeys living in an anthropogenic landscape, and I compared social networks in relation to disappearances caused by natural and human-related phenomena. Natural disappearances primarily involved dispersal events, where vervets are characterized by male-biased dispersal (Cheney 1981). In several primate species, males disperse multiple times, including at sexual maturity (i.e., natal dispersal; around five years old for vervets; Cheney et al. 1988) and later (i.e., secondary dispersal), typically to increase their dominance rank and thus their access to mating opportunities (Cheney and Seyfarth 1983; Sprague et al. 1998; Jack and Fedigan 2004). However, increasing dominance rank following dispersal was not consistently observed in vervets, although males whose rank did not increase immigrated to societies with more favorable sex ratios (L'Allier et al. 2022). Males may be evicted, where eviction is usually observed in unimale societies (e.g., Pusey and Packer 1987), but can be observed in multimale societies (e.g., white-faced capuchins, *Cebus capucinus*: Jack et al. 2012). Alternatively, males may disperse voluntarily, as is typically the case for vervets (Cheney and Seyfarth 1983; L'Allier et al. 2022). Voluntary dispersal in vervets and other species may be preceded by males “visiting” other societies (i.e., “prospecting” or male incursions) prior to their transfer, a behaviour that may occur over many days (Struhsaker 1967a; Cheney and Seyfarth 1983). During these visits, males spend less time in their own society. This behavioural change could manifest as lowered tie strength between dispersing males and others in their society. In addition to dispersal, all society members are vulnerable to natural deaths through predation or conspecific attack. Vervet predators in Amboseli National Park, Kenya include leopards, eagles,

snakes such as pythons, and baboons (Seyfarth et al. 1980). The societies around Lake Nabugabo live in a human-modified matrix such that leopards and baboons are not a threat, but domestic dogs are a main predator (Teichroeb et al. 2015). In addition, the Lake Nabugabo vervets are subject to human-related disappearances through poisoning or direct conflicts with villagers in the area (Chapman, Twinomugisha, et al. 2016). As these vervets live near a village, they are also prone to electrocution (Chapman, Twinomugisha, et al. 2016).

3.1.1 Research Questions, Hypotheses, and Predictions

In this section, I addressed the following research questions:

A. Do individual factors affect whether a vervet monkey disappears from their society?

Specifically, do these factors affect whether an individual:

- I. remains in their society or emigrates?
- II. remains in their society or has a human-related death?

B. Do individual factors affect the mode of disappearance? Namely, whether the individual emigrated or disappeared by other modes, including natural death (i.e., predation, conspecific-caused death), human-related death (i.e., poisoning, beating), death by electrocution, or unknown cause of death?

Overall, I hypothesized that individual characteristics (sex, age, rank, social centrality) can be used to predict A) the disappearance of an individual and B) their mode of disappearance.

First, I hypothesized that 1) sex-specific philopatry and dispersal would influence sociality given that female vervet monkeys are the philopatric sex (Cheney 1981), and thus spend more time in their society forming social ties relative to males (Sterck et al. 1997). Because females are philopatric, I predicted that 1a) males are more likely to disappear from their society,

and 1b) males are less central within their society compared to females (i.e., have lower degree, strength, eigenvector, and betweenness centrality). Consequently, if 1a and 1b are true, I predicted that 1c) on average, individuals who disappear from the society will be less socially central than those who remain.

Secondly, I hypothesized that 2) if male dispersals are voluntary and are aimed at avoiding inbreeding and improving reproductive success (Krause and Ruxton 2002; L'Allier et al. 2022), then male dispersals are predictable. Since inbreeding avoidance is an important reason for dispersing rather than male takeovers, I predicted that 2a) sexually mature males (i.e., adult and subadult) will be more likely to disperse compared to young males, and 2b) those who emigrated would not differ in their dominance rank nor their static social centrality from those who remained within the society. Since dispersals are voluntary and involve visiting other societies prior to emigration (Cheney and Seyfarth 1983), I predicted that males who emigrated 2c) would not show any change in their dominance rank, but these emigrating males would exhibit a decrease in their dynamic social centrality immediately before dispersal 2d) compared to individuals who remained within the society and 2e) compared to individuals who disappeared in other ways. Because males are the dispersing, non-philopatric sex, I predicted that 2f) the average static social centrality of individuals who disperse would be lower than the average social centrality of individuals who disappear in other ways, since both sexes can be involved in other modes of disappearance.

Among the other known causes of disappearance, I expected that human-related death would be the second most common cause of known disappearances, given that the study population of vervets live in a human-modified landscape where they are known to forage on crops and are generally considered a pest (Chapman, Twinomugisha, et al. 2016). The main

poison used against the vervets at Lake Nabugabo is Furadan (carbofuran). Since symptoms of lethal poisoning by carbofuran occur within approximately 12 hours (Pivariu et al. 2020), I interpreted these deaths as relatively spontaneous and therefore 3) hypothesized that neither poisoning nor other human-related causes of death would change the behaviour of the impacted monkey long before their death. Hence, I predicted that 3a) human-related disappearance events would not be predictable and thus the impacted individuals would not exhibit substantial changes in their dynamic social network position in the month preceding their death compared to their baseline network position. Furthermore, I hypothesized that 4) high-ranking individuals have priority of access to desired resources, including grooming partners and food (Struhsaker 1967a), such that socially central individuals (by having many social partners) also have priority of access to resources through tolerance and/or exchange of resources (Seyfarth 1977; Seyfarth 1980; Kapsalis and Berman 1996; Borgeaud and Bshary 2015). Because of this priority of access, namely to food, I predicted that high-ranking and socially central individuals may be more prone to human-related death rather than 4a) remaining within the society and 4b) dispersing since they may gain access to poisoned foods first or may be more likely to come in contact with humans.

Alternatively, I hypothesized that if predation is the most common non-dispersal-related cause, then 5) individuals who are more spatially peripheral are at greater risk of predation (Hamilton 1971). Individuals who are often spatially peripheral may also be less socially central because they don't associate as frequently (Kalbitzer et al. 2017). Thus, I predicted that 5a) individuals who are less socially central (static value) are more likely to disappear as a result of predation or death from conspecific aggression than to disperse. I also predicted that these natural deaths would be spontaneous and unpredictable, such that 5b) the individual's dynamic

social position would not change between their baseline position and their position the month before their disappearance (Table 1).

3.2 Methods

3.2.1 Demographic Events

Using the long-term demographic data collected by the field team between January 2012 and July 2022, I extracted all disappearance events and noted the mode of disappearance (i.e., emigration, human-related death, including poisoning and beating, death by electrocution, predation, conspecific-related death, unknown death, unknown). To test my predictions, I divided these disappearances into non-mutually exclusive categories: 1) all disappearances, 2) emigrations only, and 3) other disappearances (i.e., human-related death, death by electrocution, predation, conspecific-related death, and unknown death). In all the analyses, I included disappearances with either a confirmed or strongly suspected cause. Confirmed disappearances included those where an individual was observed in another society confirming emigration, where an individual was found dead with signs of poisoning, and so on. Strongly suspected causes included ones in which an individual was not directly observed in another society, but emigration was strongly suspected due to the timing of or behaviour prior to the disappearance. When I examined all disappearances, I did not distinguish between the modes of disappearance; that is, I included all demographic events, including those where the mode of disappearance was entirely unknown (i.e., the individual was no longer observed in the society for any reason). For analyses where I did distinguish the modes of disappearance, I erred on the side of caution and only included those disappearances with a confirmed or strongly suspected cause, or where death was confirmed (i.e., carcass found) but cause of death was undetermined. In all analyses, I only included individuals for whom sex was known since sex was a factor that I predicted would be

important in distinguishing individuals who disappeared, especially those who emigrated, from those who remained in the society.

I excluded the disappearances of infants (e.g., Lehmann and Ross 2011; Bret et al. 2013; Chapman, Friant, et al. 2016; Borgeaud et al. 2017) as there were insufficient data to define their interactions. In contrast, juveniles (> 6 months old) participate in social interactions or associations with individuals other than their mother (Struhsaker 1967b). For example, juveniles, especially larger juvenile females, direct grooming to others (Jarrett et al. 2018), including recent mothers to whom they are attracted because of their newborn infants (especially < 1 month old) (Struhsaker 1967b; Struhsaker 1971). As a result, I included demographic events involving juveniles.

3.2.2 Social Network Analysis

For each demographic event, I quantified two proximity networks for the society in which the demographic event occurred. The first corresponded to the proximity network in the month prior to the demographic event; that is between -30 and -1 days, where day 0 is the date of disappearance (i.e., the first date on which the individual was not observed) (Franz et al. 2015). I chose one month because, while demographic changes may be observed on a shorter time scale (e.g., male vervet monkeys may visit other societies over a few days prior to emigration: Cheney and Seyfarth 1983), the field team's schedule may constrain the data available within this shorter time frame. The second network constituted the proximity network in the penultimate month before the demographic event (i.e., from -60 to -31 days). This second network acted as the baseline condition (Franz et al. 2015), since I expected that changes to the social network in anticipation of the demographic event (e.g., Larson et al. 2018) would be concentrated in the month prior to disappearance (e.g., Cheney and Seyfarth 1983). Thus, I used the data from the

month prior to disappearance to examine static social centrality, and then change between the baseline and month before disappearance to examine dynamic social centrality.

3.2.3 Data Analysis

To confirm whether age and sex influenced the social network metrics, and thus whether to control for these variables by maintaining them as fixed effects, I generated separate models with the static values of the social network metrics (%degree, z-strength, z-betweenness, z-eigenvector, see sections 2.2.2 and 2.4 for definitions), derived from the baseline data (-60 to -31 days) for all events, as the outcome variables. The fixed effects were age (ordinal variable: juvenile < subadult < adult) and sex (binary variable: 0 = female, 1 = male). To account for pseudoreplication, I included the following as random effects (Schneider-Crease et al. 2020): 1) individual identity and 2) event number (i.e., an identifier for each demographic event, that is, involving one society on one date but which may involve multiple disappearances) nested within society identity. I repeated these models using the dynamic social network metric (month before disappearance minus baseline) as the outcome. I tested each model with a t-test using Satterthwaite's method. Based on the results (see section 3.3.1 below), I controlled for age and sex in all the models concerning the static values of the centrality metrics (i.e., in the month before disappearance), but not in the models regarding the dynamic social position.

To verify whether each of the static social network metrics and dominance rank were independent from one another, I next tested for correlations between these predictors. To avoid pseudoreplication of individual identities and any network changes due to impending disappearances, I chose the baseline data for one event per society from 2017 or later. At this time, we were studying all three societies and the field methods were consistent. I chose the event for which there was the greatest number of individuals whose proportional rank I could

calculate (date of events: M: 11 February 2017, baseline data: 13 December 2016 to 11 January 2017; HC: 18 May 2017, baseline: 19 March to 17 April 2017; KS: 4 August 2017, baseline: 5 June to 4 July 2017).

To answer the research questions, I performed logistic regression without permutations (Gear et al. 2009) by generating penalized binomial generalized linear mixed models (GLMMs) using the package `brglm` (Kosmidis 2021). I opted for penalized logistic regression because in several models, multicollinearity was very high (> 10), or an error was thrown by R because of quasi-complete separation within the model. Complete separation occurs when a function of an independent variable can fully predict the dependent variable, while quasi-complete separation occurs when one value of the independent variable predicts both outcomes of the dependent variable (Allison 2008). For this dataset, quasi-complete separation occurred for the outcome of emigration and the independent variables sex and age: only subadult and adult males emigrate, but not all males nor subadults/adults emigrate. One method of calculating the maximum likelihood estimate for the model when there is complete or quasi-complete separation is to instead calculate a penalized maximum likelihood estimate, where a penalty is given to the likelihood values to remove variables with little impact on the outcome and ensure maximum likelihood does not tend toward infinity (Firth 1993; Allison 2008). Given that variables with little effect are removed, researchers have suggested using penalized logistic regression to avoid overfitting even when complete separation does not exist (Pepe et al. 2013). As a result, the coefficients generated by penalized logistic regression have little bias (Allison 2008).

These logistic regressions compared the individual characteristics of the following binary outcomes:

- individuals who remained within their society (1) and those who disappeared (0) (exploratory analysis; Table 1: predictions 1a-c)
- individuals who remained (1) and those who emigrated (0) (2a-d)
- males who remained (1) and males who emigrated (0), to ensure sex was not driving the previous relationship (2a-d)
- individuals who remained (1) and individuals who had a human-related death (0) (3a, 4a); and
- individuals who emigrated (1) and those who disappeared for any other known or suspected reason (0) (2e,f, 4b).

I performed two iterations of each model. In one, I considered individual characteristics as predictor variables, including the static value of dominance rank and the social network metrics in the month immediately prior to the event (i.e., -30 to -1 days). In the other, I considered the change in individual characteristics as predictor variables, that is dynamic dominance rank and social network position from -30 to -1 days minus those values from -60 to -31 days. I quantified dominance rank (see section 2.3 for details) by extracting the Elo score of the individual of interest on the final day from which the associated social network was derived (e.g., for the network one month prior to disappearance, I extracted the Elo score on day -1). I then used the Elo scores to calculate proportional rank for all society members and used this metric in the model.

For each analysis, I created a fully nested model in which the fixed effects were sex, age, %degree, z-betweenness, and z-eigenvector (Appendix A: Tables A1-A4). For each model, I repeated the model selection procedure (section 2.4) using a limited dataset that included only individuals whose dominance rank was known, where I also included proportional rank as a

fixed effect. In all cases, proportional rank was not included in the best model (Table A2, A4); therefore, I ignored proportional rank in all analyses and used the full dataset to generate the best model. I used the same random effects as described above.

As an indicator of each model's ability to predict the outcome variable, I calculated an R^2 for each model (Nakagawa and Schielzeth 2013) and adjusted it based on the number of predictors as follows (Ezekiel 1930, cited in Raju et al. 1997):

$$R_{adj}^2 = 1 - \frac{(1 - R^2) \times (n - 1)}{n - k - 1}$$

where R^2 was generated using the function `r.squaredGLMM` (package `MuMIn`; Bartoń 2020), n is the number of observations, and k is the number of predictors. I limited k to the number of fixed effects since `r.squaredGLMM` calculates R^2 by comparing to the null model. The null model includes all random effects, so the number of random effects was already accounted for in the value of R^2 . I did not choose the best model by maximizing the adjusted- R^2 (e.g., Hu and Shao 2008) because this method is generally considered to generate poor results (McQuarrie and Tsai 1998; Burnham and Anderson 2002). Instead, I selected models based on having the lowest AICc (section 2.4), and I considered any model within two units of AICc to be equally likely top models (Burnham and Anderson 2002; Wagenmakers and Farrell 2004; Arnold 2010; Burnham et al. 2011; Lukas and Clutton-Brock 2014). Of the models where $\Delta AICc < 2$, I identified the single best model as the most parsimonious one (i.e., fewest predictors/degrees of freedom) (Burnham and Anderson 2002; Arnold 2010) that also included sex as a predictor (only for models of the static value of social network position). I confirmed this choice by performing likelihood ratio tests comparing the top models within $\Delta AICc < 2$ (Tables A1-A4). Likelihood ratio tests have been proposed as a means of determining whether an independent variable

improves the predictive power of a model while maximizing the data used to generate the model (i.e., instead of splitting the dataset into training and testing sets) (Dobbin and Simon 2011; Pepe et al. 2013).

In addition to adjusted- R^2 values, I also used a Hosmer-Lemeshow goodness-of-fit test (HL test; function `hoslem.test`, package `ResourceSelection`; Lele et al. 2019) with the number of probability bins set to $g = 10$ (i.e., bins are $< 10\%$ probability, 10-20%, etc.) to assess model calibration (Hosmer et al. 2013; Fenlon et al. 2018; Shipe et al. 2019). Model calibration verifies that the model is unbiased in generating predictions across various probabilities – e.g., $< 10\%$ bin represents the probability that the data point is of an individual who remained in the society (1) rather than disappeared (0) – by comparing the proportion of observed 1 and 0 outcomes to the expected number of 1 and 0 outcomes between the probability bins (Fenlon et al. 2018). Despite shortcomings of the HL test, namely that the number of probability bins to use is arbitrary and that the test has greater statistical power with a greater sample size, this test is used frequently as a measure of calibration (Huang et al. 2020).

I then calculated the area under the curve (AUC) of the receiver operating characteristic curve to assess model discrimination, where discrimination refers to the capacity of the model to distinguish data points that have outcomes 1 and 0 (Shipe et al. 2019). In a regression, the AUC indicates the probability that an individual with observed outcome 1 will be expected (i.e., predicted based on the model) to have a greater probability associated with it than an individual with observed outcome 0 (Shipe et al. 2019). AUC varies from 0.5 to 1 where 0.5 indicates the model randomly discriminates/predicts whether an outcome will be 0 or 1 (e.g., disappeared or remained) and 1 indicates a 100% probability that an individual who is observed to remain (outcome 1) will be assigned a greater probability of remaining in the society than an individual

who was observed to have disappeared (outcome 0) (Shipe et al. 2019). To assess the predictive capacity of a model using AUC, a training dataset (~2/3 subset of full dataset) should be used to build the model and then AUC should be calculated using a novel testing (~1/3) dataset (Shipe et al. 2019). This was not possible in the current study due to limited sample size; instead, I calculated AUC for the same dataset I used to build the model as an indicator of model fit.

3.2.4 Post-Hoc Analysis: Matrix Correlations

To assess whether mode of disappearance affects the social network of the society differently, I performed an exploratory post-hoc analysis. Following Borgeaud et al. (2017), I limited the social network to only those individuals who were present both before and after a disappearance event. I checked the matrix correlations between the social networks of a society one month before (-30 to -1 days) and after (0 to 30 days) each disappearance event (Franz et al. 2015; Pfaff et al. 2023). I limited the analysis to disappearance events for which the mode of disappearance was confirmed and where one or more individuals disappeared by the same mode; that is, I kept events that involved two emigrations on the same day, but I omitted events involving one emigration and one unknown death on the same day. I kept events that occurred at around the same time even if they did not involve the same mode of disappearance. For each event, I classified each matrix correlation based on the mode of disappearance that occurred. I also did not account for differences in the number of individuals disappearing between events because I expected that the number of affected individuals may be part of the reason why a human-related death (e.g., large-scale poisoning) and an emigration (e.g., lone or joint parallel dispersal) differed. I also expected that human-related deaths may be less predictable than emigrations, and that there would thus be a greater change in the network when the

disappearance is unexpected (Shizuka and Johnson 2020). I compared the matrix correlations around human-related deaths to those around emigrations using a Welch two sample t-test.

3.3 Results

From January 2012 (M) and July 2016 (HC, KS) to July 2022, we recorded 162 disappearances among juveniles, subadults, and adults (M: 65, HC: 30, KS: 67). Of these, I analyzed 110 disappearances (M: 42, HC: 23, KS: 45) for which I could quantify the social network position of the disappearing individual and their sex was known (Table 3, bolded column). Of the human-related deaths, two monkeys were beaten and the remaining 20 were confirmed or suspected to have been poisoned. Among all disappearances, there were 13 demographic events involving 36 individuals that occurred on the same date; this included two (N = 10), three (N = 1), six (N = 1), or seven (N = 1; poisoning event) individuals. There were nine instances in which two or more demographic events occurred within one week of each other (≤ 7 days). Among emigrations, there were four confirmed occurrences of joint and/or sequential parallel dispersal (i.e., dispersal of multiple males between the same societies within 90 days where all involved males had a confirmed dispersal: L’Allier et al. 2022), involving a total of nine males. All emigrations involved subadult or adult males.

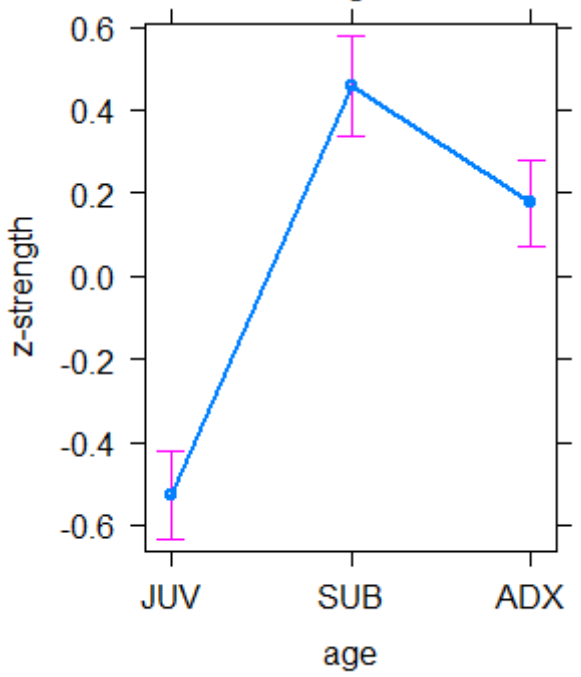
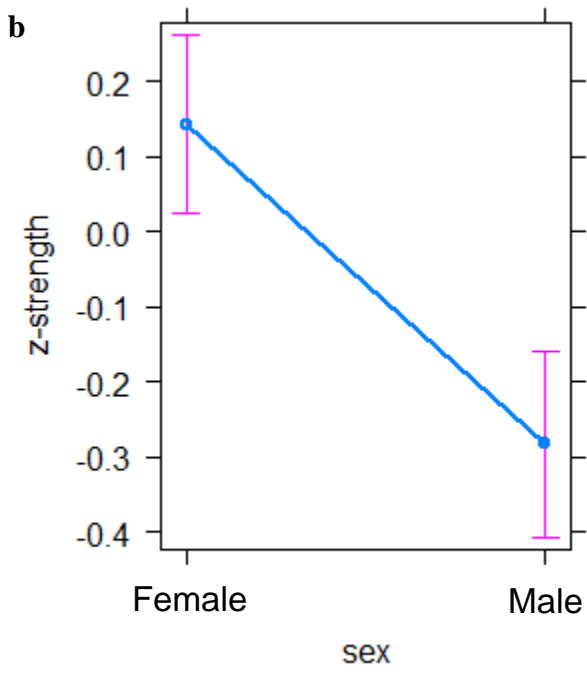
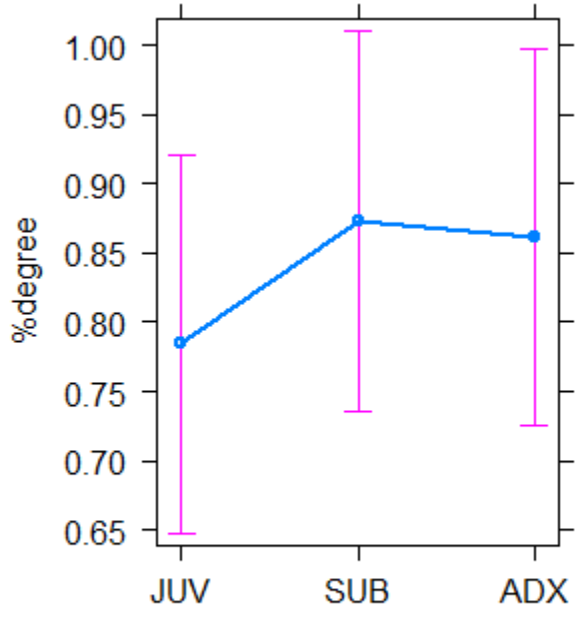
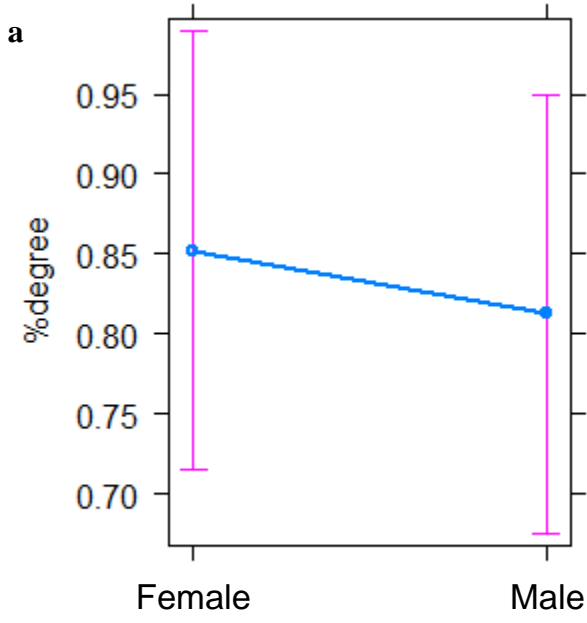
Table 3. Summary of the number of affected individuals per mode of disappearance for each model. Change refers to models concerning the change in dynamic social network position (subset of data) and static refers to models considering the static values of social network position. Events row gives the number of unique dates on which demographic events occurred.

Mode	Remained vs. all disappearances		Remained vs. emigrations		Remained vs. human-related disappearances		Emigrations vs. other disappearances	
	Change	Static	Change	Static	Change	Static	Change	Static
Emigration	29	32	29	32	-	-	29	32
Confirmed	16	19	16	19			16	19
Presumed	13	13	13	13			13	13
Human-related death	22	22	-	-	22	22	22	22
Confirmed	17	17			17	17	17	17
Presumed	5	5			5	5	5	5
Death by electrocution	2	3	-	-	-	-	2	3
Predation	2	2	-	-	-	-	2	2
Conspecific-related death	1	1	-	-	-	-	1	1
Unknown death	7	7	-	-	-	-	7	7
Unknown	37	43	-	-	-	-	-	-
Events	81	87	27	29	13	13	51	54

Bolded column indicates the summary of all disappearances analyzed.

3.3.1 Relationships Between Predictors

Sex and age were both significant predictors of the static values of the social network metrics (Table A5). Relative to females, males had a lower %degree (Figure 1a), z-strength (Figure 1b), z-eigenvector centrality (Figure 1c), and z-betweenness centrality (Figure 1d) (left panels). In turn, older individuals had a higher %degree, z-strength, and z-eigenvector than younger individuals, but only had a marginally higher z-betweenness (Figure 1, right panels). However, neither age nor sex explained the change in any of the dynamic social network metrics from baseline to the month before disappearance (t-test, all network metrics: sex: $t \leq |0.295|$, $p \geq 0.77$, age: $t \leq |1.633|$, $p \geq 0.1$; Table A6). Based on baseline data from one event per society in 2017, z-strength and z-eigenvector were highly correlated ($r = 0.9935$) while the other network metrics had low to moderate correlations (Table 4).



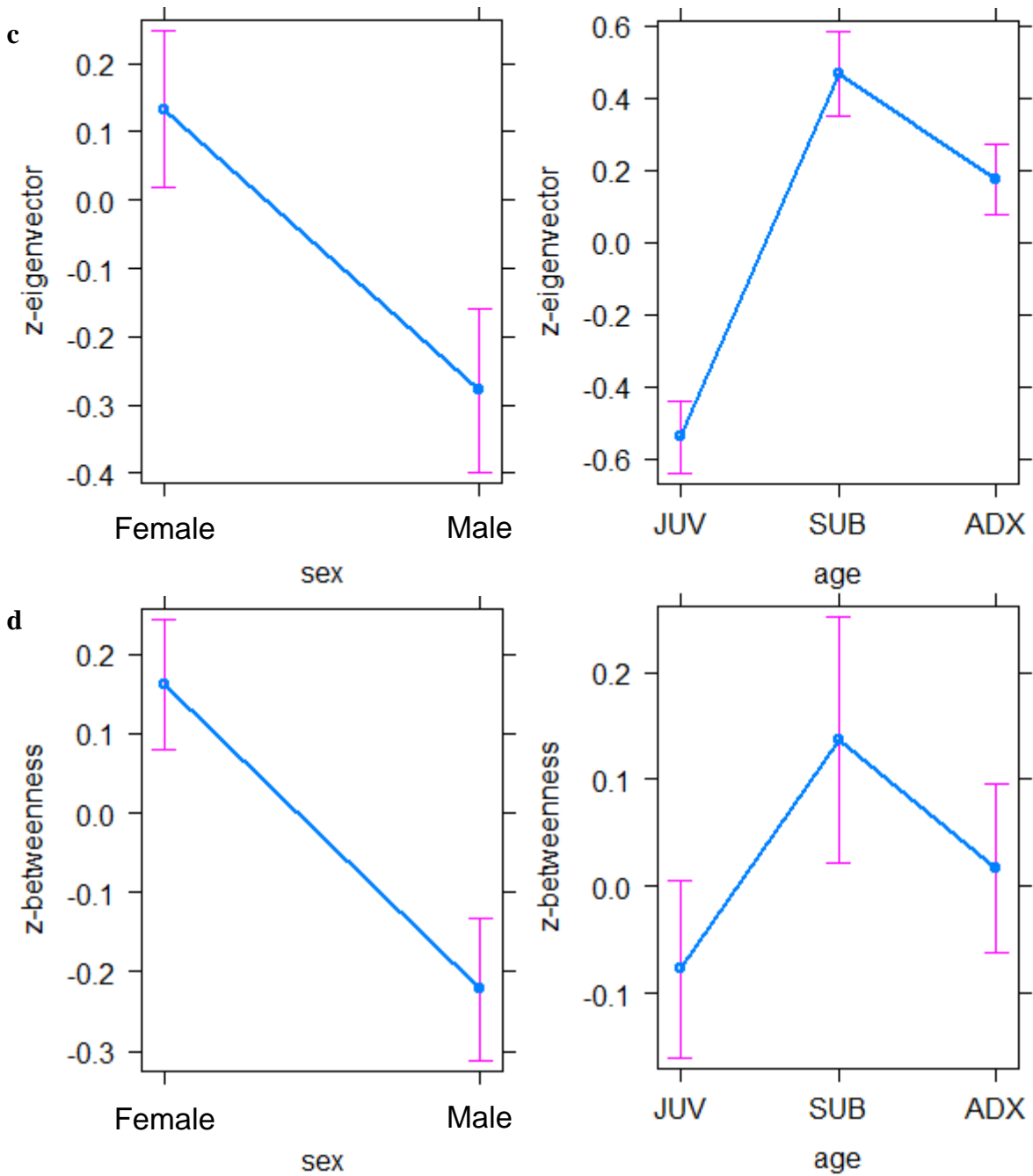


Figure 1. Relationship between social network metrics and sex (left panels) and age category (right panels) of vervet monkeys from three societies at Lake Nabugabo, Uganda. Age refers to age classes: juvenile (JUV), subadult (SUB), and adult (ADX). (a) Degree centrality as a percent of direct partners out of all potential partners in a network. (b) Strength, (c) eigenvector centrality, and (d) betweenness centrality as z-scores comparing individuals in the same network.

Table 4. Correlation coefficients (r) between social network metrics and dominance rank using the static values of each metric from the baseline data (-60 to -31 days before a demographic event occurred). One demographic event was chosen per society (M, HC, KS) at Lake Nabugabo, Uganda to avoid repeated measures per individual. The events were chosen from 2017 or later to ensure data collection techniques were consistent across societies and the specific event was chosen for having the greatest number of individuals within the network whose proportional ranks could be computed. Events occurred on: M: 2017-02-11, HC: 2017-05-18, KS: 2017-08-04. %degree refers to the proportion of individuals within a society with whom a focal animal associated. The z- metrics refer to the z-scores for each metric.

	%degree	z-strength	z-betweenness	z-eigenvector	Proportional rank
%degree	1				
z-strength	0.3382*	1			
z-betweenness	0.1102	0.6010*	1		
z-eigenvector	0.3309*	0.9935*	0.5740*	1	
Proportional rank	-0.0529	-0.1291	0.0928	-0.1362	1

*Statistically significant correlation ($p < 0.05$).

3.3.2 Remained versus All Disappearances

3.3.2.1 Change in Social Network Position

Comparing all individuals of known sex who disappeared by any mode (N = 100 with 59 males and 41 females) to those who remained within their society (Table 3), the best of five models within 2 AICc included age, sex, z-betweenness, and z-eigenvector as predictors (AICc = 810.3; Table A1). As predicted, individuals statistically more likely to disappear were older individuals (linear component of age (age.L): estimate \pm SE = -0.583 ± 0.185 , $z = -3.143$, $p = 0.002$), with a greater difference between subadults and adults rather than juveniles and subadults (quadratic component of age (age.Q): 0.422 ± 0.207 , $z = 2.036$, $p = 0.042$; Table A7). Males (sex: -0.767 ± 0.218 , $z = -3.516$, $p < 0.001$) and individuals with a decrease in z-eigenvector (0.417 ± 0.138 , $z = 3.024$, $p = 0.003$; Figure 2) were also more likely to disappear by any mode. In addition, there was a trend towards individuals with a decrease in z-betweenness being more likely to disappear (0.184 ± 0.095 , $z = 1.930$, $p = 0.054$; Figure 2). As predicted, individuals who disappeared tended to have a decrease in their social network position (z-betweenness: mean = -0.387 , z-eigenvector: -0.287) from baseline to the month prior to disappearance, while individuals who remained within the society had a small increase in their social position (z-betweenness: mean = 0.017 , z-eigenvector: 0.049 ; Figure 3). Based on the Hosmer-Lemeshow goodness-of-fit test (HL test), there was no evidence that the model was not well-calibrated ($\chi^2 = -1847.7$, $df = 8$, $p = 1$). However, the predictors explained very little variation in the outcome variable (adjusted- $R^2 = 0.017$) and the model did not discriminate well between individuals who remained versus disappeared (AUC = 0.683; Table A1).

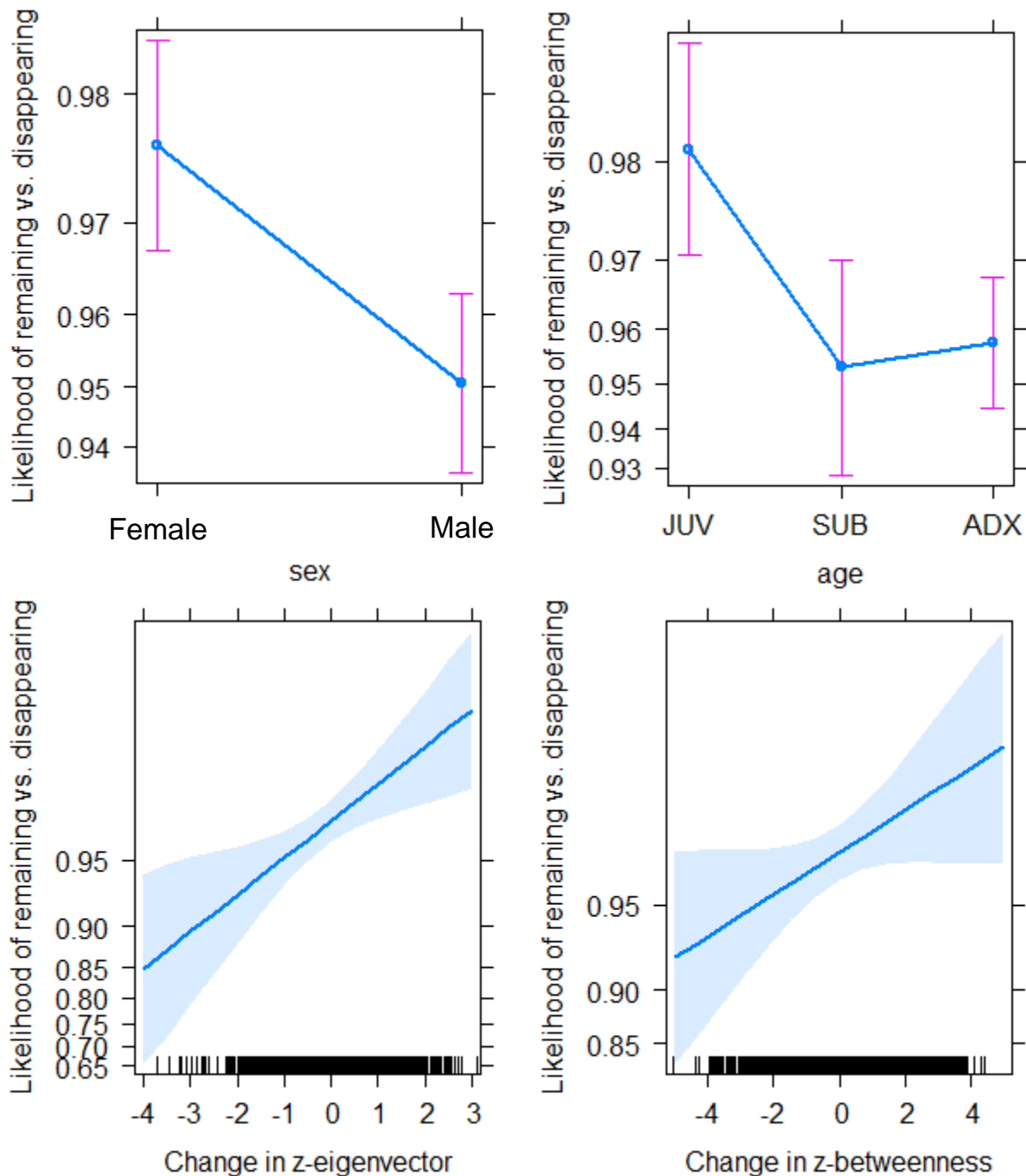


Figure 2. Relationship between individual characteristics and whether individuals remained in their society (1) or disappeared by any modes (0) among three societies of vervet monkeys at Lake Nabugabo, Uganda (M, HC, KS). Top left is the relationship to sex. Top right is the relationship between age class – juvenile (JUV), subadult (SUB), and adult (ADX) – and probability of remaining in the society. Bottom left is the association with the change in eigenvector centrality (as a z-score) from baseline (-60 to -31 days before a disappearance) to the month before a disappearance (-30 to -1 days). Bottom right is the association with the change in betweenness centrality (z-score).

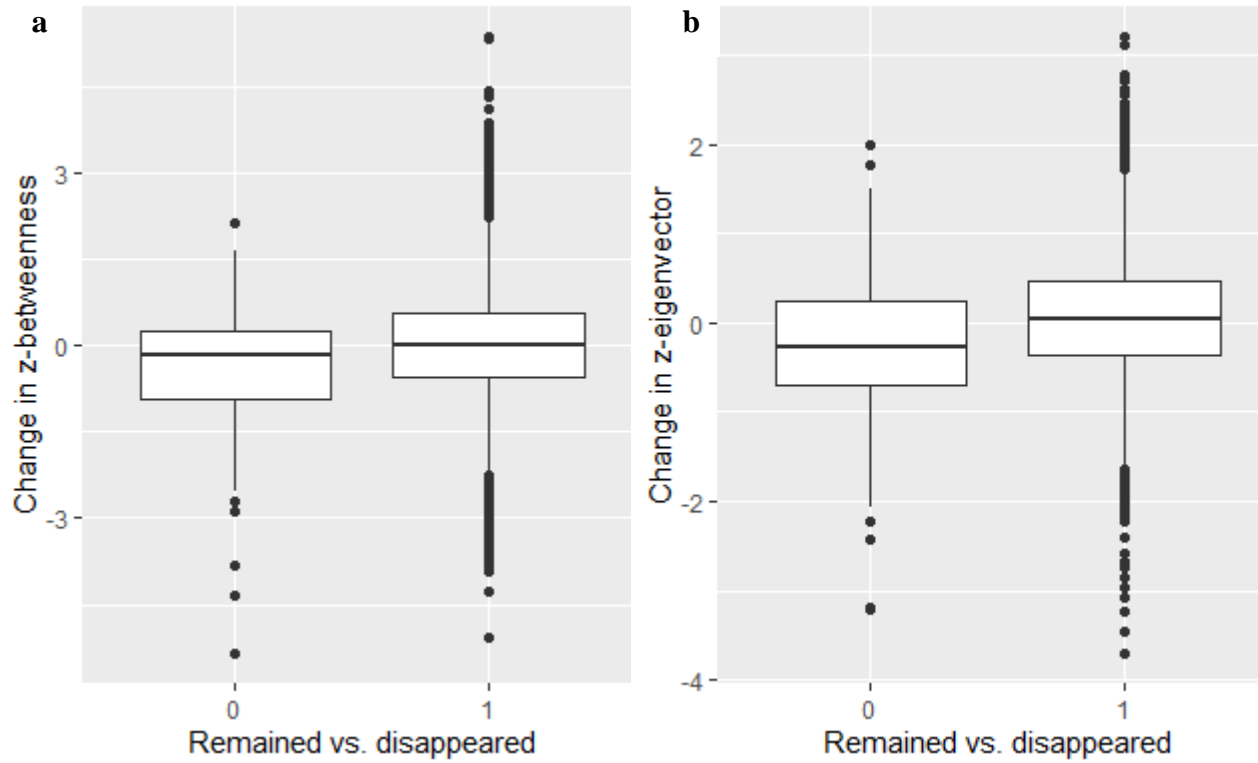


Figure 3. Distribution of the change in (a) betweenness centrality (as a z-score) and (b) eigenvector centrality (z-score) from the baseline condition (-60 to -31 days before a disappearance) to the month immediately before a disappearance (-30 to -1 days). Comparing vervet monkeys at Lake Nabugabo, Uganda (M, HC, KS societies) who disappeared from their society by any mode (0 on x-axis) to those who remained within their society (1).

3.3.2.2 Static Social Network Position

Comparing individuals who disappeared by any mode (N = 110 with 63 males and 47 females) to those who remained within their society (Table 3), the best model among three equally likely options included age, sex, z-eigenvector, and the interactions between age and sex, and age and z-eigenvector (AICc = 889.8; Table A3). Individuals statistically more likely to disappear by any mode were older (age.L: -0.783 ± 0.286 , $z = -2.737$, $p = 0.006$), male (sex: -0.846 ± 0.336 , $z = -2.518$, $p = 0.012$), and individuals with a lower z-eigenvector (0.569 ± 0.135 , $z = 4.214$, $p < 0.001$; Table A7). There was also a significant relationship between sex and the quadratic component of age (1.636 ± 0.728 , $z = 2.247$, $p = 0.025$) and z-eigenvector and the quadratic component of age (-0.679 ± 0.268 , $z = -2.529$, $p = 0.011$), where subadult males and subadults with a lower z-eigenvector were most likely to disappear (Figure 4). There was no evidence that the model was not well-calibrated (HL test: $\chi^2 = -2058.0$, $df = 8$, $p = 1$). However, the predictors explained very little variance (adjusted- $R^2 = 0.013$) and the model did not discriminate well between individuals who remained versus those who disappeared (AUC = 0.691; Table A3).

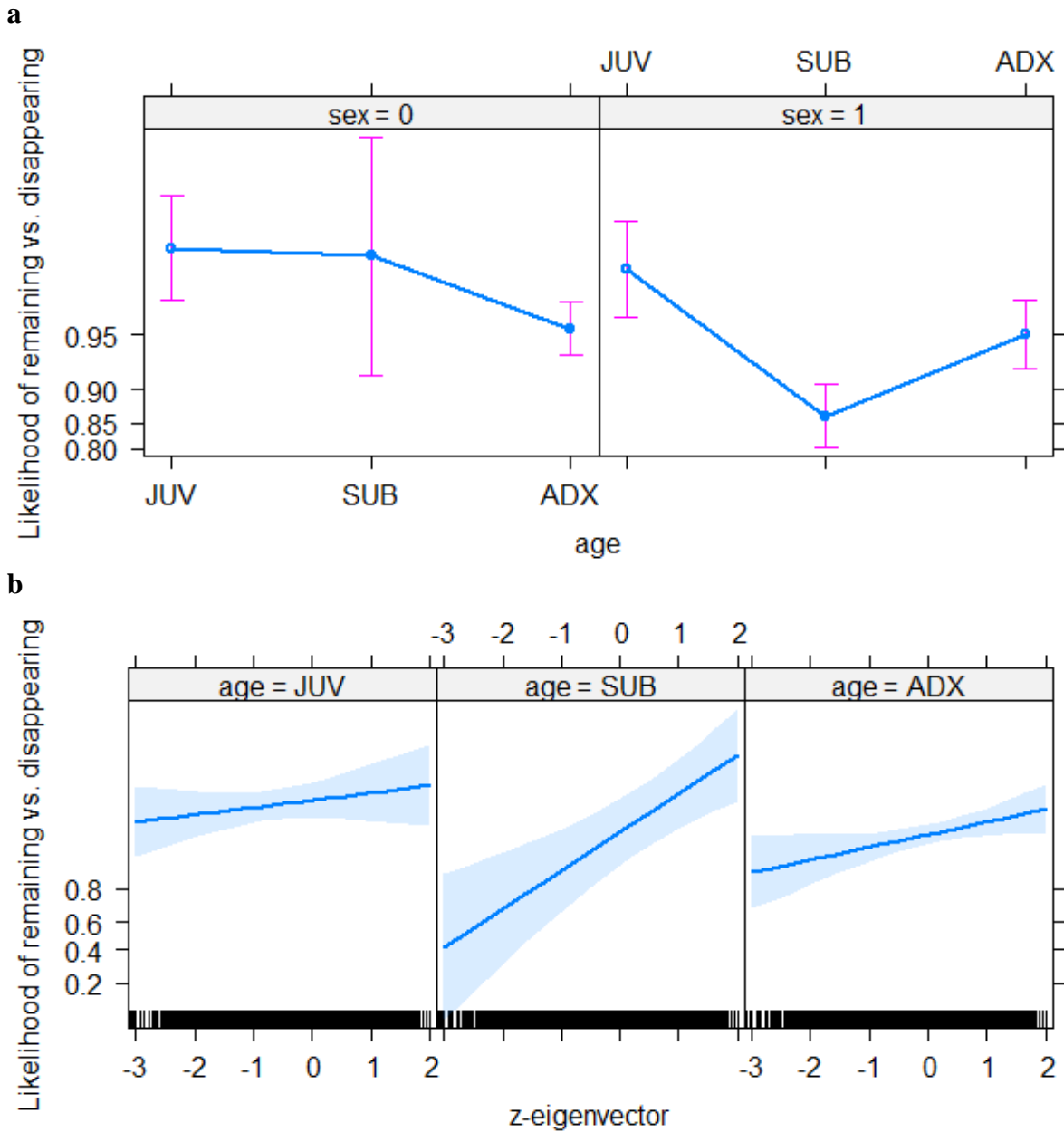


Figure 4. Relationship between individual characteristics and whether individuals remained in their society (1) or disappeared by any mode (0) among three societies of vervet monkeys at Lake Nabugabo, Uganda (M, HC, KS). (a) The relationship between age class – juvenile (JUV), subadult (SUB), and adult (ADX) – and probability of remaining within the society in reference to sex (where 0 is female and 1 is male). (b) The relationship to eigenvector centrality (as a z-score) in the month before disappearance (-30 to -1 days) in reference to age.

3.3.3 *Remained versus Emigrated*

3.3.3.1 Change in Social Network Position

When only considering confirmed or suspected emigrations (Table 3), the best of two models within 2 AICc only included age and sex as predictors (AICc = 179.4; Table A1). Older individuals were less likely to remain than to emigrate (age.L: -2.569 ± 1.018 , $z = -2.524$, $p = 0.012$), with a greater difference between subadults and adults rather than juveniles and subadults (age.Q: 1.722 ± 0.633 , $z = 2.721$, $p = 0.007$; Table A7). As predicted, males were more likely to emigrate than females (sex: -4.515 ± 1.420 , $z = -3.180$, $p = 0.001$; Figure 5). The model of remaining versus emigration showed no evidence of being poorly calibrated (HL test: $\chi^2 = 638.4$, $df = 8$, $p = 1$), and explained a greater amount of variance (adjusted- $R^2 = 0.211$) and was better able to discriminate individuals who remained within the society from those who emigrated (AUC = 0.890) than the previous model examining the likelihood of remaining versus disappearing by any mode. The results were qualitatively similar when I only considered males (i.e., age was the only significant predictor; Table A1).

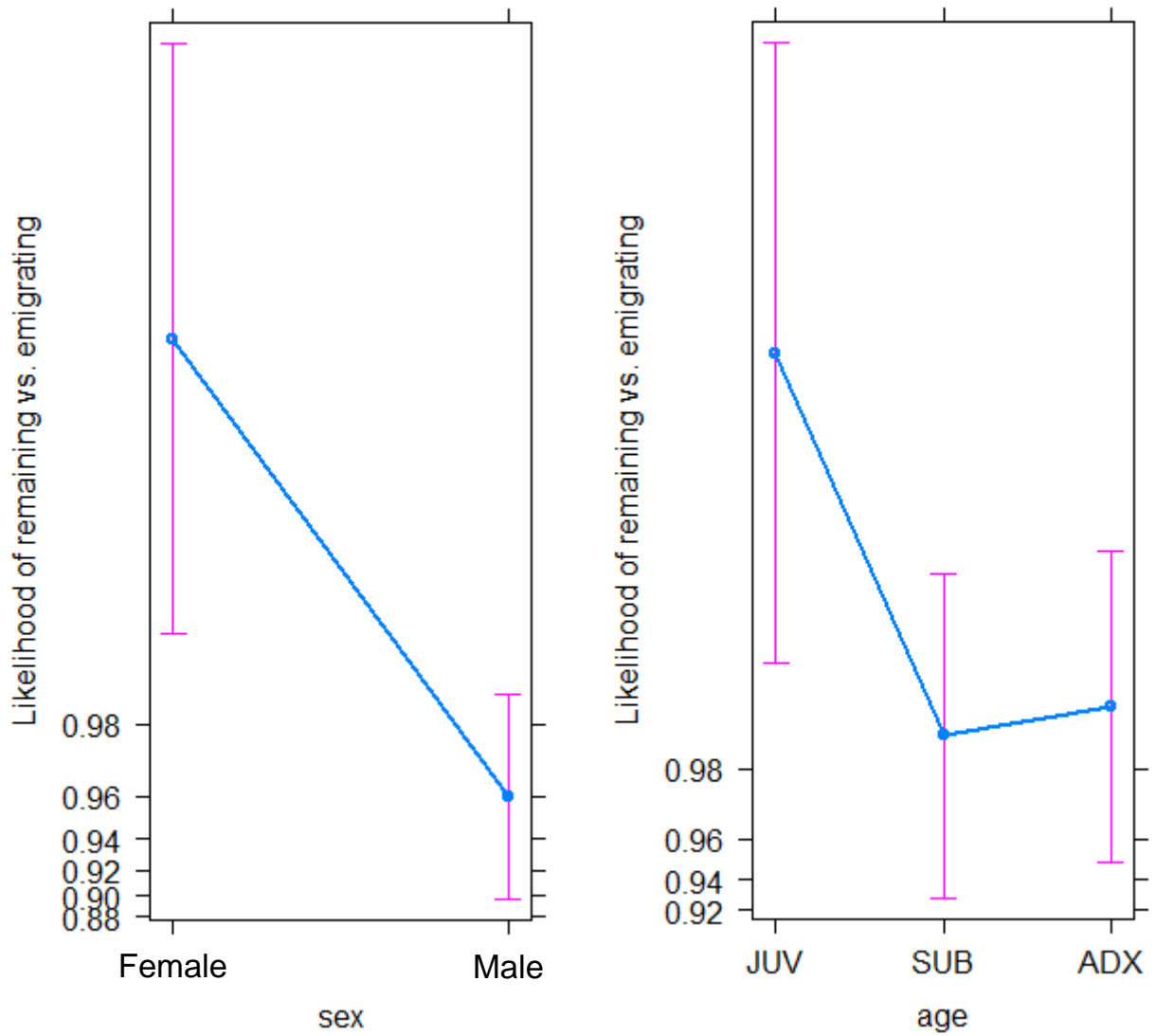


Figure 5. Relationship between sex and age and likelihood a vervet monkey remained within their society (1) or disappeared by emigration (0). Age classes are given as juvenile (JUV), subadult (SUB), and adult (ADX).

3.3.3.2 Static Social Network Position

When considering static social position, sex and age were once again the only predictors included in the best model (AICc = 195.6) among four potential models (Table A3) predicting which individuals remained in their society versus emigrated (Table 3). Males (sex: -4.543 ± 1.416 , $z = -3.208$, $p = 0.001$) and older individuals were more likely to emigrate than to remain (age.L: -2.616 ± 1.017 , $z = -2.573$, $p = 0.010$), with a greater difference between subadults and adults rather than juveniles and subadults (age.Q: 1.956 ± 0.625 , $z = 3.128$, $p = 0.002$; Table A7). The model had no evidence of being poorly calibrated (HL test: $\chi^2 = -728.3$, $df = 8$, $p = 1$), explained some variance (adjusted- $R^2 = 0.215$), and was relatively good at discriminating individuals who remained within the society from those who emigrated (AUC = 0.900) compared to the previous model of remained versus disappeared. Once again, results were qualitatively similar when I limited the data to only males (results not presented; Table A3).

3.3.4 Remained versus Human-Related Disappearance

3.3.4.1 Change in Social Network Position

Unlike emigrations which were not explained by social position, the best model (four possible models within 2 AICc) comparing individuals who remained to those who had a confirmed or suspected human-related disappearance (poisoning or beating; Table 3) included age, z-eigenvector, and %degree (AICc = 164.4; adjusted- $R^2 = 0.039$; HL test: $\chi^2 = -311.3$, $df = 8$, $p = 1$; AUC = 0.757; Table A1). Contrary to predictions, individuals who had a human-related disappearance tended to decrease in their eigenvector centrality (mean = -0.377) from baseline to the month prior to their disappearance, whereas those who remained in the society showed an increase in eigenvector (mean = 0.066 ; z-eigenvector: 1.033 ± 0.310 , $z = 3.336$, $p < 0.001$; Figure 6, 7). The interaction of age and change in degree was also a significant predictor (age.L

by %degree: 3.874 ± 1.941 , $z = 1.995$, $p = 0.046$; age.Q by %degree: -11.849 ± 4.819 , $z = -2.459$, $p = 0.014$; Table A7), where juveniles who disappeared tended to increase in their degree, subadults decreased, and, for adults, the change in degree did not predict the likelihood of a human-related disappearance (Figure 6).

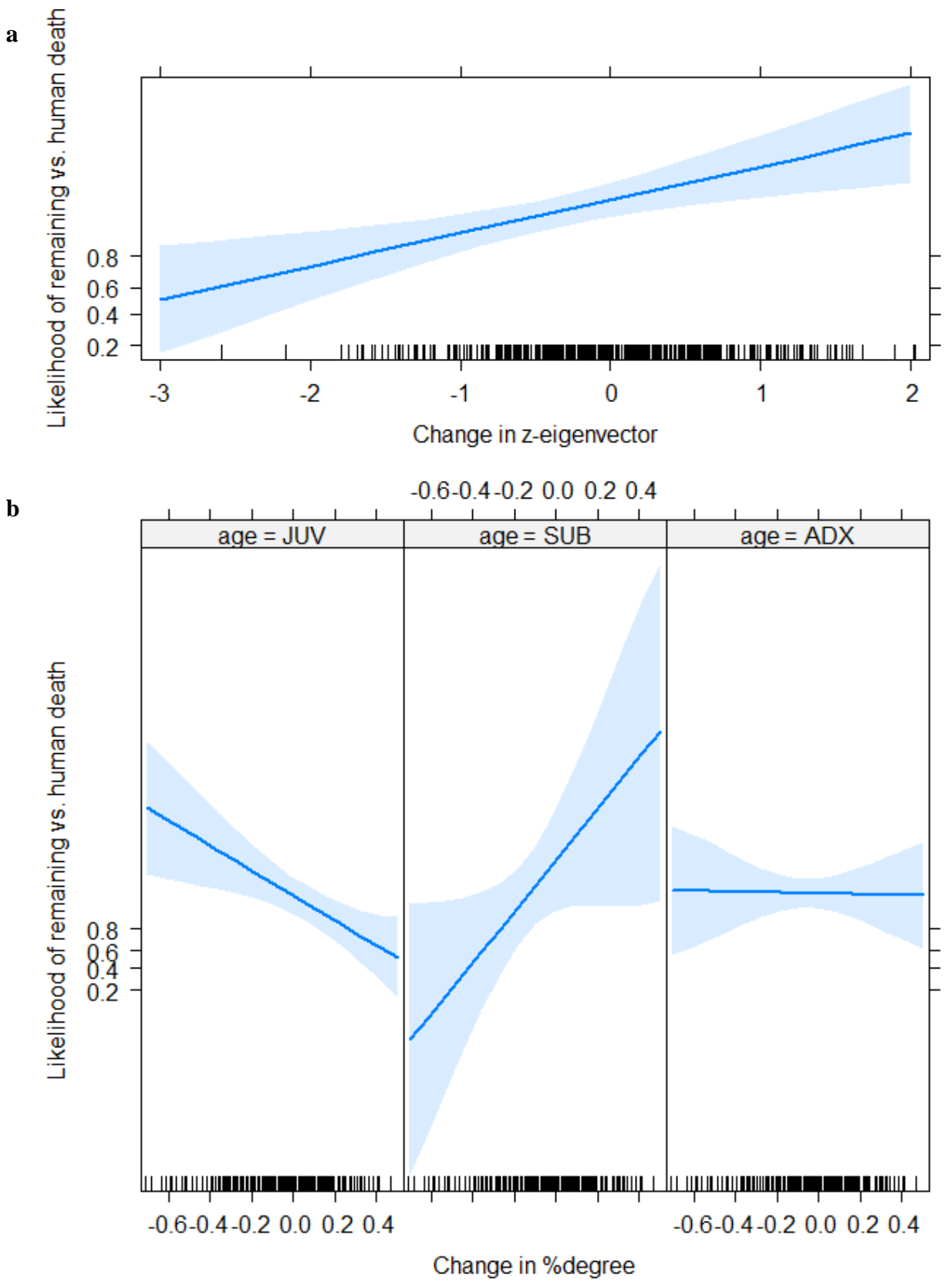


Figure 6. Relationship between individual characteristics and whether individuals remained in

their society (1) or disappeared as a result of human activities (0) among three societies of vervet monkeys at Lake Nabugabo, Uganda (M, HC, KS). (a) The relationship between likelihood of remaining in the society and change in eigenvector centrality (given as a z-score) from baseline (-60 to -31 days before a disappearance) to the month before a disappearance (-30 to -1 days). (b) The relationship between likelihood of remaining for each age class and change in degree centrality as a percent of the social network with whom an individual associated. Age classes are juvenile (JUV), subadult (SUB), and adult (ADX).

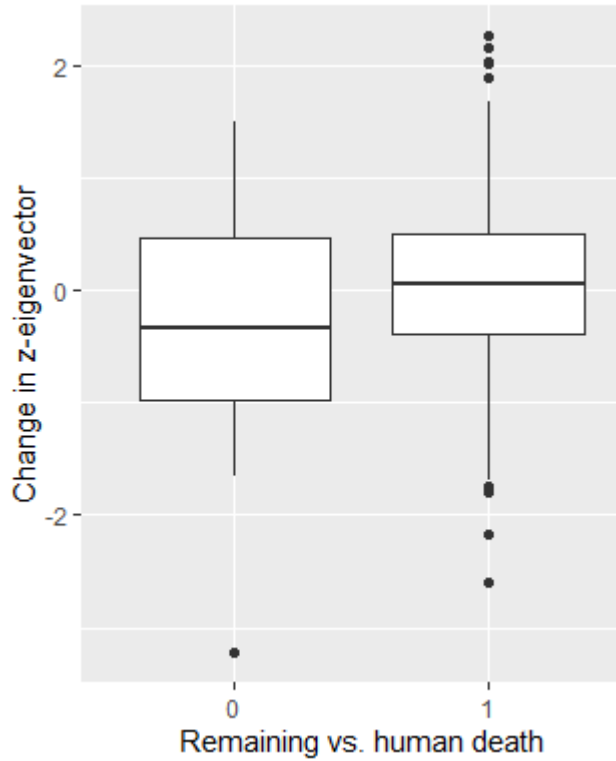
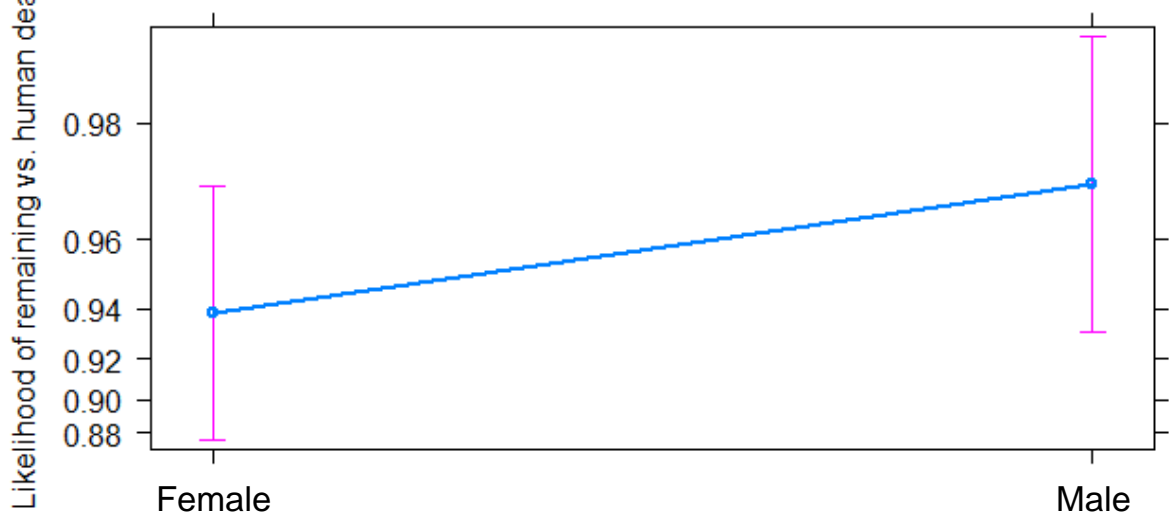


Figure 7. Distribution of the change in eigenvector centrality (as a z-score) from the baseline condition (-60 to -31 days before a disappearance) to the month immediately before a disappearance (-30 to -1 days). Comparing vervet monkeys at Lake Nabugabo, Uganda (M, HC, KS societies) who disappeared as a result of human activities (0 on x-axis) to those who remained within their society (1).

3.3.4.2 Static Social Network Position

Just as when I considered the change in social network, static social position was a predictor of whether an individual remained or had a human-related disappearance (Table 3). The best model out of seven equally likely models (AICc = 171.3; adjusted-R² = 0.223; HL test: $\chi^2 = -315.8$, df = 8, p = 1; AUC = 0.653; Table A3), incorporated age, sex, z-eigenvector, and the interaction of age and z-eigenvector as predictors. Individuals who were less socially central (z-eigenvector: 3.041 ± 1.594 , z = 1.908, p = 0.056; Figure 8) tended to be more likely to have a human-related death than to remain in the society. I controlled for age (age.L: -0.259 ± 0.388 , z = -0.667 , p = 0.505) and sex (0.786 ± 0.520 , z = 1.511, p = 0.131) in the best model despite not being significant predictors (Table A7).

a



b

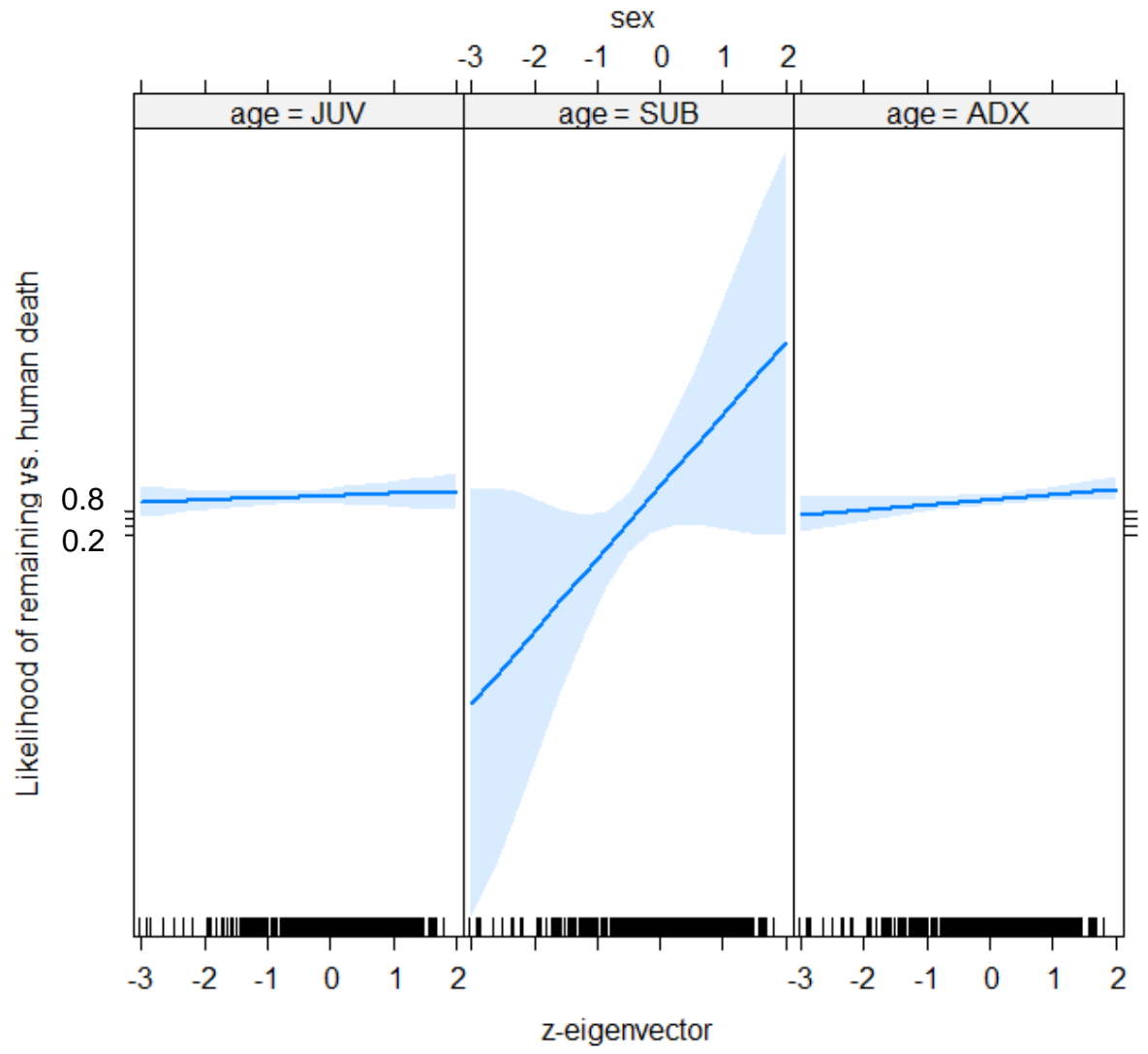


Figure 8. Relationship between individual characteristics and whether individuals remained in their society (1) or disappeared as a result of human activities (0) among three societies of vervet monkeys at Lake Nabugabo, Uganda (M, HC, KS). The left figure indicates the relationship between sex and probability of remaining within the society. The right figure is the relationship to eigenvector centrality (as a z-score) in the month before disappearance (-30 to -1 days) in reference to age class – juvenile (JUV), subadult (SUB), and adult (ADX).

3.3.5 *Emigration versus Other Modes of Disappearance*

3.3.5.1 Change in Social Network Position

When comparing individuals who emigrated and those who disappeared by any other known or suspected modes (i.e., human-related, electrocution, predation, conspecific-related, unknown death; Table 3), four individuals disappeared twice, either emigrating twice or emigrating and then having a human-related disappearance. Out of four models within 2 AICc, the best model comparing emigrations and other disappearances included only sex and age as predictors (AICc: 45.9; Table A1). Males (sex: 4.982 ± 1.595 , $z = 3.124$, $p = 0.002$) and older individuals (age.L: 2.965 ± 1.181 , $z = 2.511$, $p = 0.012$; Figure 9) were more likely to emigrate than to disappear by other modes (Table A7). There was no evidence the model was poorly calibrated (HL test: $\chi^2 = -45.9$, $df = 8$, $p = 1$). The model also discriminated well between those who emigrated and those who disappeared by other modes (AUC = 0.906), and it explained a lot of variance (adjusted- $R^2 = 0.648$; Table A1).

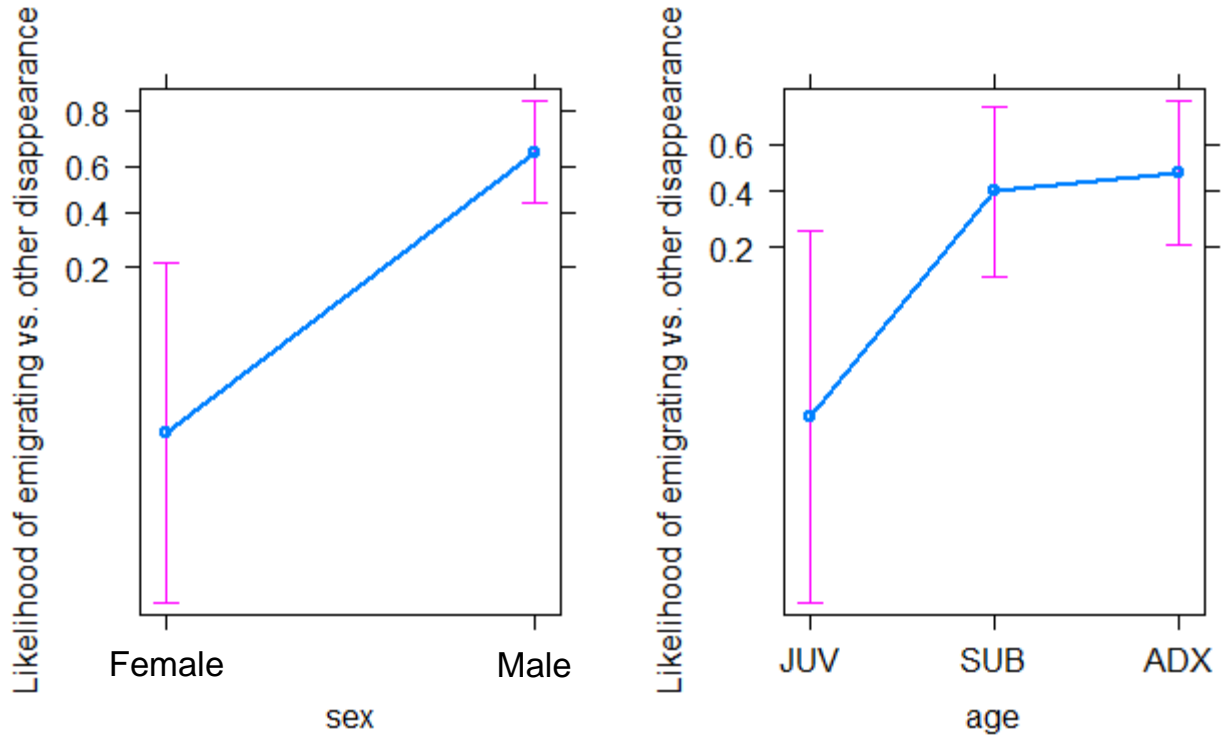


Figure 9. Relationship between sex and age and likelihood a vervet monkey emigrated from their society (1) or disappeared by any other known or suspected modes (0). Age classes are given as juvenile (JUV), subadult (SUB), and adult (ADX). Figure based on dataset looking at dynamic social network position.

3.3.5.2 Static Social Network Position

Based on the best of three possible models (AICc = 47.2; adjusted-R² = 0.655; HL test: $\chi^2 = -45.8$, df = 8, p = 1; AUC = 0.904; Table A3), sex and age were the only two factors that predicted whether an individual would emigrate or disappear by other known or suspected modes (Table 3). Males were more likely to emigrate than to disappear by other modes (5.041 ± 1.592 , $z = 3.167$, p = 0.002), and there was a greater difference between juveniles and subadults than between subadults and adults (age.Q: -1.607 ± 0.813 , $z = -1.976$, p = 0.048), but only a trend toward older individuals being more likely to emigrate (2.966 ± 1.181 , $z = 2.510$, p = 0.121; Table A7).

3.3.6 Post-Hoc Analysis: Matrix Correlations

The mean correlation coefficient of matrices before and after emigrations was 0.913, while the mean coefficient before and after human-related deaths was 0.898. The matrix correlations did not differ significantly between these two modes of disappearance ($t(21.756) = 0.582$, p = 0.567).

3.4 Discussion

Overall, sex, age, and social centrality, especially eigenvector centrality, explained various disappearance patterns. Sex and age were the most important factors in explaining which individuals were most likely to disappear. Males, older individuals, and those with a lower eigenvector centrality or a decrease in their eigenvector were more likely to disappear. Likewise, males and older vervets tended to be more likely to emigrate than to remain or to disappear by other modes (i.e., human-related disappearance, predation, electrocution, conspecific-related death, unknown death), although age was not consistently a significant predictor. In contrast to

emigrations, human-related disappearances were not significantly explained by sex nor age. Instead, vervets who had a human-related death tended to decrease in or have a lower social centrality compared to individuals who survived, though the pattern differed based on age category. Consequently, sex and age alone explained emigrations and influenced the mode of disappearance of the vervets while social centrality explained human-related deaths.

3.4.1 All Disappearances and Emigrations

The finding that sex was a predictor of various disappearance modes supported the prediction (1a, Table 1) that, on average, males are more likely to disappear than females, which is consistent with female philopatry and male-biased dispersal (Cheney 1981). Compared to males and younger vervets, females and older individuals were more socially central (1b): they had more partners, as a percent of realized to potential partners (%degree centrality), associated more frequently (z-strength) and with partners who also associated with others frequently (z-eigenvector), and they connected more individuals within the network (z-betweenness), although age was only marginally significant in predicting z-betweenness. That females, the philopatric sex, tended to be more socially central than males was consistent with other primate studies (Perry 1996; Sterck et al. 1997; Lehmann and Ross 2011; Borgeaud et al. 2017), though this did not preclude males, the dispersing sex, having differentiated relationships (Lehmann and Boesch 2009).

Unlike sex, there have been mixed results regarding the influence of age on sociality. Among wild vervets, one study found younger individuals were more socially central than adults in the grooming network (higher degree and unweighted eigenvector; Canteloup et al. 2021) while another study showed a non-significant trend toward older individuals being more socially central (Borgeaud et al. 2017). In the grooming network of rhesus macaques, individuals of each

age-class did not differ significantly in their degree centrality, strength, eigenvector, nor betweenness, although adults had the greatest betweenness values (Liao et al. 2018). Ultimately, both juveniles and adults were central in different networks (approach, grooming, play), but juveniles tended to interact with many partners whereas adults interacted at the same frequency (i.e., similar strength) with fewer partners (Liao et al. 2018). Similarly, female Barbary macaques tended to have a lower eigenvector and degree centrality as they aged (Sosa 2016). Compared to juveniles, adult olive baboons initiated grooming more frequently and received grooming from more partners, but juveniles were more central in terms of betweenness, partners they directed grooming toward, and frequency of grooming received (Fedurek and Lehmann 2017). These differences may result from other studies using direct interactions (namely grooming or play) to define the social network rather than using the proximity network.

When considering all disappearances, the mode of disappearance for most events was unknown, followed by both confirmed and presumed emigrations, and then human-related deaths. Since emigrations made up 29% of all disappearances (48% when excluding unknowns, Table 3), it followed that males would be more likely to disappear than females (1a). Likewise, emigrations were limited to subadults and adults, so the pattern that older individuals were more likely to emigrate also followed the results for all disappearances. Focusing on unknown modes of disappearance, these may include any of the modes discussed, such as dispersal, human- or conspecific-related death, predation, electrocution, in addition to water and food stress (Young et al. 2019), old age/senescence (Frye et al. 2021), or disease/poor health (Fairbanks and McGuire 1986). Nutritional or hydration stress are unlikely in the Nabugabo population since natural food availability is relatively consistent over time (Schwegel et al. 2022), the vervets are known to forage crops, raid kitchens, and receive tourist handouts (Chapman, Twinomugisha, et al. 2016),

and the population lives along the edge of a freshwater lake. Given the Lake Nabugabo research site is a forest-agriculture matrix, it is possible that an individual's body may not have been discovered, but it is more likely that the body was somehow moved, whether by dispersing to a new society, being predated, or being scavenged. As such, I would expect that human- or conspecific-related death and electrocution would be less likely causes of "unknown" disappearances. Considering predation, disease, and senescence as potential modes of "unknown" disappearance, older individuals would sensibly be more likely to disappear by one of these modes, although young individuals may also be prone to predation (Janson and van Schaik 1993). For example, age and gait speed (i.e., time to traverse a certain distance) were inversely related in captive vervets (*Chlorocebus aethiops sabaesus*) (Frye et al. 2021), such that older individuals may be more vulnerable to predators (Fuller and Keith 1980; but see Janson and van Schaik 1993). However, the relationship of age and predation may be mediated by the preferences of predators: birds of prey, such as martial eagles, and baboons tend to target younger vervets whereas leopards may aim for adults, and snakes, such as pythons, may be more flexible (Cheney and Seyfarth 1981). The main predators of the Nabugabo vervets are snakes, dogs (Teichroeb et al. 2015), and birds of prey (unpublished data), for whom prey preferences are not necessarily known. Regarding disease and senescence, both are related to aging (McHugh and Gil 2018), and individuals may become socially peripheral as their health declines (Veenema et al. 1997; Shizuka and Johnson 2020). Likewise, individuals who are or became socially peripheral may be more likely to be predated (Hamilton 1971). Being socially peripheral in the proximity network may indicate that an individual is more frequently spatially separated or spatially peripheral to the society relative to more socially central monkeys (Kalbitzer et al. 2017). Among vervets, females and dominant individuals tend to be spatially central when the

society is at rest (Teichroeb et al. 2015). In turn, dominant primates are often socially central (Schino 2001; Silk et al. 2003; Sueur, Petit, et al. 2011; Bret et al. 2013), although this was not the case for the Nabugabo vervets. When the society is at rest, individuals at the periphery are at greater risk of predation (Hamilton 1971), suggesting lower-ranking, and presumably socially peripheral, individuals may be more likely to be predated. However, when the society is moving, high-ranking individuals tend to be at the leading edge (Teichroeb et al. 2015) and are at greater risk of predation (Bumann et al. 1997). Consistent with predictions surrounding predation risk and disease/senescence, I found that vervets were more likely to disappear by any mode than to remain within their society if they had a lower eigenvector centrality (especially among subadults) or a decrease in their eigenvector, and there was a similar trend for those who decreased in betweenness centrality. Consequently, my results supported the prediction that individuals who disappeared by any mode would be less socially central than those who remained in the society (1c). Alongside the finding that males are less socially central than females and males are more likely to disappear, the hypothesis (1) that sex-specific philopatry and dispersal influence sociality was supported.

Consistent with my prediction (2a), older male vervets were more likely to emigrate than younger individuals or females. The field team only recorded subadult and adult males emigrating from the studied societies, which is consistent with vervets having male-biased dispersal and the goal of emigration being inbreeding avoidance (i.e., sexually mature individuals are the ones dispersing). However, this pattern was not universal: we recorded five adult and subadult females immigrating into these study societies alongside two short-term immigrant juveniles of unknown sex. I could not include these data in the analyses, though, because they involved immigrations from unknown societies, and thus there was no social

network context for why these vervets may have dispersed. Female dispersal in a female philopatric species tends to be rare but not absent. For example, female dispersals among white-faced capuchins do not appear to be related to inbreeding avoidance and instead tended to occur following a male takeover, likely to avoid infanticide (Jack and Fedigan 2009). Overall, the few observations of Nabugabo females dispersing suggest that the models of emigration are biased against female and juvenile dispersals, and that our record of presumed emigrations may be incomplete since females are generally discounted as having dispersed.

Unlike age and sex, social centrality and dominance rank did not explain emigration patterns. As predicted (2b), the static social position and dominance rank of emigrating males in the month prior to disappearance was similar to the social position and rank of individuals (males and females together, and males alone) who remained within the society. Specifically, neither static centrality nor rank explained which individuals dispersed. A difference in static social centrality could have indicated the emigrating males were on the verge of eviction (Larson et al. 2018), and thus no difference helps support that dispersals were voluntary. The lack of relationship between disappearance via emigration and social centrality may reflect how dispersal decisions are made. Among the Lake Nabugabo vervets, dispersals are all voluntary rather than due to eviction (L'Allier et al. 2022), suggesting dispersals are timed rather than forced. Accordingly, dispersals occurred around the same time as the mating season and males dispersed into a society with an improved sex-ratio and/or where they increased their dominance rank (L'Allier et al. 2022). Moreover, natal dispersals occurred around the time a male reached the age of sexual maturity and the tenure length of non-natal males coincided approximately with the time it would take their daughters to reach sexual maturity, suggesting males were ultimately avoiding inbreeding (L'Allier et al. 2022). Together, these results indicate that the timing of male

dispersals is related to avoiding inbreeding and improving their reproductive success (hypothesis 2). While social centrality tends to improve reproductive success (Weidt et al. 2008; Cameron et al. 2009; Brent et al. 2013; Cheney et al. 2016; Kalbitzer et al. 2017; McFarland et al. 2017), this improvement occurs primarily within the society. If the individual remains in their society longer than the time for them or their daughters to reach sexual maturity, they may risk lower reproductive success via inbreeding. Consequently, social position would likely not be a factor in determining whether an individual disperses or not, and thus, individuals of any social position should be susceptible to dispersing. Just as social position did not predict emigration, male dominance rank also varied among the emigrating Nabugabo males (L'Allier et al. 2022), and thus did not predict emigrations. Among yellow-bellied marmots, characterized by male-biased dispersal where most males emigrate at one year but about 50% of females also emigrate, female marmots who were more central, particularly in the affiliative network, were less likely to disperse compared to less central females, consistent with the social cohesion hypothesis (Blumstein et al. 2009). However, centrality, as measured by embeddedness and degree, did not affect whether a male marmot dispersed (Blumstein et al. 2009). These results suggest male dispersal decisions are not based on social integration (Blumstein et al. 2009), but rather based on natural history.

Both findings (2a,b) – that older males were more likely to disperse and emigrating males did not differ in static social centrality – are in line with inbreeding avoidance, and, by extension, that dispersals are voluntary. However, I anticipated males would visit or prospect to other societies prior to emigration with consequences for the social network. As predicted (2c), I observed no drop in the rank of emigrating individuals from baseline to the month prior to disappearance relative to individuals who remained in their society or disappeared by other

means. This finding is further evidence that male dispersals are voluntary in that the males did not receive aggression that prompted their emigration. However, contrary to my prediction regarding social centrality (2d,e), I did not observe a decrease in a male's centrality prior to his dispersal relative to individuals who remained or those who disappeared by other modes.

Theoretically, voluntarily dispersing males will visit or prospect other societies prior to emigration to investigate reproductive opportunities and barriers to immigration within the new society (Teichroeb et al. 2011). Visiting and becoming fully integrated into a new society may occur over several days (Cheney and Seyfarth 1983) or up to a couple of months (53 days; Struhsaker 1967a). During this time, vervets would presumably not be associating with co-residents as frequently, and thus show a decrease in their social position. If visiting typically occurs over a shorter period, this decrease in position may have been overshadowed by data from the rest of the month, since I used 30-day periods to quantify the social network, or these periods of visiting may have been missed entirely owing to the rotating field schedule between societies. Alternatively, if visiting tends to occur over a longer period, then the "baseline" month (-60 to -31 days) may not have been an appropriate indicator of an individual's baseline social position.

In addition, the proximity network may not have been the most appropriate network for observing changes in the social network in reference to dispersals. There are different hypotheses for how social centrality within a given network type influence dispersals (reviewed in Kurvers et al. 2014). For instance, individuals who are central or have many kin in the affiliative network may be less likely to disperse while those who have many kin in the agonistic or mating networks may be more likely to disperse (reviewed in Kurvers et al. 2014). Alternatively, seeing no drop in social centrality prior to disappearance may have been an accurate observation since males may not always visit other societies in preparation for dispersal. Instead, vervets may use

intersociety encounters to prospect other societies (Arseneau-Robar et al. 2018), and thus would not leave their society in preparation for emigration. While prospecting through intersociety encounters occurred relatively infrequently (i.e., 3% of encounters successfully doubled as prospecting), subadult males tended to capitalize most on these opportunities (Arseneau-Robar et al. 2018). Ultimately, attempts should be made to quantify the social network of dispersing individuals in other ways (e.g., grooming network) or to assess the methods of prospecting. Taken together, there was partial support for the hypothesis (2) that male dispersals are voluntary and primarily aim to avoid inbreeding.

3.4.2 Human-Related Disappearances

Unlike for emigrations, social centrality did influence human-related disappearances. Contrary to my prediction (2f, 4b), individuals who disappeared by other means, primarily through a human-related death, did not differ in their social centrality nor dominance rank from emigrating individuals. Here, I expected other disappearances would involve both males and females while emigrations would be limited to males, so the centrality of individuals disappearing by other modes would average higher. However, the other disappearances were dominated by human-related deaths, where, contrary to my prediction (4a), there was a trend toward individuals with a lower static eigenvector centrality being more likely to have a human-related disappearance than to remain in their society, especially among subadults. Thus, given the lower average social centrality of individuals who faced human-related deaths, it is unsurprising that individuals who disappeared by other means were not more socially central than emigrating males. Consequently, it does not appear that high-ranking and socially central vervets are more susceptible to human-related disappearances compared to lower-ranking or socially peripheral individuals because of priority of access to poisoned foods (hypothesis 4).

Likewise, I rejected the hypothesis (3) that other disappearances, primarily human-related deaths, were unpredictable and spontaneous, meaning there would be no change in social behaviour from baseline to the month prior to disappearance (3a). Namely, individuals who experienced a decrease in eigenvector centrality were more likely to have a human-related death than to survive and remain in their respective society. Interestingly, juveniles who increased in degree centrality and subadults who decreased in degree were more likely to have a human-related death. For juveniles, an increase in degree centrality may indicate that the juvenile was more tolerated by others, such as while feeding, and thus those juveniles that were more socially central may have had greater access to poisoned foods. However, as mentioned, there was otherwise no support for the hypothesis (4) that socially central vervets have priority of access to poisoned foods, so this result should be further investigated. As for the decreases in social centrality, these changes in network position suggest that non-emigration-related disappearances are either predictable (i.e., the individual drops in social centrality because of conditions related to these disappearance types, such as sickness behaviours; Nunn et al. 2015), or more likely, lowered social centrality makes them more susceptible to disappearances by these means. Because of the relatively few records of confirmed predation, I could not test hypothesis 5.

Although relatively little research has considered social networks in the context of human-wildlife interactions, my findings are somewhat consistent with those reported for a study of moor macaques (*Macaca maura*) whose home range intersects with a road used by food and forest-product vendors (Morrow et al. 2019). As I found with the Nabugabo vervets, moor macaques (particularly males) who, by association, were socially central in the proximity network (i.e., associated most with an individual who had a high eigenvector centrality) were *less* likely to be found along the road in proximity to humans (Morrow et al. 2019). In contrast,

however, those individuals who themselves had a high betweenness centrality were *more* likely to be along the road (Morrow et al. 2019). Ultimately, the conclusions regarding which macaques were more likely to take risks depended on the social network metric being considered (Morrow et al. 2019). These results are reflected in my findings in that the social network metric that was most important differed between my models.

Personality may link social centrality and susceptibility to human-related deaths. Given the potential costs associated with human interactions, risk-taking and/or boldness are expected to increase the chance of human-wildlife interactions (Morrow et al. 2019; Brooks et al. 2020). Life history traits may be used to predict boldness; for instance, male moor macaques were more likely than females to be found along the road, but, unexpectedly, juveniles were not more risk averse (Morrow et al. 2019). Personality may also be reflected in the social network of the species. For example, yearling rhesus macaques who were less active and calmer (i.e., equable), tended to have fewer associations (i.e., lower degree) than less equable monkeys while there was a trend toward monkeys that were confident (including bold among other traits) spending more time playing with peers (i.e., greater strength) (Weinstein and Capitanio 2008). Similarly, more socially central house finches, based on strength but not eigenvector, tended to be more exploratory in a novel environment (Moyers et al. 2018). Those who explored more areas also tended to have greater baseline corticosterone levels (Moyers et al. 2018). Contrary to my findings, these results hint that more socially central individuals may be more active or bolder, and, by extension, may be more likely to approach humans.

Aside from personality, other mechanisms may contribute to human-related deaths. Rather than less socially central individuals being more likely to be poisoned by humans, less socially central individuals may instead be more likely to succumb to the poison (i.e., die rather

than recover). In general, sociality is associated with overall health: for example, when kept in unstable social conditions (i.e., different number and composition of individuals with whom to interact for a prescribed time), rhesus macaques had fewer affiliative interactions, more aggressive ones, and did not spend as much time in close proximity or contact compared to monkeys in a stable social environment (Capitanio et al. 1998). In turn, those in unstable environments showed decreased activation of the Type I interferon genes which are needed for the innate immune system's antiviral response (Capitanio and Cole 2015).

Beyond immunity, social networks can directly and indirectly influence individual health through grooming. Proximity networks, as used in this study, indicate which individuals may interact (Whitehead and Dufault 1999), and in some studies, proximity and grooming networks are correlated (Crofoot et al. 2011; Canteloup et al. 2020; but see Castles et al. 2014). Assuming the centrality of the vervets in the proximity network gives some indication of their grooming tendencies, it follows that less socially central vervets may engage in less grooming. In turn, grooming is associated with improved health in various ways. For instance, rhesus macaques infected with simian immunodeficiency virus (SIV) who were involved in grooming more often showed a lower viral load whereas individuals who received more aggression tended to have a greater viral load (Capitanio et al. 1998). Moreover, social grooming serves the immediate purpose of removing ectoparasites (Struhsaker 1967a; Tanaka and Takefushi 1993; Akinyi et al. 2013) or fungal infections (Rosengaus et al. 2000) from individuals, where both can weaken or lead to the death of the host (Rosengaus et al. 2000; Akinyi et al. 2013), and ectoparasites may act as vectors of disease (Hutchins and Barash 1976). While grooming removes ectoparasites, direct contact between individuals may actually increase endoparasite or disease transmission (Wey et al. 2008; Nunn et al. 2015). For instance, infection with an internal nematode,

Strongyloides fuelleborni, was more common among socially central Japanese macaques (*Macaca fuscata yakui*), whereas the presence of other parasites was more common among high-ranking individuals (MacIntosh et al. 2012). Conversely, individuals infected with parasites may exhibit sickness behaviours, including reducing activities such as grooming (Nunn et al. 2015). For example, infection with *Trichuris* sp. (whipworm) was associated with vervet monkeys spending less time grooming or being in direct contact with others (Wren et al. 2021; but see Chapman, Friant, et al. 2016). Thus, lower social centrality may be an indicator that vervets are infected with endoparasites, and consequently less healthy overall. For instance, infection with a helminth parasite may increase susceptibility to or exacerbate the effects of other infections, such as malaria and liver and blood flukes (Mabbott 2018). Likewise, high-ranking female Sykes' monkeys were less likely to have a *Trichuris* or *Trichostrongylus* infection, where these infections were associated with energetic stress (Foerster et al. 2015). Often, though not in this study, high rank is associated with social centrality (Schino 2001; Silk et al. 2003; Sueur, Petit, et al. 2011; Bret et al. 2013), supporting that less socially central individuals may show greater infection rates. Regarding stresses, grooming can also play a role in the stress response. Elevated levels of glucocorticoids (GCs), such as cortisol, have been used as a proxy for perceived stress (e.g., Schoof et al. 2016; Young, Ganswindt, et al. 2017). Among brown capuchins (*Cebus [Sapajus] apella*), long-term cortisol levels were lower in socially central individuals, based on information centrality (Table 2) in the affiliative network, and higher among individuals who received more aggression (Schrock et al. 2019). Somewhat consistent with these results, the relationship between cortisol and social centrality in pregnant rhesus macaques depended on dominance rank: high-ranking females who had a high reach (i.e., greater number of individuals within their network and that of their direct partners) tended to have high cortisol levels whereas

low-ranking females with high reach tended to have low cortisol levels (Brent et al. 2011). Importantly, chronic elevations in glucocorticoids can be detrimental to health (Sapolsky et al. 2000) with less socially central individuals variably showing higher glucocorticoid levels.

3.4.3 Dominance Rank and Other Considerations

Dominance rank was not available for all individuals studied, so I re-tested a subset of the data for each model, including dominance rank as a potential predictor, and performed automated model selection (Table A2, A4). In all cases, the top model that included proportional rank as a predictor was not a better model, based on AICc, than the best model previously chosen for that analysis based on the full dataset. In other words, proportional rank did not better explain why or by what mode certain individuals disappear. Similarly, dominance rank was only weakly negatively correlated with degree, strength, and eigenvector centrality, and weakly positively correlated with betweenness centrality (Table 4).

These results are somewhat consistent with other studies. The Nabugabo vervets show a similar pattern to brown capuchins where social centrality in the affiliative network was not related to dominance rank (Schrock et al. 2019). However, various other studies, including in several macaque species (Sueur, Petit, et al. 2011), indicated that high-ranking individuals tended to be more socially central than lower-ranking individuals (e.g., Japanese macaques: MacIntosh et al. 2012; Barbary macaques: Sosa 2016; vervets: Borgeaud et al. 2017; reviewed in: Schino 2001). However, apart from Borgeaud et al. (2017), the studies all considered grooming rather than proximity networks, particularly grooming received by a high-ranking individual. In contrast, considering the agonistic network of Barbary macaques, high-ranking individuals tended to be less socially central than low-ranking individuals (Sosa 2016).

Dominance rank and social centrality, specifically related to grooming, are expected to be related since individuals may try to exchange grooming a high-ranking monkey for tolerance, such as when feeding (Seyfarth 1977; Seyfarth 1980; Kapsalis and Berman 1996; Borgeaud and Bshary 2015). That I found no association between rank and centrality metrics in the proximity network suggests that proportional rank is not an indicator of access to social partners (Struhsaker 1967a) in this population of vervet monkeys. Taken at face value, that social centrality, without rank, was included in the models of all disappearances and of human-related disappearances suggests that competitive ability within the species and/or society does not make it more or less likely that the individual disappeared. For example, despite their intrasociety competitive ability, top-ranking male vervets may be at greater risk of predation because they tend to take on the role of mobbing predators during an attack (Baldellou and Henzi 1992).

The disconnect between rank and centrality may result from various issues. To begin, the proximity network is sometimes correlated with the grooming network (Crofoot et al. 2011; Canteloup et al. 2020) and is an indicator of social tie strength (Cords 1997). However, proximity is not a direct proxy of access to social partners because it only indicates which individuals may interact, not which ones do. Next, the choice of dominance rank metric may be important. Proportional rank was the most suitable metric for this analysis since it represents a standardization that allowed me to control for dominance hierarchy size across multiple societies and multiple time periods. However, in baboons, Levy et al. (2020) reported that ordinal rank (i.e., an integer representing an individual's place in the hierarchy) is a better measure to examine how dominance rank relates to social partner access. Finally, I considered the male and female dominance hierarchies separately since they reflect competitive ability and matriline (Bramblett et al. 1982; McGuire 1982), respectively. However, both inter- and intrasexual ties

exist within a society, with female-female and female-male affiliative interactions occurring more often than male-male ones (Freeman 2012; Jarrett et al. 2018). Dominance rank is thus limited to within the sex whereas social position considers interactions within and between sexes. As a result, dominance rank may not reflect an individual's overall access to social partners.

3.4.4 Post-Hoc Analysis: Matrix Correlations

Based on the post-hoc analysis, the correlations of the social network matrices of remaining society members before and after a disappearance did not differ when the demographic event was an emigration or a human-related death. This result suggests that the social associations between the individuals who remain in the society are quite resilient to demographic changes, regardless of the cause of that demographic change. This resilience has also been observed in redfronted lemurs, *Eulemur rufifrons* (Pfaff et al. 2023). Based on social differentiation (i.e., differences in tie strength) and affiliative and agonistic rates before and after either an emigration or a predation event, disappearances did not affect the interaction rates or social stability (based on social differentiation) of the lemurs (Pfaff et al. 2023). However, given there were fewer partners with whom to interact and no change in interaction rates, interactions were necessarily redistributed among the remaining members of the society (Pfaff et al. 2023). Similarly, among yellow baboons (*Papio cynocephalus*), female grooming networks experienced a small decrease in the average number of grooming partners in the month immediately after the disappearance of a high-ranking male but returned to baseline in the following month (Franz et al. 2015). The same was true of Barbary macaques where the structure of the grooming network, but not the agonistic network, remained the same following a massive loss of individuals during a harsh winter (Fedurek et al. 2022). In other species, the loss of individuals significantly

changes social structure (e.g., pig-tailed macaques, *Macaca nemestrina*: Flack et al. 2006).

Ultimately, the network considered (affiliative, proximity, agonistic) may influence the result.

3.4.5 Conclusion

In summary, sex and age explained various disappearance modes for the Nabugabo vervets, with males and older individuals being more likely to disappear in general and to emigrate. This pattern was consistent with female philopatry and male-biased dispersal among vervets. However, sex and age did not explain which individuals were more likely to have a human-related death. Instead, human-related deaths and disappearances by any mode tended to be more likely among individuals who had a lower social centrality or decreased in their social centrality. This pattern may be explained by socially peripheral individuals being more susceptible to poisoning than central individuals. Overall, the social structure of the Nabugabo vervets was relatively resilient to demographic changes regardless of the cause of the change.

4.0 Reproductive Success

4.1 Introduction

Among numerous taxa, group-living is employed as a strategy to improve an individual's fitness over solitary individuals (Alexander 1974; Krause and Ruxton 2002). For the evolution of group-living to have occurred, namely the formation of social ties between conspecifics, social ties must confer an advantage to individuals in terms of improving survival and reproduction (Brent 2015). Accordingly, numerous studies have found that social tie measures at the individual, intermediate, and group (society) levels are associated with fitness. In these studies, fitness has been variably operationally defined by lifespan (e.g., rats, *Rattus norvegicus*: Yee et al. 2008; chacma baboons, *Papio hamadryas ursinus*: Silk et al. 2010b; rock hyraxes, *Procavia capensis*: Barocas et al. 2011; bottlenose dolphins, *Tursiops* sp.: Stanton and Mann 2012; yellow baboons, *Papio cynocephalus*: Archie et al. 2014), survival in harsh conditions and after significant loss of society members (e.g., Barbary macaques, *Macaca sylvanus*: McFarland and Majolo 2013; Lehmann et al. 2016; feral horses, *Equus caballus*: Nuñez et al. 2015), number and/or probability of producing offspring (e.g., house mice, *Mus domesticus*: Weidt et al. 2008; feral horses: Cameron et al. 2009; rhesus macaques, *Macaca mulatta*: Brent et al. 2013; chacma baboons: McFarland et al. 2017), and infant survival (e.g., feral horses: Cameron et al. 2009; chacma baboons: Cheney et al. 2016; McFarland et al. 2017; white-faced capuchins, *Cebus capucinus imitator*: Kalbitzer et al. 2017). Most studies agree that socially central animals, in either the grooming, proximity, or agonistic networks, experience higher relative fitness than less central individuals (but see Kalbitzer et al. 2017).

Dominance rank may also have consequences for survival and/or reproductive success. Dominance influences an individual's access to resources, such as food, space, and social

partners (Struhsaker 1967a). With priority of access to these resources, namely food, high-ranking females may be in better physical condition and thus exhibit greater fitness than low-ranking females through improved survival (Wrangham 1981), higher birth rates (Fairbanks and McGuire 1984), and a greater chance of giving birth during suboptimal conditions (van Noordwijk and van Schaik 1999). In turn, social position and dominance rank are often related. Individuals who have a high dominance rank tend to be more socially central (Schino 2001; Silk et al. 2003; Sueur, Petit, et al. 2011) since others may try to interact with high-ranking society members, such as by grooming them, in exchange for tolerance when accessing resources (Seyfarth 1977; Seyfarth 1980; Kapsalis and Berman 1996; Borgeaud and Bshary 2015).

Studies on animal SNA often focus on wild populations that have little contact with humans or on captive populations that, by definition, have neutral or positive (e.g., food provisioning) contact with humans. However, few studies consider wild populations that live close to, and have negative interactions with, humans (e.g., Chapman, Twinomugisha, et al. 2016). Proximity to people may influence social behaviour or social position; for instance, moor macaques interacted or associated more frequently but with fewer partners while along a road in proximity to people than while in the forest away from people (Morrow et al. 2019). Proximity to humans may also change the relationship between social position or dominance and reproductive success. For example, species living around humans may supplement their natural diet by crop foraging (Chiyo et al. 2011; Chapman, Twinomugisha, et al. 2016; Cancelliere et al. 2018). While crops may not have greater nutritional value compared to wild foods, individuals may benefit from crop foraging because of the accessibility (Cancelliere et al. 2018), density, and digestibility of these resources (reviewed in Hill 2018). Dominance may also influence which individuals are most likely to gain access to these resources. For instance, central and dominant

Japanese macaque matriline benefitted most from food provisioning by experiencing greater increases in their matriline size (Sugiyama and Ohsawa 1982). In turn, access to provisioned foods (Sugiyama and Ohsawa 1982) and/or crops (Higham et al. 2009) improved infant survival rates and lowered interbirth intervals among primates.

Given that access to human foods may mediate how dominance and social centrality affect reproductive success, I considered these factors in vervet monkeys living in an anthropogenic landscape around Lake Nabugabo, Uganda. The Nabugabo vervets are moderately seasonal breeders with a birth peak between October and January (Schwegel et al. 2022). My previous research has shown that female dominance is associated with reproductive success in this population, as higher-ranking females tend to have shorter interbirth intervals (IBIs), with a population-wide mean of around 12 months (Schwegel et al. 2022). Variation also exists in the survival of infants to juvenescence (e.g., Hauser 1993; Kavanagh et al. 2011), but factors affecting this variation (e.g., maternal rank, infant sex) have yet to be quantified in the Nabugabo societies. In Amboseli National Park, Kenya, infants have a mortality rate of 57% within their first year, and maternal rank was not associated with likelihood of infant survival (Hauser 1993). However, among captive vervets, the infant mortality rate was 34%, with female infants being more likely to survive than males (Kavanagh et al. 2011). Furthermore, lower-ranked captive females were less likely to have a surviving infant (Kavanagh et al. 2011).

4.1.1 Research Question, Hypothesis, and Prediction

In this section, I wanted to examine how a female's social position affects her reproductive success. I hypothesized that socially central individuals are afforded (within society) protection by their position (Young, McFarland, et al. 2017) and/or access to resources. As a result, I predicted that socially central females would be more likely to have infants that

survived (Cameron et al. 2009; Cheney et al. 2016; Kalbitzer et al. 2017; McFarland et al. 2017) to one year than less central females (Table 1).

4.2 Methods

4.2.1 Reproductive Success

As a proxy measure of fitness, I operationally defined a female's reproductive success according to whether her infant, born in a given reproductive year, survived ≥ 365 days. I defined a reproductive year as April to March inclusively (e.g., 2017 was April 2017 to March 2018), because only one infant throughout the entire study period was born in early March, providing a natural break in the reproductive cycle of the population (Schwegel et al. 2022). Given the definition of a reproductive year and that there was a six-month period following the beginning of the study of each society during which the field team learned individual identities and habituated the society, I used 2012 as the first reproductive year for M, and 2017 as the first for HC and KS; I included 2019 as the final reproductive year (i.e., infant born between April 2019 and March 2020 and survival to March 2021). I excluded five infants from the analysis because their mother died prior to the end of the reproductive year (i.e., March 31st; two from M and three from KS), and infants often die following their mother's death (Cheney et al. 1981).

4.2.2 Social Network Analysis and Dominance Rank

To be consistent with the analyses in section 3, I computed a proximity network based on the gambit of the group for each reproductive year (see section 2.2 for additional details). I then extracted the degree, strength, betweenness, and eigenvector centrality for all the females who gave birth during that year. For dominance rank, I extracted the Elo scores (section 2.3) of all

mothers on the final day from which I derived the associated social network (i.e., March 31st of the reproductive year).

4.2.3 Data Analysis

I generated a binomial GLMM (function: `glmer`, package: `lme4`; Bates et al. 2020), of infant survival to ≥ 365 days (1) versus infant death at < 365 days (0). As fixed effects, I included the mother's social network position (%degree, z-betweenness, z-eigenvector; section 2.4) and proportional rank on the last day of the reproductive year in which the infant was born. To avoid pseudoreplication, I included mother identity nested within society as a random effect. I also included the reproductive year in which the infant was born as a random effect to account for repeated measures and since external conditions during that year may result in similar outcomes across infants. For example, following a male immigration, there is a greater risk of injury to society members (Schneider-Crease et al. 2020), such as mothers, which may impact infant survival. Likewise, greater rainfall at Lake Nabugabo in 2019 and 2020 (Schwegel et al. 2022) may also have affected survival.

4.3 Results

Considering survival within the first two years of life among vervets born between January 2012 (M) or July 2016 (HC and KS) and August 2019 (N = 103), most deaths occurred before reaching 365 days old (31 of 36 deaths recorded among individuals ≤ 730 days; Figure 10). Following approximately one year, the survival rate of the Nabugabo vervet monkeys stabilized for several months before continuing to drop slowly (Figure 11).

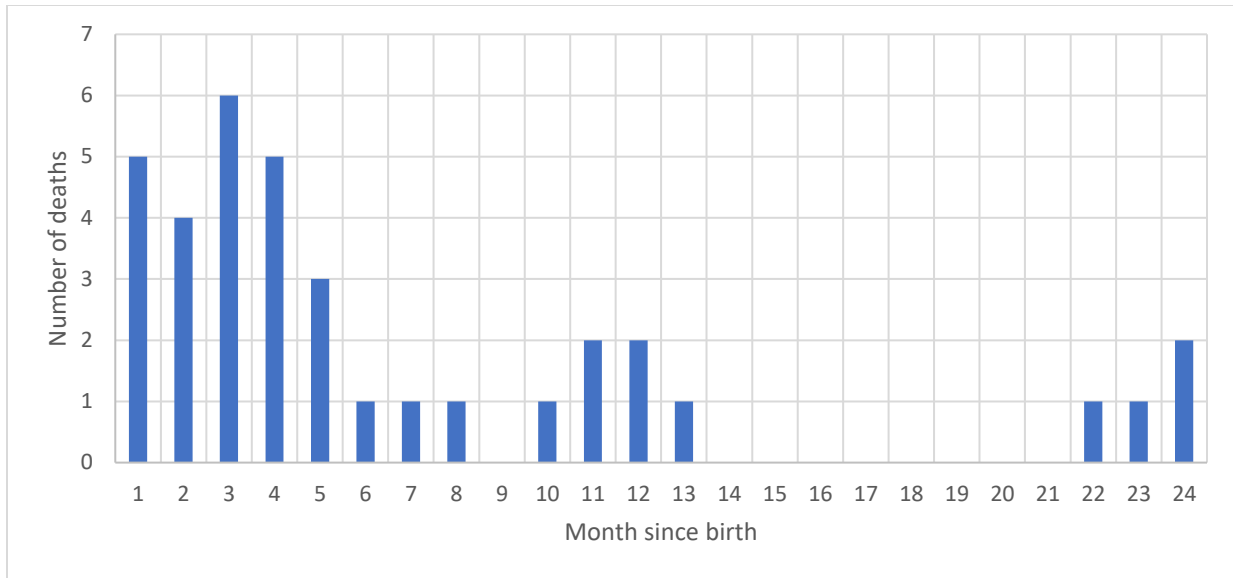


Figure 10. Number of deaths (up to two years) per month following birth among 103 vervet monkeys born between January 2012 (M society) or July 2016 (HC and KS societies) and August 2019 at Lake Nabugabo, Uganda. Month since birth indicates the period of time during which individuals died (i.e., month 1 indicates deaths from [0, 30.4) days, month 2 is from [30.4, 60.8) days).

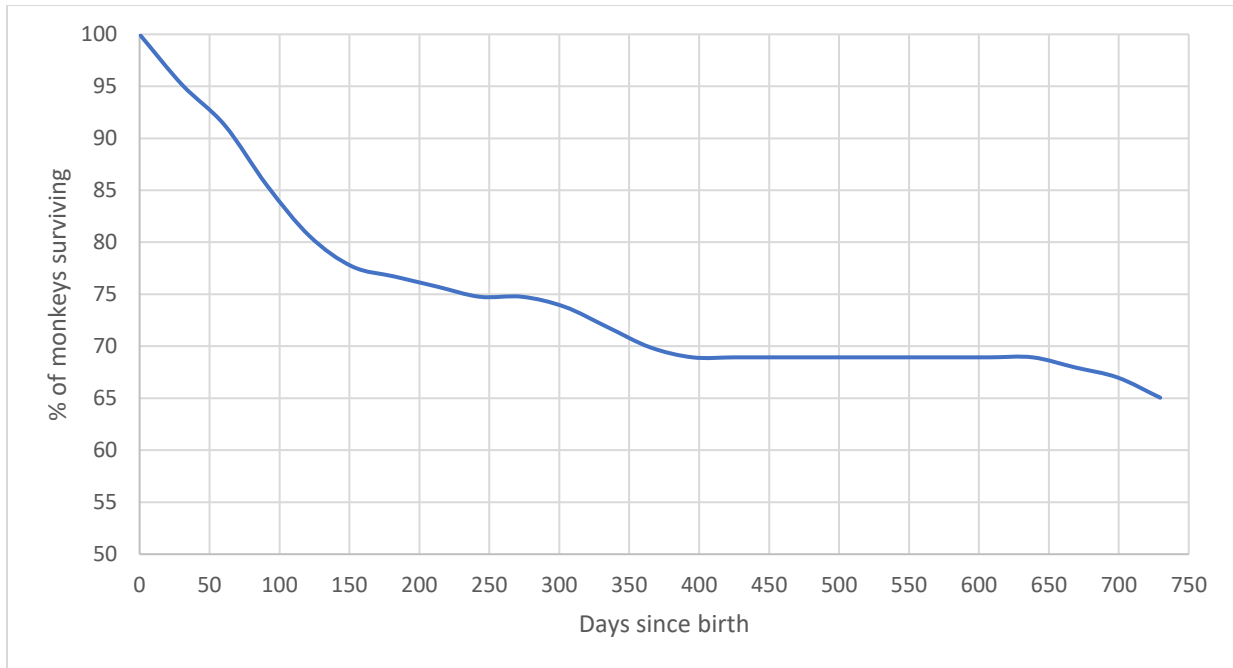


Figure 11. Survivorship curve up to two years of 103 vervet monkeys born from January 2012 (M society) or July 2016 (HC, KS) until August 2019 at Lake Nabugabo, Uganda. Y-axis indicates the percentage of the 103 monkeys who are surviving a given number of days after their birth. Note the y-axis shows from 50 to 100% survivorship to better observe the trend in survivorship.

From April 2012 (M) and April 2017 (HC and KS) to March 2020, 124 infants were born (M: 76, HC: 12, KS: 36). Of these, five infants were stillborn or died soon after birth and a total of 41 infants did not survive to at least one year (Table 5).

Table 5. Summary of infants born in each reproductive year (e.g., 2017 is April 2017 to March 2018) in three societies (M, HC, KS) at Lake Nabugabo, Uganda. Summarizing infants born from April 2012 (M) or April 2017 (HC and KS) to March 2020. Male immigrations indicates the number of males who immigrated into the society during the reproductive year. Survived indicates the number of infants who survived ≥ 365 days and died indicates the number who survived < 365 days. % survived is the proportion of the total number of infants born in a given reproductive year and society who survived to one year.

<i>Reproductive Year</i>	Society	Male immigrations	Infants Born	Survived	Died	% Survived	% Survived total
2012	M	0	8	6	2	75.0%	75.0%
2013	M	0	9	5	4	55.6%	55.6%
2014	M	0	8	4	4	50.0%	50.0%
2015	M	1	10	7	3	70.0%	70.0%
2016	M	1	9	8	1	88.9%	88.9%
2017	M	1	10	10	0	100%	66.7%
	HC	1	3	0	3	0.0%	
	KS	1	11	6	5	54.5%	
2018	M	3	8	6	2	75.0%	65.2%
	HC	0	5	2	3	40.0%	
	KS	1	10	7	3	70.0%	
2019	M	0	14	6	8	42.9%	66.7%
	HC	0	4	4	0	100%	
	KS	3	15	12	3	80.0%	

For 119 births, the best model of infant survival to one year only included maternal z-betweenness as a fixed effect (0.383 ± 0.184 , $z = 2.078$, $p = 0.038$; AICc = 153.4; adjusted- $R^2 = 0.03044$; HL test: $\chi^2 = -66.235$, $df = 8$, $p = 1$; AUC = 0.623; Figure 12), such that the infants of females who had higher betweenness scores were more likely to survive. Results were similar when I excluded two infants whose mothers had not engaged in any agonistic behaviours prior to their birth, and thus I could not calculate dominance rank (results not presented).

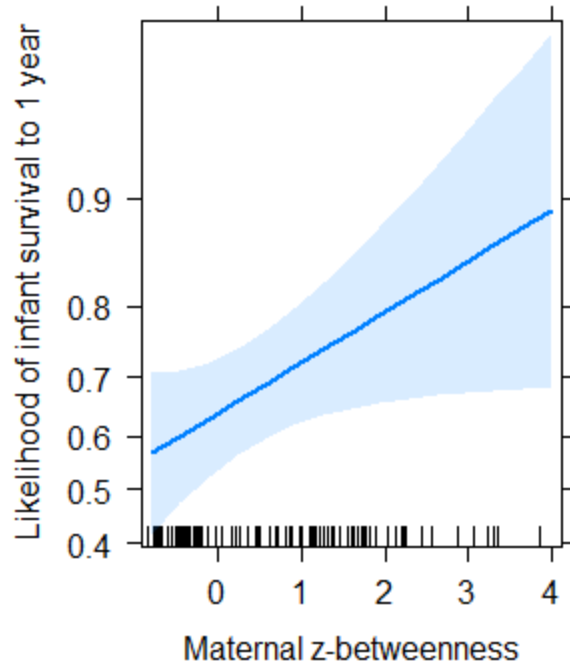


Figure 12. Probability of a vervet monkey surviving ≥ 365 days in reference to the betweenness centrality (as a z-score) of their mother within the reproductive year in which the infant was born. Reproductive year is from April to March. Located at Lake Nabugabo, Uganda (M, HC, KS societies).

4.4 Discussion

At Lake Nabugabo, most deaths among infants and juveniles occur within the first year, particularly within the first five months, after which the mortality rate (30.1% at 365 days, with 23.3% before six months and 6.8% between six months and one year) levelled off. Controlling for the reproductive year, maternal identity, and society, mothers who had a greater betweenness centrality (z -betweenness) were more likely to have an infant that survived to one year in a given reproductive year. Thus, the hypothesis (6) that socially central females have higher reproductive success was supported.

High betweenness centrality indicates that an individual is important in connecting others (Lehmann et al. 2016); this means they are important for uniting the society (Lehmann and Dunbar 2009), as well as for the transmission of resources, culture, information, and disease, among others (Freeman 1977; Brent 2015). Thus, individuals with high betweenness centrality are at both a disadvantage, in that they tend to be at higher risk of getting (Christley et al. 2005) and spreading disease (Klov Dahl et al. 2001), and an advantage in terms of information transfer between separate sections of a network. For example, among tits (blue tit: *Cyanistes caeruleus*, great tit: *Parus major*, marsh tit: *Poecile palustris*), the individuals who were most likely to find a new food patch were those who had a high betweenness centrality (at one site) or a high eigenvector centrality (other site) (Aplin et al. 2012). Similarly, there was evidence that information about food patches was transmitted through the social network, with connected individuals being more likely to arrive next at the new food patch (Aplin et al. 2012). Social ties may thus confer an advantage to individuals by allowing them access to information (Aplin et al. 2012), particularly from disparate areas of a network when considering betweenness centrality. In support of this notion, male chimpanzees with a high betweenness centrality within the

coalitionary network were more likely to increase their dominance in the following season and had a greater reproductive output (i.e., were more likely to sire at least one offspring in the following two years) than those with lower betweenness (Gilby et al. 2013). Here, it is suggested that the males with high betweenness (i.e., whose direct partners did not tend to form coalitions with one another) were choosing the “correct” partners that allowed them to increase in rank and reproductive output (Gilby et al. 2013). Similarly, vervet males who were integrated in the female social network, that is who had a high eigenvector centrality in the grooming network and, to a lesser extent, a high degree in the proximity network, were more likely to improve their dominance rank, suggesting that connectedness to females deters aggression from other males (Young, McFarland, et al. 2017). However, among the chimpanzees there was no evidence that friends of friends refrained from directing agonism toward the individual with high betweenness, so the significance of having high betweenness was not elucidated in this study (Gilby et al. 2013). Speculatively, instead of betweenness preventing an individual from being targeted by friends of friends (i.e., to maintain the relationship with the mutual friend; Gilby et al. 2013), having high betweenness may instead allow the individual to gain protection from separated areas of the network. That is, there would be few, or no conflicts of interest should the individual with high betweenness solicit aid from an individual within one part of the network against an individual in the other part. However, the willingness to assist in a coalition would likely depend on the kin relationships of the individuals, where kin are more likely to support one another than to support non-kin, as well as the rank of individuals, where coalitions tend to be directed toward subordinates (Smith et al. 2010; Barrett et al. 2015).

Despite somewhat similar results from other studies, using betweenness centrality as a predictor of reproductive success is not ideal. Unlike degree (primarily received, i.e., in-degree),

strength (received and initiated), and eigenvector centrality, the betweenness centrality of vervet monkeys in South Africa was not consistent across seasons (Błaszczuk 2018). However, unlike in South Africa (Błaszczuk 2018), Lake Nabugabo does not show much environmental seasonality, where natural food availability remains approximately the same across months and the primary seasonal change involves the amount of precipitation (Schwegel et al. 2022). Moreover, betweenness centrality may differ based on environmental context. For instance, moor macaques had a lower betweenness centrality when they were found around a road (i.e., directly or indirectly in proximity to humans) compared to when they were in the forest (Morrow et al. 2019). Aside from inconsistency over time and space, betweenness centrality is also less accurate in high density networks, that is, where most individuals interact or associate with most others within the network (Silk et al. 2015). As I used the gambit of the group to identify proximity associations, I found relatively little variation in the degree of individuals, where most individuals did associate with most others in the network. Therefore, the Lake Nabugabo vervets had high density networks, and thus betweenness was likely not as telling of a social network metric compared to eigenvector centrality, for example. Ultimately, these issues mean that betweenness centrality would likely not be a good indicator of whether a female was likely to have many surviving offspring over the years.

Beyond just betweenness centrality, socially central individuals, measured by various metrics, tend to have greater reproductive success (Silk, Altmann, et al. 2006) because individuals who associate often may have fewer agonistic interactions (Cameron et al. 2009; Lehmann and Boesch 2009), improved health (Struhsaker 1967a; Tanaka and Takefushi 1993; Capitanio et al. 1998; Rosengaus et al. 2000; Akinyi et al. 2013; Capitanio and Cole 2015; Schrock et al. 2019), or greater social support in protecting offspring (Palombit et al. 1997), all

of which may improve the female's ability to conceive or rear offspring (Brockman and van Schaik 2005; Cameron et al. 2009). From an ultimate perspective, natural selection favoured the evolution of sociality, particularly behaviours that form social ties, because individuals incurred survival and reproductive advantages by displaying these behaviours (Brent 2015). Coinciding with this evolutionary perspective, various studies have linked social centrality, in the affiliative, proximity, and/or agonistic networks, and fitness as indicated by 1) individual lifespan and/or probability of survival (e.g., strength and stability of social ties in the affiliative network of baboons: Silk et al. 2010b; Archie et al. 2014; degree centrality in the proximity network of feral horses: Nuñez et al. 2015), 2) reproductive rate (e.g., eigenvector centrality in the proximity network and out-strength in the agonism network of rhesus macaques: Brent et al. 2013), and 3) infant survival (e.g., strength in the affiliative network of white-faced capuchins: Kalbitzer et al. 2017).

While in some species it is centrality in the agonism network that predicts fitness, female dominance rank was not included as a predictor of offspring survival in the Nabugabo vervets. There have been mixed results regarding the influence of rank on reproduction; for example, in Amboseli National Park, dominance rank did not affect reproduction (Cheney et al. 1988), while at Nabugabo, more dominant females tended to have shorter interbirth intervals, though there was not much variance in interbirth intervals (Schwegel et al. 2022). Dominance rank may play a varied role in vervets based on the availability of resources, where high-ranking females tended to have more infants (i.e., higher birth rate) in societies where food was clumped, whereas there were no rank differences when food was evenly distributed (Whitten 1983).

Despite correlations observed between centrality and reproductive success, few studies have considered the mechanism(s) that mediate this relationship (reviewed in Thompson 2019).

Some have considered the role of glucocorticoids (GCs) – a group of hormones released during the stress response – where elevated levels of GCs have been used as a proxy for perceived stress (e.g., Schoof et al. 2016; Young, Ganswindt, et al. 2017). Acute elevations in GC levels prepare and allow individuals to defend themselves against aversive stimuli while preventing the stress response from being overactive; however, chronic elevations can be detrimental to health (Sapolsky et al. 2000). For example, dominance rank has been linked to energetic stress, where lower-ranking individuals – especially in societies where subordinates are subject to greater levels of aggression and lower levels of social support (Abbott et al. 2003) – showed greater GC levels, but these levels were partially mitigated by grooming relationships (Foerster et al. 2011). Maintaining body temperature by huddling with social partners has also been introduced as a potential mechanism improving individual survival (McFarland and Majolo 2013). Furthermore, lowered rates of aggression and/or harassment have been proposed (Stanton and Mann 2012) and supported (Cameron et al. 2009) as mediating factors between the prevalence/strength of social ties and fitness. Harassment and injury decreased individual reproductive success in various species (e.g., feral horses: Linklater et al. 1998; bruchid beetles, *Callosobruchus maculatus*: Gay et al. 2009; damselflies, *Ischnura senegalensis*: Takahashi and Watanabe 2010; gelada baboons, *Theropithecus gelada*: Schneider-Crease et al. 2020), and are thus relevant factors to consider as potential social mechanisms leading to the fitness benefits associated with social ties. These mechanisms should be further studied in the future.

In addition to these potential mechanisms, future studies should also place greater emphasis on the mother's role during the offspring's infancy and juvenescence that may impact the likelihood of surviving to adulthood. For example, I only omitted individuals whose mother did not survive to the end of the reproductive year. However, most infants at Lake Nabugabo

tend to be born between October and January (Schwegel et al. 2022), where an infant born in October would have reached six months (juvenescence) by the end of the reproductive year (March 31st), but infants born in January would not. Vervet monkeys whose mother died when they are young, especially before they reached six months but even up to eight months, also tended to die (Cheney et al. 1981). Particularly during the first three to four months of life, vervet monkeys are particularly dependent on their mother because their main food source is milk up until this point (Hauser 1994). Therefore, one should consider omitting any infants whose mother died before they reached six months, or even one year, since vervets spend a lot of time with their mother in their first year, such as learning which foods are appropriate (Hauser 1993).

Aside from maternal deaths, maternal characteristics and/or mothering styles may also be considered. Despite dominance rank not influencing infant survival to one year among the Nabugabo vervets, captive low-ranking vervet females (*Chlorocebus aethiops sabaesus*) were more likely to have an infant die within the first 30 days, potentially because higher-ranking females may be more inclined to take the infant, resulting in dehydration or starvation (Kavanagh et al. 2011). Because of these threats some mothers seek contact with their infants more often, retrieving them from allomothers (Hauser and Fairbanks 1988), while other mothers may allow greater contact between their infant and other society members (Struhsaker 1967b; Struhsaker 1971). Notably, the infants of low-ranking mothers tend to be targeted more, potentially since the status of high-ranking mothers deters others from approaching (Struhsaker 1971). There was also a trend toward high-ranking mothers rejecting (i.e., preventing nipple contact) female infants more and male infants less than low-ranking mothers (Lee 1984). These rejection patterns meant that female infants tended to gain independence from their mother earlier than male infants (Lee 1984). Rejection patterns also differed between the infants born

early in the breeding season compared to those born later, where later born infants were rejected less frequently (Lee 1984). Given the association with independence, rejection pattern differences between mothers of different dominance ranks and infants born in different periods of the breeding season may have consequences for survival.

Finally, I omitted infant sex and male reproductive success from this analysis, both of which may be relevant factors to consider. I ignored infant sex as a predictor since many infants who died prior to reaching one year did not have their sex identified because of difficulties characterizing genitalia on young vervet monkeys. However, infant sex is hypothesized to be related to maternal energy expenditure, with male infants of primiparous females in some primate species having lower survival rates than females (Bercovitch et al. 1998). In addition, I only considered a female's direct reproductive success because genetic data was not available, so I could not assess paternal relatedness (i.e., male reproductive success) nor the kin relationships of females who were present at the beginning of the long-term study (i.e., indirect fitness of females). Future studies should consider including both infant sex and paternity as a predictor of survival.

In summary, just as in wild populations that are not in proximity to human developments, I found evidence that social centrality influences infant survival in a species living near humans. This finding forms the basis for future research that may consider the mechanism(s) linking social centrality and reproductive success. These studies can then be used to further compare wild populations that are and are not subject to human-wildlife interactions.

5.0 General Discussion

5.1 Summary

The use of social network analysis (SNA) has been increasing over the years as a means of explaining behaviour and other biological phenomena at the individual or group (society) level (Wey et al. 2008; Croft et al. 2011; Farine and Whitehead 2015). While various approaches for performing statistics on network data exist (Croft et al. 2011; Hart et al. 2021; Hart et al. 2022) and the validity of permutation tests to account for non-independence in the data has been questioned (Weiss et al. 2021), SNA remains a useful umbrella for elucidating social networks. In this study, I used techniques in SNA to explain how social position influences disappearances and deaths of vervet monkeys in a society and how centrality affects the reproductive success of females.

In section 3, I explored various modes of disappearance and/or death among the vervet monkeys at Lake Nabugabo, comparing individuals based on whether they disappeared or remained within their society and by which mode they disappeared. Most disappearances were unknown, where the monkey was no longer observed and no carcass was recovered. In decreasing order, the next most common types of disappearance resulted from emigrations, human-related deaths (particularly poisoning), unknown deaths where a carcass was found but cause of death was undetermined, death by electrocution, predation, and conspecific-related death. Comparing individuals who emigrated to both those who remained in the society and those who disappeared by any other mode (i.e., human- or conspecific-related, electrocuted, predated, unknown death), sex and age were the only predictors included in the best model, where older individuals and males were more likely to emigrate. However, when considering all disappearances, sex, age, and social centrality explained which individuals disappeared rather

than remained. Specifically, when I investigated the change in dynamic social centrality of the monkeys from their baseline month (i.e., the penultimate month) to the month immediately prior to disappearance, older individuals, males, and those who showed a decrease in their eigenvector centrality and a trend towards a decrease in their betweenness centrality were more likely to disappear from their society than to remain within it. When I considered only the static value of social centrality in the month prior to disappearance, I found that older individuals, males, and those with a lower eigenvector, especially subadults, were more likely to disappear than to remain. Narrowing the scope to only consider individuals who had a human-related death relative to individuals who remained in the society, monkeys who decreased in their eigenvector centrality, and juveniles who increased in their degree or subadults who decreased in degree centrality were more likely to have a human-related death. Considering the static values of social network, I observed a trend toward individuals who had a lower eigenvector, particularly subadults, being more likely to have a human-related death than to remain.

These results suggested that emigrations are based on the natural history of the species and inbreeding avoidance rather than being dependent on the social integration of the individual, particularly when considering the dispersing sex (Blumstein et al. 2009). Emigrations were also not predicted by a change in social network position, though this may be the result of missing the change by investigating the wrong timeline, or that there is no change in social position because prospecting other societies may not be limited to leaving one's own society to visit another (Arseneau-Robar et al. 2018). In contrast, disappearances in general and human-related disappearances were both preceded by a decrease in social position and primarily involved individuals of lower social position. For all the disappearances, this trend may result from predation events where less socially central individuals may be at greater risk (Hamilton 1971;

Kalbitzer et al. 2017). As for human-related disappearances, proximity to humans may change the social behaviour of individuals (Morrow et al. 2019), and those who are less socially central may have poorer health or a suppressed immune response compared to those who are socially central (Struhsaker 1967a; Tanaka and Takefushi 1993; Capitanio et al. 1998; Rosengaus et al. 2000; Akinyi et al. 2013; Capitanio and Cole 2015; Schrock et al. 2019; Wren et al. 2021).

While the models described above performed best among the various combinations of predictors, most of these models explained little variance in the outcome variable. This lack of explanatory value is likely because of logistical limitations that affected how I defined my variables and resulting quasi-complete separation. Specifically, since exact ages were not known for many of the Nabugabo vervets, I grouped individuals into age classes that may have a wide range (i.e., infants: < 6 months; juveniles: 6 months to about 3 years; subadults: approximately 3 to 4 years; adults: > 4 or 5 years; Struhsaker 1967b). Because of this range, where emigration depends on age at sexual maturity for natal males and tenure length for secondary dispersers (L'Allier et al. 2022), age class may not give specific insight into which individuals are likely to emigrate. As a result of these age classes, models often had quasi-complete separation because I found that only subadult and adult males emigrated despite there being a few records of females or juveniles immigrating into the study societies. However, just because an individual is male or adult does not indicate that they will necessarily emigrate, so age and sex are not catch-all predictors. Mating season, tenure length, attainment of sexual maturity, and reproductive opportunities in other societies may all influence the likelihood of a male dispersing (L'Allier et al. 2022). Furthermore, in the case of the models that considered all and/or other disappearances, each mode of disappearance was expected to have a different underlying mechanism that affected how social centrality played into the likelihood of disappearing. For instance, among the

dispersing sex, social integration does not necessarily affect whether the individual will emigrate (Blumstein et al. 2009). In comparison, less socially central, and thus more spatially peripheral (Kalbitzer et al. 2017), individuals may be at greater risk of predation (Hamilton 1971).

In section 4, I found that females who had a greater betweenness centrality were more likely to have infants that survived past one year. Betweenness has previously been associated with greater reproductive success among male chimpanzees (Gilby et al. 2013). More generally, in various mammalian species, individuals who were more socially central tended to have greater reproductive success than less socially central individuals (Weidt et al. 2008; Yee et al. 2008; Cameron et al. 2009; Silk et al. 2010b; Barocas et al. 2011; Stanton and Mann 2012; Brent et al. 2013; McFarland and Majolo 2013; Archie et al. 2014; Nuñez et al. 2015; Lehmann et al. 2016; McFarland et al. 2017), including exhibiting greater infant survival (Cameron et al. 2009; Cheney et al. 2016; Kalbitzer et al. 2017; McFarland et al. 2017). My results are thus consistent with the pattern of sociality improving reproductive success, even in a wild population that is subject to human-wildlife interactions. However, the mechanism that links sociality and reproductive success is still to be determined.

5.2 Limitations

Because of the nature of field work and behavioural observations, there are various limitations to this study. To begin, in many cases, there were insufficient data to accurately construct the social network for all the demographic events I studied (Farine 2018). Namely, I would need a minimum of 20 observations of each dyad to do so (Hoppitt and Farine 2018). This problem could be fixed by using a longer period of time prior to the demographic event to assess social network position (e.g., Lehmann et al. 2016; Larson et al. 2018). However, considering network connections too long before the event may limit the biological significance of the

network, that is, a longer period may mask changes in social position that occur in the society before the demographic event. Alternatively, a shorter period prior to the event (e.g., using 7 or 15 days instead of 30) may be more appropriate since changes in the network may occur on a shorter time scale (e.g., visiting may occur over a few days; Cheney and Seyfarth 1983). Nevertheless, I did not shorten the period prior to the event because, based on an exploratory analysis, networks created based on 15 and 30 days were approximately equivalent in showing differentiated social associations. Concurrently, based on the field schedules, there is theoretically up to 15 days during which data from a society is not collected (Schwegel et al. 2022), so 30 days better captures whether relevant data exist for a particular event.

Another factor affecting data availability is that sampling effort was not consistent over time (Farine 2018) because of the addition of two new study societies that required changes to the study protocol in 2016. For instance, the field team started collecting data on each society for two instead of three weeks in a four-week period and decreased the scan sampling interval from 30 to 15 minutes. In addition, unforeseeable issues such as illness among the field team, safety concerns from inclement weather, or the vervets' location occasionally limited data collection. As a result, data around each demographic event or within each year may not be entirely consistent and/or comparable. However, to compensate for this inconsistency, I calculated tie strength using the half-weight index (HWI) which controls for gregariousness (Thompson 2019), and ultimately differences in how often an individual is observed (dependent on sampling effort), by giving a proportion of samples in which an individual was interacting relative to the total number of samples in which that individual was observed. While correcting for gregariousness may mask the relationship of interest, particularly when gregariousness affects how often the individual will be observed (Franks et al. 2021), not correcting for this trait may erroneously

suggest gregarious individuals avoid less gregarious ones (Whitehead 2008). The HWI has been criticized for being arbitrary in assigning weights to observations of individuals observed apart rather than together (Hoppitt and Farine 2018), but using the HWI was justifiable for making this study more comparable to many before it.

At a broader level, I determined associations and the HWI using the gambit of the group (Whitehead and Dufault 1999; Franks et al. 2010; Hoppitt and Farine 2018), which also has drawbacks. By using the gambit of the group, I was able to consider all associations, not just those occurring between nearest neighbours, and thus I did not ignore any individuals who were associating. However, the gambit of the group is less conservative in its estimation of how many individuals may interact; that is, the gambit assumes all individuals within a group of the society will interact with one another equally (Whitehead and Dufault 1999), and that they are in proximity for a social reason rather than a non-social one, such as accessing food (Whitehead 2008). Based on the scan data, these assumptions cannot be verified. However, previous research indicates that vervets show triadic closure (i.e., if A and B are friends and B and C are friends, then A and C are friends) (Borgeaud et al. 2016), which partially validates using the gambit of the group.

5.3 Future Directions

Given the limitations regarding the gambit of the group and that benefits of social position are often attributed to grooming relationships, this study could be repeated using the grooming network rather than the proximity one to see if results are consistent. I did not use grooming because grooming is less commonly observed than proximity, so the disappearances of some individuals would need to be ignored since no social centrality information would have

been available for them in the month prior to disappearance. Likewise, a minimum number of observations is required to properly illustrate social network structure (Hoppitt and Farine 2018). As a result, there would be fewer data points. Despite these drawbacks, the grooming network would have the added benefit of not only directly measuring affiliative interactions between individuals, but also being more precise in those interactions. That is, instead of assuming all individuals are equally likely to interact within a group (based on the gambit of the group), I would only consider those individuals who did interact. That said, interactions involving more than two individuals (e.g., if three individuals are mutually grooming) would likely be ignored.

In addition to considering the grooming network, kin relationships should also be incorporated as these relationships may affect individual social behaviour. For example, females within the high-ranking matriline tend to be more socially central in the agonism network compared to females from other matrilines (Sosa 2016). Similarly, females are more likely to groom matrilineal kin than other individuals (Silk et al. 1999). Kin tend to be preferred partners because of inclusive fitness benefits: by investing energy in helping kin, such as by providing coalitionary support (Smith et al. 2010) or by grooming them and removing ectoparasites (Struhsaker 1967a; Tanaka and Takefushi 1993; Akinyi et al. 2013), the individual may improve the chances their kin will survive and reproduce, and thus the individual may improve their own indirect fitness (Hamilton 1964). I did not include kinship in my models because only maternal kin were known in the Nabugabo vervets, and I did not know the genetic relationships between individuals who were already present in the society when the study began. However, I did include dominance rank, which doesn't directly control for kinship but may account for matrilineal hierarchies (Bramblett et al. 1982) to some extent. Ultimately, SNA should be

combined with genetic studies to identify maternal and paternal kin, and associate these with social behaviour.

Finally, I did not consider the presence of individuals from the same age cohort as a confounding factor in the social network. I omitted age cohort because for most individuals, namely those born prior to the beginning of the study, those who were part of their age cohort were unknown (i.e., who was born in the same reproductive year). In many primate species, individuals prefer to associate with others from their same age cohort because those individuals may be paternal kin (Altmann 1979; Alberts et al. 2006; Jack and Fedigan 2006; Silk, Altmann, et al. 2006; Muniz et al. 2010; but see Minkner et al. 2018). If genetic data were incorporated in the analysis, age cohort would not need to be considered separately. However, individuals may also prefer those within their age cohort who are not paternal kin (Silk, Altmann, et al. 2006), perhaps because of familiarity and/or because peers may engage in parallel dispersal, in which case age cohort or age differences would need to be included in the model.

5.4 Conclusion

This study contributes to the relatively limited literature using social network position to predict whether disappearances occur and by what mode. For example, Lehmann et al. (2016) considered the social networks of Barbary macaques in the six months prior to the death of many individuals during a harsh winter to identify what factors predicted which individuals were more likely to survive. Similarly, Larson et al. (2018) studied the social networks of rhesus macaques in the two years leading up to the eviction of numerous females, assessing how their position changed in advance of the eviction. To the best of my knowledge, this study is unique in considering social network position and changes in position on a short-term scale (one to two months) as a means of assessing which individuals are more likely to disappear. That I found

individuals who decreased in their social centrality were more likely to disappear by any mode than to remain in their society indicates that social networks on a short-term scale may be a useful benchmark in future studies. Furthermore, this study is among the few that consider a wild population living in a human-modified environment. Overall, my results suggest that emigration, particularly in a species with sex-biased dispersal, is explained primarily by the natural history of that species whereas disappearances in general, particularly human-related deaths, and the reproductive success of individuals depends on their social integration. Likewise, the social network of vervet monkeys, and potentially other species, is quite resilient to demographic changes, regardless of the cause of the demographic change (i.e., natural or human-induced). As a result, conservation strategies designed for wild populations could be adapted for populations living in proximity to humans. Similarly, living in a human-modified matrix may not unduly modify or stress the social networks of vervets or other species.

6.0 References

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Appendix A

Table A1. Model selection statistics for models considering the change in social position of vervets at Lake Nabugabo, Uganda from the penultimate (baseline) month to the month immediately prior to an individual's disappearance. Models were run on the full dataset and excluded dominance rank as a predictor. Predictors include age, sex, change in betweenness centrality as a z-score (Δz_{bet}), change in eigenvector centrality as a z-score (Δz_{eig}), change in degree centrality as a percent of realized social partners ($\Delta \%deg$), and the interactions of these predictors (:). AICc is the Akaike Information Criterion corrected, while $\Delta AICc$ is the difference from the AICc of the model with the lowest AICc. R^2 is the variance explained by the fixed effects and the full model (calculated using the delta method) since the random effects did not explain any variance. The adjusted- R^2 (R^2 -adj) is adjusted for the number of fixed effects. LRT is the likelihood ratio test using up to two models as baseline conditions. AUC is the area under the receiver operating characteristics curve as a test of model discrimination. Hosmer-Lemeshow Test measures model calibration. df is degrees of freedom.

Outcome	Predictors	AICc	Δ AICc	R ²	R ² -adj	LRT_1		LRT_2		AUC	Hosmer-Lemeshow Test				
						χ^2	df	χ^2	df		χ^2	df			
													df	p	
Remained (1) vs. disappeared (any modes; 0)	age + sex + Δ zbet + Δ zeig + age:sex	809.50	0	0.019	0.016	24.844	4	< 0.001	8.488	3	0.037	0.693	-1846.4	8	1
	age + sex + Δ zbet + Δ zeig + age:sex + sex: Δ zbet	810	0.51	0.018	0.015	26.346	5	< 0.001	9.989	4	0.041	0.691	-1845.7	8	1
	† age + sex + Δ zbet + Δ zeig	810.3	0.84	0.019	0.017	19.985	2	< 0.001	3.629	1	0.057	0.683	-1847.7	8	1
	age + sex + Δ zbet + Δ zeig + sex: Δ zbet	810.9	1.36	0.018	0.015	21.475	3	< 0.001	5.119	2	0.077	0.679	-1846.6	8	1
	age + sex + Δ zeig + age:sex	811	1.51	0.017	0.014	21.319	3	< 0.001	4.963	2	0.084	0.684	-1844.7	8	1
	age + sex + Δ zbet + Δ zeig + Δ %deg + age:sex	811.5	1.99	0.019	0.016	24.868	5	< 0.001	8.511	4	0.075	0.693	-1845.4	8	1
	age + sex + Δ zbet + Δ zeig + age:sex + sex: Δ zeig	811.6	2.05	0.019	0.015	24.812	5	< 0.001	8.455	4	0.076	0.693	-1845.4	8	1
	age + sex + Δ zbet + Δ zeig + age:sex + sex: Δ zbet + sex: Δ zeig	811.8	2.32	0.018	0.015	26.55	6	< 0.001	10.193	5	0.07	0.691	-1844.8	8	1
	age + sex + Δ zbet + Δ zeig + Δ %deg + age:sex + sex: Δ zbet	812	2.44	0.018	0.014	26.431	6	< 0.001	10.075	5	0.073	0.691	-1844.7	8	1
	**age + sex + Δ zeig	812	2.46	0.017	0.015	16.357	1	< 0.001				0.674	-1845.7	8	1
	age + sex + Δ zbet + Δ zeig + Δ %deg	812.3	2.81	0.019	0.017	20.026	3	< 0.001	3.67	2	0.16	0.683	-1846.6	8	1

Outcome	Predictors	AICc	Δ AICc	R ²	R ² -adj	LRT_1		LRT_2		AUC		Hosmer-Lemeshow Test		
						χ^2	df	p	χ^2	df	p	χ^2	df	p
Emigrated (1) vs. other disappearance (0)	age + sex + Δ zbet	44.8	0	0.673	0.65	3.466	1	0.063			0.942	34.1	8	1
	age + sex + Δ zbet + Δ %deg	45.8	1.03	0.684	0.657	4.886	2	0.087			0.957	39.2	8	1
	† *age + sex	45.9	1.1	0.665	0.648						0.906	45.9	8	1
	age + sex + Δ %deg	46.8	1.96	0.665	0.641	1.502	1	0.22			0.933	48.6	8	1

^MThe dataset was limited to only include males

†The chosen “best” model for each outcome

*The reference model for LRT_1

**The reference model for LRT_2

Table A2. Model selection statistics for models considering the change in social position of vervets at Lake Nabugabo, Uganda from the penultimate (baseline) month to the month immediately prior to an individual's disappearance. Models included those individuals for whom dominance rank could be determined and were used to determine whether proportional rank (prop) should be included in the final model. Predictors include age, sex, change in betweenness centrality as a z-score (Δz_{bet}), change in eigenvector centrality as a z-score (Δz_{eig}), change in degree centrality as a percent of realized social partners ($\Delta \%deg$), and the interactions of these predictors (:). AICc is the Akaike Information Criterion corrected, while $\Delta AICc$ is the difference from the AICc of the model with the lowest AICc. LRT is the likelihood ratio test using up to two models as baseline conditions. df is degrees of freedom.

Outcome	Predictors	AICc	$\Delta AICc$	LRT		
				χ^2	df	p
Remained (1) vs. disappeared (any modes; 0)	*age + sex + Δz_{eig} + age:sex	591.1	0			
	age + sex + Δz_{eig} + $\Delta \%deg$ + age:sex	591.4	0.35			
	age + sex + Δz_{bet} + Δz_{eig} + age:sex	592.2	1.11			
	age + sex + Δz_{bet} + Δz_{eig} + $\Delta \%deg$ + age:sex	592.2	1.15			
	age + sex + Δz_{eig} + age:sex + age: Δz_{eig}	592.4	1.29			
	age + sex + Δz_{eig} + $\Delta \%deg$ + age:sex + age: Δz_{eig}	592.5	1.44			
	age + sex + Δz_{eig} + age:sex + sex: Δz_{eig}	592.6	1.48			
	age + sex + Δz_{eig} + prop + age:sex	593.0	1.92	0.102	1	0.750
Remained (1) vs. emigrated (0)	*age + sex + $\Delta \%deg$	164.2	0			
	age + sex + Δz_{eig} + $\Delta \%deg$	166.1	1.93			
	age + sex + $\Delta \%deg$ + prop	166.2	2.06	0.018	1	0.893
^M Remained (1) vs. emigrated (0)	*age + $\Delta \%deg$	161.2	0			
	age + Δz_{eig} + $\Delta \%deg$	163.2	1.96			
	age + $\Delta \%deg$ + prop	163.3	2.07	0.010	1	0.919
Remained (1) vs. human-related death (0)	age + Δz_{eig} + $\Delta \%deg$ + age: $\Delta \%deg$	122.5	0			
	age + Δz_{bet} + Δz_{eig} + $\Delta \%deg$ + age: $\Delta \%deg$	122.6	0.12			
	* Δz_{eig}	122.7	0.17			
	age + Δz_{eig}	123.3	0.8			
	Δz_{bet} + Δz_{eig}	123.4	0.9			
	age + Δz_{bet} + $\Delta \%deg$ + age: $\Delta \%deg$	123.8	1.32			
	age + Δz_{bet} + Δz_{eig}	124.0	1.44			
	sex + Δz_{eig}	124.3	1.77			
	age + Δz_{eig} + $\Delta \%deg$ + age: $\Delta \%deg$ + age: Δz_{eig}	124.4	1.87			
	age + Δz_{bet} + Δz_{eig} + $\Delta \%deg$ + age: $\Delta \%deg$ + age: Δz_{eig}	124.5	1.95			
	age + sex + Δz_{eig} + $\Delta \%deg$ + age: $\Delta \%deg$	124.5	1.96			
Δz_{eig} + prop	124.6	2.1	0.157	1	0.692	

Emigrated (1) vs. other disappearance (0)	*sex	36.5	0			
	sex + Δz_{bet}	36.6	0.12			
	sex + $\Delta \%deg$	37.8	1.29			
	sex + Δz_{bet} + $\Delta \%deg$	38.0	1.51			
	sex + Δz_{eig}	38.4	1.86			
	sex + prop	38.8	2.23	0.033	1	0.856

^MThe dataset was limited to only include males

*The reference model for LRT

Table A3. Model selection statistics for models considering the static value of social position of vervets at Lake Nabugabo, Uganda in the month immediately prior to an individual's disappearance. Models were run on the full dataset and excluded dominance rank as a predictor. Predictors include age, sex, static betweenness centrality as a z-score (zbet), static eigenvector centrality as a z-score (zeig), static degree centrality as a percent of realized social partners (%deg), and the interactions of these predictors (:). AICc is the Akaike Information Criterion corrected, while $\Delta AICc$ is the difference from the AICc of the model with the lowest AICc. R^2 is the variance explained by the fixed effects and the full model (calculated using the delta method) since the random effects did not explain any variance. The adjusted- R^2 (R^2 -adj) is adjusted for the number of fixed effects. LRT is the likelihood ratio test using up to two models as baseline conditions. AUC is the area under the receiver operating characteristics curve as a test of model discrimination. Hosmer-Lemeshow Test measures model calibration. df is degrees of freedom.

Outcome	Predictors	AICc	ΔAICc	R ²	R ² -adj	LRT_1			LRT_2			AUC			Hosmer-Lemeshow Test		
						χ ²	df	p	χ ²	df	p	χ ²	df	p	χ ²	df	p
Remained (1) vs. disappeared (any modes; 0)	age + sex + zbet + zeig + age:sex + age:zeig	889.1	0	0.018	0.015	21.971	5	< 0.001	9.952	3	0.019	0.695	-2059	8	1		
	† age + sex + zeig + age:sex + age:zeig	889.8	0.71	0.016	0.013	19.245	4	< 0.001	7.226	2	0.027	0.691	-2058	8	1		
	age + sex + zbet + zeig + %deg + age:sex + age:zeig	890.7	1.57	0.018	0.014	22.412	6	0.001	10.39	4	0.034	0.695	-2057	8	1		
	age + sex + zeig + %deg + age:sex + age:zeig	891.4	2.28	0.016	0.013	19.693	5	0.001	7.674	3	0.053	0.692	-2057	8	1		
	age + sex + zbet + zeig + age:sex	892	2.96	0.02	0.018	14.985	3	0.002	2.966	1	0.085	0.692	-2059	8	1		
	**age + sex + zeig + age:sex	893	3.91	0.018	0.016	12.019	2	0.003				0.686	-2058	8	1		
	age + sex + zbet + zeig + age:sex + sex:zbet	893.1	4.01	0.021	0.019	15.945	4	0.003	3.926	2	0.14	0.693	-2058	8	1		
	age + sex + zbet + zeig + age:sex + sex:zeig	893.6	4.55	0.021	0.018	15.406	4	0.004	3.387	2	0.184	0.692	-2058	8	1		
	age + sex + zbet + zeig + %deg + age:sex	893.7	4.61	0.02	0.018	15.346	4	0.004	3.327	2	0.189	0.693	-2058	8	1		
	age + sex + zeig + age:sex + sex:zeig	894.3	5.17	0.02	0.017	12.771	3	0.005	0.752	1	0.386	0.688	-2058	8	1		
	age + sex + zeig + %deg + age:sex	894.6	5.55	0.019	0.016	12.396	3	0.006	0.378	1	0.539	0.688	-2056	8	1		
	age + sex + zbet + zeig + %deg + age:sex + sex:zbet	894.7	5.63	0.022	0.019	16.339	5	0.006	4.32	3	0.229	0.694	-2057	8	1		
	*age + sex + zeig	901	11.96	0.015	0.013							0.667	-2054	8	1		

Outcome	Predictors	AICc	ΔAICc	R ²	R ² -adj	LRT_1			LRT_2			AUC			Hosmer-Lemeshow Test		
						χ ²	df	p	χ ²	df	p	χ ²	df	p	χ ²	df	p
Remained (1) vs. emigrated (0)	age + sex + zeig + age:zeig	193.8	0	0.199	0.194	7.901	3	0.048	5.129	2	0.077	0.913	-727.5	8	1		
	**age + sex + zeig	194.9	1.07	0.212	0.208	2.772	1	0.096				0.907	-732.1	8	1		
	age + sex + zbet + zeig + age:zeig	195.1	1.31	0.209	0.203	8.626	4	0.071	5.855	3	0.119	0.913	-729.8	8	1		
	† *age + sex	195.6	1.82	0.218	0.215							0.9	-728.3	8	1		
	age + sex + zeig + %deg + age:zeig	196	2.16	0.199	0.193	7.773	4	0.1	5.002	3	0.172	0.909	-728	8	1		
	age + sex + %deg	196.7	2.92	0.219	0.216	0.926	1	0.336				0.901	-730.8	8	1		
	age + sex + zeig + %deg	196.7	2.92	0.213	0.209	2.946	2	0.229	0.174	1	0.676	0.909	-731.9	8	1		
	age + sex + zbet + zeig	197	3.2	0.211	0.206	2.665	2	0.264	0.106	1	0.744	0.907	-730.9	8	1		
	age + sex + zbet	197.3	3.48	0.214	0.21	0.364	1	0.546				0.9	-732.9	8	1		
	age + sex + zbet + zeig + %deg + age:zeig	197.3	3.49	0.208	0.201	8.486	5	0.131	5.714	4	0.222	0.911	-728.2	8	1		

Outcome	Predictors	AICc	ΔAICc	R ²	R ² -adj	LRT_1		LRT_2		AUC	Hosmer-Lemeshow Test			
						χ ²	df	p	χ ²		df	p	χ ²	df
M Remained (1) vs. emigrated (0)	age + zeig + age:zeig	190.8	0	0.171	0.16	7.945	3	0.047	5.147	2	0.076	352.6	8	1
	**age + zeig	191.9	1.03	0.229	0.223	2.798	1	0.094				289	8	1
	age + zbet + zeig + age:zeig	192.1	1.31	0.172	0.159	8.71	4	0.069	5.913	3	0.116	1575	8	< 0.001
	† *age	192.6	1.79	0.22	0.216							280.6	8	1
	age + zeig + %deg + age:zeig	193	2.19	0.17	0.157	7.829	4	0.098	5.031	3	0.17	343.6	8	1
	age + %deg	193.7	2.89	0.222	0.217	0.937	1	0.333				284.2	8	1
	age + zeig + %deg	193.7	2.9	0.231	0.223	2.982	2	0.225	0.185	1	0.667	290.2	8	1
	age + zbet + zeig	194	3.16	0.228	0.22	2.72	2	0.257	0.077	1	0.781	288.8	8	1
	age + zbet	194.3	3.43	0.22	0.214	0.398	1	0.528				282.7	8	1
	age + zbet + zeig + %deg + age:zeig	194.3	3.52	0.171	0.156	8.58	5	0.127	5.782	4	0.216	4087.1	8	< 0.001

Outcome	Predictors	AICc	ΔAICc	R ²	R ² -adj	LRT_1			LRT_2			AUC			Hosmer-Lemeshow Test		
						χ ²	df	p	χ ²	df	p	χ ²	df	p	χ ²	df	p
Remained (1) vs. human-related death (0)	† age + sex + zeig + age:zeig	171.3	0	0.233	0.223	14.38	3	0.002	2.205	1	0.138	0.653	315.8	8	1		
	**age + zeig + age:zeig	171.5	0.14	0.234	0.226	12.175	2	0.002				0.637	315.7	8	1		
	age + sex + zeig + %deg + age:zeig	171.8	0.51	0.12	0.106	15.944	4	0.003	3.768	2	0.152	0.68	314.6	8	1		
	age + zeig + %deg + age:zeig	171.9	0.56	0.112	0.1	13.816	3	0.003	1.641	1	0.2	0.687	314.7	8	1		
	age + sex + zbet + zeig + age:zeig	172.6	1.29	0.232	0.22	15.167	4	0.004	2.992	2	0.224	0.663	315.2	8	1		
	age + sex + zbet + zeig + %deg + age:zeig	173	1.62	0.126	0.11	16.916	5	0.005	4.741	3	0.192	0.698	314.2	8	1		
	age + zbet + zeig + age:zeig	173.2	1.83	0.232	0.221	12.546	3	0.006	0.371	1	0.543	0.649	314.8	8	1		
	*age + zeig	179.5	8.2	0.008	0.001							0.598	308.8	8	1		
	age + sex	182.8	11.5	0.001	-0.01	3.289	0	< 0.001				0.557	306.7	8	1		
	age + sex + zeig	180.5	9.1	0.011	0.002	1.115	1	0.291				0.613	308.6	8	1		
Emigrated (1) vs. other disappearance (0)	† *age + sex	47.2	0	0.671	0.655							0.904	45.8	8	1		
	age + sex + zbet	47.9	0.68	0.696	0.677	1.657	1	0.198				0.923	41.72	8	1		
	age + sex + %deg	49.1	1.85	0.676	0.655	0.487	1	0.485				0.927	40.56	8	1		

^MThe dataset was limited to only include males

[†]The chosen “best” model for each outcome

*The reference model for LRT_1

**The reference model for LRT_2

Table A4. Model selection statistics for models considering the static value of social position of vervets at Lake Nabugabo, Uganda in the month immediately prior to an individual's disappearance. Models included those individuals for whom dominance rank could be determined and were used to determine whether proportional rank (prop) should be included in the final model. Predictors include age, sex, static betweenness centrality as a z-score (zbet), static eigenvector centrality as a z-score (zeig), static degree centrality as a percent of realized social partners (%deg), and the interactions of these predictors (:). AICc is the Akaike Information Criterion corrected, while $\Delta AICc$ is the difference from the AICc of the model with the lowest AICc. LRT is the likelihood ratio test using up to two models as baseline conditions. df is degrees of freedom.

Outcome	Predictors	AICc	$\Delta AICc$	LRT_1			LRT_2		
				χ^2	df	p	χ^2	df	p
Remained (1) vs. disappeared (any modes; 0)	**age + sex + zeig + age:sex + age:zeig	647.8	0						
	age + sex + zbet + zeig + age:sex + age:zeig	648.1	0.31						
	age + sex + zeig + %deg + age:sex + age:zeig	649.1	1.37						
	age + sex + zbet + zeig + %deg + age:sex + age:zeig	649.4	1.64						
	age + sex + zeig + prop + age:sex + age:zeig	649.5	1.7				0.323	1	0.570
	*age + sex + zeig + age:sex	653.3	3.56						
	age + sex + zbet + zeig + age:sex	653.3	3.6						
	age + sex + zeig + %deg + age:sex	654.5	4.73						
	age + sex + zbet + zeig + %deg + age:sex	654.5	4.74						
	age + sex + zeig + age:sex + sex:zeig	654.9	5.19						

	age + sex + zeig + prop + age:sex	655.0	5.25	0.322	1	0.571			
	age + sex + zbet + zeig + age:sex + sex:zbet	655.0	5.26						
	age + sex + zbet + zeig + prop + age:sex	655.1	5.39						
	age + sex + zbet + zeig + age:sex + sex:zeig	655.2	5.46						
Remained (1) vs. emigrated (0)	*age + sex + zeig + age:zeig	173.5	0						
	age + sex + zbet + zeig + age:zeig	174.8	1.26						
	age + sex + zeig + prop + age:zeig	175.4	1.88	0.169	1	0.682			
^M Remained (1) vs. emigrated (0)	*age + zeig + age:zeig	170.6	0						
	age + zbet + zeig + age:zeig	171.8	1.27						
	age + zeig + prop + age:zeig	172.5	1.91	0.196	1	0.658			
Remained (1) vs. human- related death (0)	*age + sex + zeig + age:zeig	115.1	0						
	age + sex + zeig + %deg + age:zeig	116.4	1.29						
	age + sex + zbet + zeig + age:zeig	116.8	1.62						
	age + sex + zeig + prop + age:zeig	117.3	2.12	0.012	1	0.912			
Emigrated (1) vs. other disappearance (0)	*sex	37.7	0						
	sex + zbet	39.4	1.76						
	sex + %deg	39.8	2.13						
	sex + prop	40.0	2.35	0.109	1	0.742			

^MThe dataset was limited to only include males

*The reference model for LRT_1

**The reference model for LRT_2

Table A5. Relationship between the baseline static social network metrics (i.e., between -60 to -31 days before all demographic events) and age and sex. Each of the models was produced using lmerTest. The random effects were individual identity and event number (nested within society identity) to control for pseudoreplication. Sex is given in reference to females (0). Age.L refers to the linear relationship between the levels of age (where juvenile < subadult < adult) and age.Q refers to the quadratic relationship. df is degrees of freedom.

Social network metric	Predictor	Estimate \pm standard error	df	t-value	p-value
Degree (% of partners)	Sex	-0.039 \pm 0.015	125	-2.628	0.010
	Age.L	0.054 \pm 0.006	1232	9.078	< 0.001
	Age.Q	-0.041 \pm 0.006	2584	-7.238	< 0.001
Strength (z-score)	Sex	-0.424 \pm 0.083	148	-5.100	< 0.001
	Age.L	0.498 \pm 0.036	890	13.889	< 0.001
	Age.Q	-0.516 \pm 0.039	2604	-13.383	< 0.001
Eigenvector centrality (z-score)	Sex	-0.411 \pm 0.083	147	-4.968	< 0.001
	Age.L	0.504 \pm 0.036	1068	14.082	< 0.001
	Age.Q	-0.528 \pm 0.038	2663	-13.812	< 0.001
Betweenness (z-score)	Sex	-0.383 \pm 0.062	166	-6.175	< 0.001
	Age.L	0.067 \pm 0.037	667	1.795	0.073
	Age.Q	-0.136 \pm 0.047	2278	-2.880	0.004

Table A6. Relationship between the change in social network metrics (i.e., between -60 to -31 days and -30 to -1 days before all demographic events) and age and sex. Each of the models was produced using lmerTest. The random effects were individual identity and event number (nested within society identity) to control for pseudoreplication. Sex is given in reference to females (0). Age.L refers to the linear relationship between the levels of age (where juvenile < subadult < adult) and age.Q refers to the quadratic relationship. df is degrees of freedom.

Social network metric	Predictor	Estimate ± standard error	df	t-value	p-value
Degree (% of partners)	Sex	0.002 ± 0.006	122	0.295	0.769
	Age.L	-0.003 ± 0.004	279	-0.756	0.451
	Age.Q	0.008 ± 0.006	1257	1.291	0.197
Strength (z-score)	Sex	-0.005 ± 0.034	128	-0.143	0.886
	Age.L	-0.039 ± 0.025	284	-1.568	0.118
	Age.Q	0.046 ± 0.037	1072	1.249	0.212
Eigenvector centrality (z-score)	Sex	-0.008 ± 0.033	132	-0.252	0.802
	Age.L	-0.040 ± 0.024	288	-1.633	0.104
	Age.Q	0.055 ± 0.036	1066	1.501	0.134
Betweenness (z-score)	Sex	-0.011 ± 0.051	171	-0.217	0.828
	Age.L	-0.008 ± 0.038	363	-0.214	0.830
	Age.Q	0.017 ± 0.057	1225	0.295	0.768

Table A7. Estimates and significance of predictors for the chosen best models concerning disappearances of vervet monkeys at Lake Nabugabo, Uganda from their society. (1) and (0) indicate which outcome was considered positive for each binary model. Network type refers to whether the model was based on the dynamic social network of the vervets (i.e., change from penultimate to ultimate month prior to a disappearance event) or the static social network (i.e., social centrality metrics taken in the ultimate month prior to disappearance).

Outcome	Network type	Predictor	Estimate \pm standard error	z-value	p-value
Remained (1) vs. disappeared (any modes; 0)	Dynamic	Intercept	3.668 \pm 0.184	19.899	< 0.001
		age.L	-0.583 \pm 0.185	-3.143	0.002
		age.Q	0.422 \pm 0.207	2.036	0.042
		sex	-0.767 \pm 0.218	-3.516	< 0.001
		z-betweenness	0.184 \pm 0.095	1.930	0.054
		z-eigenvector	0.417 \pm 0.138	3.024	0.003
	Static	Intercept	3.691 \pm 0.307	12.021	< 0.001
		age.L	-0.783 \pm 0.286	-2.737	0.006
		age.Q	-0.334 \pm 0.696	-0.479	0.632
		sex	-0.846 \pm 0.336	-2.518	0.012
		z-eigenvector	0.569 \pm 0.135	4.214	< 0.001
		age.L:sex	0.150 \pm 0.384	0.392	0.695
		age.Q:sex	1.636 \pm 0.728	2.247	0.025
		age.L:z-eigenvector	0.112 \pm 0.194	0.578	0.563
age.Q:z-eigenvector	-0.679 \pm 0.268	-2.529	0.012		
Remained (1) vs. emigrated (0)	Dynamic	Intercept	7.584 \pm 1.480	5.126	< 0.001
		age.L	-2.568 \pm 1.018	-2.524	0.012
		age.Q	1.722 \pm 0.633	2.721	0.007
		sex	-4.515 \pm 1.420	-3.180	0.001
	Static	Intercept	7.679 \pm 1.477	5.200	< 0.001
		age.L	-2.616 \pm 1.017	-2.573	0.01
		age.Q	1.956 \pm 0.625	3.128	0.002
		sex	-4.543 \pm 1.416	-3.208	0.001
Remained (1) vs. emigrated (0); males only	Dynamic	Intercept	3.069 \pm 0.492	6.235	< 0.001
		age.L	-2.568 \pm 1.024	-2.508	0.012
		age.Q	1.721 \pm 0.636	2.705	0.007
	Static	Intercept	3.135 \pm 0.490	6.397	< 0.001
		age.L	-2.617 \pm 1.023	-2.559	0.011
		age.Q	1.956 \pm 0.629	3.110	0.002
Remained (1) vs. human-	Dynamic	Intercept	3.419 \pm 0.456	7.491	< 0.001
		age.L	0.073 \pm 0.353	0.208	0.835

related death (0)		age.Q	-1.271 ± 1.037	-1.226	0.22
		z-eigenvector	1.033 ± 0.310	3.336	0.001
		%degree	1.917 ± 2.157	0.889	0.374
		age.L:%degree	3.874 ± 1.941	1.995	0.046
		age.Q:%degree	-11.849 ± 4.819	-2.459	0.014
	Static	Intercept	2.971 ± 0.762	3.901	< 0.001
		age.L	-0.259 ± 0.388	-0.667	0.505
		age.Q	-1.005 ± 1.725	-0.583	0.56
		sex	0.786 ± 0.520	1.511	0.131
		z-eigenvector	3.041 ± 1.594	1.908	0.056
		age.L:z-eigenvector	0.235 ± 0.352	0.667	0.505
	age.Q:z-eigenvector	-6.432 ± 3.883	-1.657	0.098	
Emigrated (1) vs. other disappearance (0)	Dynamic	Intercept	-4.998 ± 1.624	-3.079	0.002
		age.L	2.965 ± 1.181	2.511	0.012
		age.Q	-1.453 ± 0.819	-1.774	0.076
		sex	4.982 ± 1.595	3.124	0.002
	Static	Intercept	-4.995 ± 1.620	-3.083	0.002
		age.L	2.966 ± 1.181	2.510	0.121
		age.Q	-1.607 ± 0.813	-1.976	0.048
		sex	5.041 ± 1.592	3.167	0.002