MALE MATING EFFORT AND FEMALE PREFERENCE IN RELATION TO MALE DOMINANCE RANK, TENURE LENGTH, AND AGE IN WILD VERVET MONKEYS (*CHLOROCEBUS PYGERYTHRUS*)

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Abstract

In this study, we aimed to evaluate the effect of male dominance rank, tenure, and age on male mating effort and female choice while quantifying four sociometric variables of male dominance hierarchy (stability, linearity, directional consistency, steepness) in two groups of wild vervet monkeys (*Chlorocebus pygerythrus*) at Lewa-Borana Conservancy, Kenya. We collected a total of 305 hours of behavioural data across a 4-month field season in 2022 on 13 adult/subadult males. Overall, adult, high-ranking males who had been in the group for a shorter amount of time, generally put forth more mating effort, copulated more frequently, and were preferred by females. The male dominance hierarchies for both groups were stable (mean $S = 0.9844 \pm 0.001$), quasi-linear (mean $h' = 0.7554 \pm 0.018$), unidirectional (mean $DCI = 0.7017 \pm 0.121$), and moderately steep (mean $D_{ij} = 0.6437 \pm 0.044$).

Keywords: Male dominance hierarchy, dominance characteristics, sexual strategies, primates

Dedication

This thesis is dedicated to my dad, Andrew Fane, who gave me a childhood filled with nature walks, rehabilitating wildlife, and collecting animal bones. He sparked the wonder in me and lives on within it.

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1.0 Introduction

1.1 Dominance Hierarchies

Social dominance hierarchies are present in most species with social organization and social behaviour (Cant & Field, 2005; Chiao, 2010; Ramsay & Ratcliffe, 2003). Dominance rank refers to the position of one individual in a dominance hierarchy and is often attained through repeated agonistic interactions between group members (Drews, 1993; Majolo et al., 2012). Dominance may give rise to various fitness-related benefits such as preferential access to food, water, shelter (Appleby, 1980; Clutton-Brock et al., 1984; Dunbar & Dunbar, 1977; Majolo et al., 2012) and/or sexual partners (Alberts et al., 2006; Altmann, 1962; Majolo et al., 2012); as a result, dominance rank can have a profound impact on an individual's survival and reproductive success (Filby et al., 2010; Freeman, 2012; Majolo et al., 2012; Packer & Pusey, 1987; Silk, 2007).

Access to fertile females is the primary limiting resource for male reproductive success (Emlen & Oring, 1977; Freeman, 2012). In many group-living species, dominant males attain increased mating opportunities through winning direct competition with subordinate males (Ellis, 1995; Kutsukake & Nunn, 2009). The 'priority of access model' of male mating strategies developed by Altmann (1962) has been an influential framework for understanding the relationship between male dominance rank and reproductive success in relation to access to fertile females for group-living primates (Bissonnette et al., 2011). Altmann (1962) suggested that male rank should correlate with reproductive success because dominant males should be more effective at monopolizing fertile females than lower-ranking competitors, causing a strong reproductive skew. Reproductive skew is the unequal distribution of reproductive opportunities among same-sex group members (Kutsukake & Nunn, 2009; Wikberg et al., 2016), and following the priority of access model, we would predict strong skew towards one or a few high-ranking males.

Males can monopolize access to females by winning direct competitions against subordinate males, mate-guarding, and influencing female mate choice (Altmann & Alberts, 2003; Majolo et al., 2012). Due to the unavailability of genetic data, and because many female primates, including vervet monkeys (*Chlorocebus pygerythrus*), show no external morphological changes associated with ovulation (Andelman, 1987; Sillen-Tullberg & Moller, 1993), observational studies can only estimate male reproductive success by recording the frequency of copulations by each individual (Cheney et al., 1989). Thus, mating success often serves as a proxy for male reproductive (paternity) success in observational studies. In this thesis, we examine the role of male dominance rank, male tenure length, and male age-class in sociosexual behaviour and intersexual affiliation in two vervet monkey groups at Lewa-Borana, Kenya while also quantifying and comparing four sociometric parameters of the male dominance hierarchy (linearity, steepness, directional consistency, and stability).

The relationship between male rank and mating success in primates has been well documented in the literature but produces variable results both within and across taxa (for reviews see Cowlishaw & Dunbar, 1991; Ellis, 1995; Majolo et al., 2012). The discrepancies in the literature are likely due to the unique socioecological circumstances of individual species and groups which influence the degree to which males can monopolize access to mates and in turn, influences the reproductive benefits associated with dominance rank (Emlen & Oring, 1977; Gartland et al., 2021; Majolo et al., 2012; van Hooff & van Schaik, 1994). Factors such as the history of the social group, male tenure length and age, group composition, relationships with females, fighting ability and opportunities for sneak mating will all influence the relationship between male dominance rank and mating success (Berard, 1999; Cowlishaw & Dunbar, 1991; Inoue & Takenaka, 2008; Otani et al., 2020)

1.2 Factors that Affect Male Dominance as a Mating Strategy

In many primate species, female mate choice can impact the effectiveness of dominance as a mating strategy, which in turn, affects the reproductive skew (Huffman, 1987; Wong & Candolin, 2005; for review see Paul, 2002). In primate species such as the vervet monkey where females have concealed ovulation and sexual dimorphism is less marked, female choice is expected to play an important role in mating behaviour. This is in contrast to species where mate-guarding is favoured by honest signals of female fertility and males are able to physically dominate females to force copulation through sexual coercion (Muller & Wrangham, 2004; van Schaik et al., 2004). Females often select male partners based on dominance status, novelty, familiarity, or age (for review see Small 1989) and attractive males can be identified as those that females willingly mate with (measured through mating presentations and mating refusals) as well as those that females preferentially interact with (measured through affiliative interactions and proximity indices) (Perloe, 1992; Soltis et al., 1997).

Females are frequently assumed to show preference for male partners based on competitive ability (e.g., dominance status) because they provide protection, access to resources and may sire healthier offspring (Altmann, 1962; Cowlishaw & Dunbar, 1991; Georgiev et al., 2015; Small, 1989). Female preference for dominant males has been seen in numerous primate species, including rhesus macaques (*Macaca mulatta)* (Altmann, 1962; Kaufmann, 1965), crab-eating macaques, (*Macaca fascicularis*) (van Noordwijk, 1985), olive baboons (*Papio anubis*) (Packer, 1979b), yellow baboons (*Papio cynocephalus*) (Hausfater, 1975; Seyfarth, 1978) tufted capuchins (*Cebus apella*) (Janson, 1984), and orangutans (*Pongo pygmaeus*) (Utami, 2002). Likewise, female vervet monkeys have been documented expressing mate preference for dominant males. In captive vervets, females direct more affiliative behaviour towards alpha males than subordinate males and direct more agonistic behaviour towards subordinate males than dominant males (Keddy Hector et al., 1989). Furthermore, female vervets have shown mate preference for alpha males over subordinate males in both captive and wild settings (Andelman, 1987; Keddy Hector, 1986). Thus, female preference for dominant males can strengthen the reproductive skew in these populations.

In primates species, including vervets, where females remain in their natal group and commonly reach sexual maturity during the reproductive tenure of their father or other close relatives, females often show preference for novel males who are sexually unfamiliar (Berard, 1999; Henzi & Lawes, 1987; Huffman, 1992; Packer, 1979a, b; Smuts, 1985). This selection for novel males likely evolved to avoid inbreeding depression (i.e., reduced survival and fertility of offspring of related individuals) (Bengtsson, 1978; Kokko & Ots, 2006; Small, 1989; Szulkin et al., 2013; Waser et al., 1986). Females may also choose to mate with newer males to increase the genetic variability among their offspring (Small, 1989). Female preference for novel males has been observed in rhesus macaques (Berard, 1999) and Japanese macaques (*Macaca fuscata*) (Huffman, 1992; Wolfe, 1984). Likewise, in vervets and other group living primates, females increase genetic variation by mating with extra-group males (Henzi & Lawes, 1987; Minkner et al., 2018; for review see Miller et al., 2021). Thus, extra-group copulations may be a strategy used by males and females to increase genetic diversity and by subordinate males to increase reproductive success (Gibson, 2010; Overduin-De Vries et al., 2012; Parga, 2006; Setchell, 2008).

Many group living primates live in multi-male groups where females are philopatric and males disperse from their natal group at sexual maturity (Greenwood, 1980; Pusey & Packer, 1987). If female mate preference for novel males is a strategy to increase genetic variation and avoid inbreeding, then age-class may also play a role in mate selection, with females showing preference for mating with immigrant adult males over natal subadult males (Blouin & Blouin, 1988; Kokko & Ots, 2006; Perry, 2008; Pusey & Wolf, 1996; Small, 1989; Spong et al., 2008; Waser et al., 1986). Female mate preference for immigrant adult males over natal subadult males has been seen in Japanese macaques (Takahata, 1980) and ruffed lemurs (*Varecia variegata*) (Foerg, 1982). Thus, inbreeding avoidance can decrease reproductive skew in some populations if females choose to mate with less related subordinate adult males over dominant subadult males who are in their natal group (Altmann et al., 1996; Godoy et al., 2016; Muniz et al., 2006).

Female preference for males can be expressed through sociosexual interactions (e.g., mating presentations and mating refusals) as well as through affiliative interactions (e.g., grooming, proximity) (Perloe, 1992; Soltis et al., 1997). Although we expect female sociosexual preference to positively correlate with affiliative behaviour in most cases (i.e., females should show preference for specific males through mating presentations and refusals as well as through proximity maintenance and grooming), the relationship becomes less straightforward when you consider subadult males residing in their natal groups. Due to the degree of relatedness between natal subadult males and the females residing with them, we would expect a reverse relationship between sociosexual and affiliative behaviour where females show sociosexual mate preference for immigrant adult males over natal subadult males, while showing preference for affiliative interactions with related subadult males over adult males. There is broad evidence in many primate species, including vervets, that individuals form stronger social bonds with related individuals over unrelated individuals (Amici et al., 2019; Johnson et al., 1980; Langergraber et al., 2007; Silk et al., 2006; for reviews see Chapais, 2001; Silk, 2002). Therefore, female preference for forming social bonds with kin may affect the degree that dominant males can monopolize affiliative access to females when natal subadult males are present in a group.

In mammals, females are expected to have stronger mate preference than males due to larger female reproductive investment (Trivers, 1972), but mechanisms should still exist in males to avoid inbreeding (Tennenhouse, 2014). Group-living males can avoid inbreeding by dispersing from their natal group (Moore, 1993; Pusey & Packer, 1987) or by exerting mate choice for unrelated mates (Pusey & Packer, 1987). In baboons, father-daughter pairs have substantially lower probabilities of consorting than unrelated pairs (Galezo et al., 2022). Similarly, alpha males in group-living primates often exert mate choice and avoid mating with their mature offspring (Godoy et al., 2016; Griffin et al., 2003; Muniz et al., 2006; Vigilant et al., 2015). Thus, male mate choice for unfamiliar mates can also affect the efficacy of dominance as a mating strategy if dominant males avoid mating with related females in their group.

Multi-male groups are subject to greater intrasexual competition than uni-male groups (Plavcan & van Schaik, 1997). An increase in the number of males in a group should reduce the effectiveness of dominance as a mating strategy, since an increase in the number of competitors increases the likelihood that high-ranking males can be displaced through coalitions of lower-ranking co-residents (Cowlishaw & Dunbar, 1991). Additionally, when there are more males in a group, the power differential between dyads (hierarchal steepness) is likely to decrease because an increase in the number of males increases the likelihood that there will be individuals of similar competitive ability (Harcourt, 1987); this, in turn, decreases the likelihood that one or a few dominant males will be able to monopolize access to multiple females (Cowlishaw & Dunbar, 1991).

An increase in the total number of females in a group may also reduce the efficacy of dominance as mating strategy as a single male cannot be in multiple places at once and an abundance of females should make it more difficult for high-ranking individuals to prevent lower-ranking competitors from gaining access to mating opportunities. Likewise, in species where female mate choice is a factor, an increased number of females would allow individual females to exercise greater mate choice due to the reduced capacity for dominant males to guard a high proportion of mates (Dunbar, 1988). The ratio of sexually receptive females to sexually active males (operational sex ratio) also plays an important role in the intensity of intrasexual competition for access to mating opportunities. When the operational sex ratio is skewed toward males, more males are ready to mate than females are in a group and the level of intrasexual competition among males for access to fertile females increases which should increase the benefit of dominance as a male mating strategy (de Jong et al., 2012; Emlen & Oring, 1977; Kvarnemo & Ahnesjo, 1996). In populations where breeding seasonality is synchronous, many of the group females are ovulatory at the same time, skewing the operational sex ratio towards females, and it should be more difficult for a single male to monopolize access to mating opportunities. Therefore, dominance as a mating strategy will be favoured in more asynchronous populations, where females become fertile at different times (de Jong et al., 2012; Emlen & Oring, 1977).

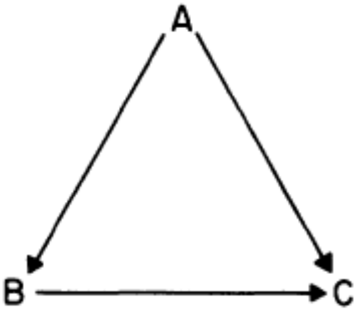
1.2.1 Dominance Hierarchy Characteristics

Dominance hierarchies are a representation of the patterning of dominance relationships at a group level, where dominance relationships are the outcome of competitive encounters between one or more pairs of individuals within a group (Altmann, 1962; de Vries, 1998). Dominance hierarchies have been found to vary both within and across species (for review see Majolo et al., 2012). Van Schaik (1989) coined the term “despotic” to describe dominance hierarchies that are “steep and linear” as well as the term “egalitarian” to describe dominance hierarchies that are “weakly linear and shallow”. Many authors similarly use the term hierarchy “strength” to describe varying features among dominance hierarchies, with strong hierarchies being steep and linear while weak hierarchies are shallow and non-linear (Wikberg et al., 2013).

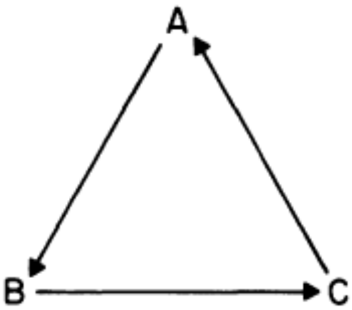
There exists a negative relationship between hierarchy strength and resource abundance. Hierarchy strength increases when resources are limited, whereas when resources are abundant, hierarchy strength decreases (Emlen & Oring, 1977; Grant et al., 1995; Isbell et al., 2002; Sterck et al., 1997). This is because when limiting resources are scarce and/or clumped, more competitive individuals are able to monopolize access to a greater portion of the available resources and dominance rank should influence an individual’s survival and reproductive success. In contrast, resources are less monopolisable when they are abundant and/or widespread and the benefits of dominance as a reproductive strategy decrease, resulting in weaker dominance hierarchies (Emlen & Oring, 1977; van Hooff & van Schaik, 1994). Many hierarchies are also shaped by changes to group composition. In ursine colobus (*Colobus vellerosus*), hierarchy expression is greater in larger groups (Teichroeb & Sicotte, 2009). Changes to group composition, through the immigration of new males, has also been reported to lead to hierarchy instability in wild crested macaques (*Macaca nigra*) (Neumann et al., 2011). Additionally, the number of individuals present in groups of domestic sow has been found to predict hierarchy strength, with groups with more individuals being weaker (Fels et al., 2014). These findings suggest that dominance characteristics are shaped by several factors including resource availability and group demographics.

The drawback of characterizing hierarchies in terms such as “despotic” or “egalitarian”, and “strong” or “weak” is that they are not inherently specific and can be interpreted in several ways, making it difficult to compare hierarchies across studies (Wikberg et al., 2013). It is therefore useful to describe dominance hierarchies in terms of several specific sociometric parameters (i.e., linearity, steepness, directional consistency, and stability) to better characterize similarities and differences between species and populations.

Linear hierarchies are primarily composed of transitive triads, while non-linear hierarchies are composed of high numbers of intransitive (circular) triads. In a transitive triad, individual A dominates B, B dominates C, and A also dominates C (Figure 1), while in an intransitive triad, individual A dominates B, B dominates C, but C then dominates A (Figure 1). The more intransitive relationships within a hierarchy, the further from linearity (Chase, 1982; de Vries, 1998).



Transitive



Intransitive

Figure 1. The configuration of relationships in transitive and intransitive triads. Reprinted from "Dynamics of Hierarchy Formation: The Sequential Development of Dominance Relationships", by Chase, I. D., 1982, Behaviour, 80(3–4), 218–239.

The steepness of a dominance hierarchy refers to the absolute difference in overall success in winning competitive encounters between adjacently ranked individuals (de Vries et al., 2006). When the measure of steepness between adjacent individuals is high, the dominant individual will frequently win competitive encounters, whereas when the measure of steepness between adjacent individuals is low, the proportion of wins and loses between the dyad will be more even. Thus, a greater difference between adjacent individuals results in a steeper dominance hierarchy (de Vries et al., 2006).

Another useful sociometric parameter for characterizing dominance hierarchies is directional consistency which describes the directional proportion of agonistic interactions between dyads. Complete unidirectionality between two individuals occurs when an individual within a dyad wins competitive encounters 100% of the time, while bidirectionality occurs when each dyad member wins 50% of competitive encounters (van Hooff & Wensing, 1987).

Finally, hierarchy stability refers to rates of changes in dominance ranks. When a hierarchy is stable, the dominance rank of each individual is fixed over time, while unstable hierarchies experience higher rates of rank change between individuals (McDonald & Shizuka, 2013; Neumann et al., 2011).

Variability in the characteristics of dominance hierarchies will affect the ability of dominant males to monopolize access to mates. Dominant males are predicted to win more agonistic interactions in stable, steep, and linear hierarchies with strong directional consistencies than in unstable, shallow, non-linear hierarchies with weak directional consistencies. Therefore, the reproductive benefits associated with dominance rank should be higher in hierarchies with stronger expression (Vehrencamp, 1983). In this study, we quantify and compare four sociometric parameters of the male dominance hierarchy (linearity, steepness, directional consistency, and stability) for two vervet monkey groups which enables us to make stronger inferences about the relationship between male dominance rank and mating success in vervet monkeys.

1.3 Study Organism

Vervet monkeys live in multi-male, multi-female groups year-round, where females are philopatric and males disperse from their natal groups at sexual maturity (~ 5 years of age) and can engage in secondary dispersal (Cheney & Seyfarth, 1983; Isbell et al., 1991; Struhsaker, 1967b). Females reach sexual maturity at around 4 years of age and do not show any visual signs of ovulation (Andelman, 1987; Cheney et al., 1988). Wild vervet populations have moderate to high breeding seasonality (*sensu* van Schaik et al., 1999, with > 67% of births within three consecutive months) (Schwegel et al., 2022) and wean at 9-21 months (Cheney et al., 1988; Whitten, 1982). Vervet monkeys are an excellent species to study male dominance status and its relationship to mating success because they have easily quantifiable, sex-specific hierarchies (Cheney & Seyfarth, 1990) and their semi-terrestrial lifestyle make their behaviour easier to observe than arboreal species (Ellis et al., 1995). While female hierarchies are stable and established through maternal descent (Bramblett et al., 1982), male hierarchies are less stable and based primarily on competitive ability (Cheney & Seyfarth, 1983; Freeman, 2012; Henzi, 1982; Isbell, 1995). Males typically disperse to neighbouring groups during the breeding season to increase their dominance rank and access to mating opportunities (Cheney & Seyfarth, 1983;

Freeman, 2012; L'Allier et al., 2022). Vervet monkeys are only mildly sexually dimorphic with adult males weighing an average of 1.4 times that of adult females in the wild and females often win encounters against males both individually and through alliances with other females (Minkner et al., 2018; Struhsaker, 1967b). Thus, females are able to resist mating attempts by males, suggesting that they have the ability to play a considerable role in mate choice (Freeman, 2012; Keddy Hector, 1986). Andelman (1987) found that female vervets reject as many as 50% of male mating attempts. In captive vervets, females direct more affiliative behaviour towards alpha males than subordinate males and direct more agonistic behaviour towards subordinate males than dominant males (Keddy Hector et al., 1989). Furthermore, captive female vervets have shown mate preference for alpha males over subordinate males (Keddy Hector, 1986).

While captive vervet studies have found a positive correlation between male dominance rank and mating success (Keddy Hector, 1986) and reproductive success (Weingrill et al., 2011), studies of wild vervets are more variable. Cheney et al. (1988) studied three groups of vervet monkeys at Amboseli, Kenya, and found no significant correlation between male rank and mating success. However, research on two groups of vervet monkeys at Samara Private Game Reserve, South Africa over multiple years found a significant negative correlation in one study period (Freeman, 2012) and a significant positive correlation in another (Freeman et al., 2016). Similarly, Minkner et al. (2018) studied three groups of vervet monkeys at Samara Private Game Reserve, South Africa over four mating seasons and found that the relationship between male dominance rank and mating success was positive across all groups and mating seasons, with the exception of one group during a single mating season. Variation among research sites in breeding seasonality, number of adult males/females, operational sex ratios and male dominance hierarchy characteristics are likely affecting the ability of dominant males to monopolize access to fertile females, leading to the discrepancies seen between captive and wild studies, as well as between years in wild populations. Thus, further studies are needed to assess factors that affect the relationship between male dominance and mating success in vervet monkeys.

1.4 Hypotheses and Predictions

In this paper, we test several hypotheses about the patterns of male sociosexual behaviour in two groups of vervets at Lewa-Borana Conservancy in Kenya. First, we examine how male sociosexual behaviour (Table 1) and intersexual behaviour (Table 2) are influenced by male rank, tenure length, age class, and group membership.

Table 1. Hypothesis 1: Male sociosexual behavioural interactions are influenced by 1) male rank, 2) tenure length, 3) age-class, and 4) group identity.

Prediction	Predictor	Response
Rank 1 a) Higher-ranking males will put forth more mating effort than lower-ranking males.	Average ordinal rank	Rate of mating effort
1 b) Higher ranking males will have more copulations than lower-ranking males.	Average ordinal rank	Rate of copulations
1 c) Higher-ranking males are preferred by females and will therefore receive a higher rate of mating presentations from females than lower-ranking males.	Average ordinal rank	Rate of received female mating presentations
1 d) Higher ranking males are preferred by females and will therefore receive a lower rate of mating refusals from females than lower-ranking males.	Average ordinal rank	Rate of received female mating refusals
1 e) Higher-ranking males are preferred by females and will therefore receive a lower rate of mating refusals per mating effort from females than lower-ranking males.	Average ordinal rank	Rate of received female mating refusals per mating effort
Tenure Length		

2 a) Males with shorter tenure are preferred by females and will therefore have more copulations than males with longer tenure.	Minimum tenure length	Rate of copulations
2 b) Males with shorter tenure are preferred by females and will therefore receive a higher rate of mating presentations from females than males with longer tenure.	Minimum tenure length	Rate of received female mating presentations
2 c) Males with shorter tenure are preferred by females and will therefore receive a lower rate of mating refusals from females than males with longer tenure.	Minimum tenure length	Rate of received female mating refusals
2 d) Males with shorter tenure are preferred by females and will therefore receive a lower rate of mating refusals per effort from females than males with longer tenure.	Minimum tenure length	Rate of received female mating refusals per mating effort
Age-class		
3 a) Adult males will put forth more mating effort than subadult males.	Age-class	Rate of mating effort
3 b) Adult males will have more copulations than subadult males.	Age-class	Rate of copulations
3 c) Adult males are preferred by females and will therefore receive a higher rate of mating presentations from females than subadult males.	Age-class	Rate of received female mating presentations
3 d) Adult males are preferred by females and will therefore receive a lower rate of mating refusals from females than subadult males.	Age-class	Rate of received female mating refusals
3 e) Adult males are preferred by females and will therefore receive a lower rate of mating refusals per effort from females than subadult males.	Age-class	Rate of received female mating refusals per mating effort
Group Identity		
4 a) The group with the highest number of adult males will put forth the most mating effort.	Group Identity	Rate of mating effort
4 b) The group with the highest number of adult males will have the highest copulation rate.	Group Identity	Rate of copulations

4 c) The group with the highest number of adult males will receive the highest rate of mating presentations from females.	Group Identity	Rate of received female mating presentations
4 d) The group with the highest number of adult males will receive the lowest rate of mating refusals from females.	Group Identity	Rate of received female mating refusals
4 e) The group with the highest number of adult males will receive the lowest rate of mating refusals per effort from females.	Group Identity	Rate of received female mating refusals per mating effort

Table 2. Hypothesis 2: Intersexual affiliation is influenced by 1) male rank, 2) tenure length, 3) age-class, and 4) group identity.

Prediction	Predictor	Response
Rank		
1 a) Females will prefer to interact with higher-ranking males over lower-ranking males and therefore, male rank will be positively correlated with rates of intersexual grooming.	Average ordinal rank	Rate of females grooming males, Rate of males grooming females
1 b) Higher-ranking males are preferred by females, and therefore females will maintain proximity at a higher rate to higher-ranking males than to lower-ranking males (e.g., Higher-ranking males will have a lower Hinde's index).	Average ordinal rank	Hinde's index
1 c) Higher-ranking males are better at monopolizing females and therefore, higher-ranking males will have higher rates of female proximity relative to lower-ranking males.	Average ordinal rank	Rate of female proximity
Tenure Length		
2 a) Females will prefer to interact with novel males over males with longer tenure and therefore, male tenure length will be negatively correlated with rates of intersexual grooming.	Minimum tenure length	Rate of females grooming males, Rate of males grooming females
2 b) Novel males are preferred by females, and therefore females will maintain proximity at a higher rate to novel males than to lower males	Minimum tenure length	Hinde's index

with longer tenure (e.g., novel males will have a lower Hinde's index).		
2 c) Novel males are preferred by females, and therefore novel males will have higher rates of female proximity relative to males with longer tenure.	Minimum tenure length	Rate of female proximity
Age-class		
3 a) Females will prefer to interact with natal subadult males over unrelated adult males and therefore, subadult males will have higher rates of intersexual grooming relative to adult males.	Age-class	Rate of females grooming males, Rate of males grooming females
3 b) Females will prefer to interact with natal subadult males over unrelated adult males and therefore, females will maintain proximity at a higher rate to subadult males relative to adult males (e.g., subadults will have a lower Hinde's index).	Age-class	Hinde's index
3 c) Females will prefer to interact with natal subadult males over unrelated adult males and therefore, subadult males will have higher rates of female proximity relative to adult males.	Age-Class	Rate of female proximity
Group Identity		
4 a) The group with the highest number of adult males will have the lowest rates of intersexual grooming.	Group Identity	Rate of females grooming males, Rate of males grooming females
4 b) Females will maintain proximity at a lower rate to the group with the highest number of adult males (e.g., the group with the highest number of adult males will have a higher Hinde's index).	Group Identity	Hinde's index
4 c) The group with the highest number of adult males will have the lowest rates of female proximity.	Group Identity	Rate of female proximity

2.0 Methods

2.1 Study Site

We collected behavioural data in two habituated groups of vervet monkeys (Boma & Marwell, ~45 individuals) at Lewa-Borana Conservancy in Isiolo, Kenya (0.20°N, 37.42°E), a 375 km^2 black rhinoceros (*Diceros bicornis*) protected area that supports over 70 species of mammals (Dupuis-Desormeaux et al., 2016, 2023). The habitat at Lewa-Borana is primarily savannah grassland, Acacia bushland, wetland, grassland and indigenous forest interspersed with a network of roads, pastures, and villages (Davidson et al., 2019; Dupuis-Desormeaux et al., 2018; Szapary, 2000). The altitude varies from 1,500 to 2,000 meters and the annual rainfall is 500 to 600 mm (Szapary, 2000). Electrical fences surround the perimeter of Lewa-Borana with six migratory fence gaps to allow wildlife movement while restricting the movement of rhinoceros (Davidson et al., 2019; Dupuis-Desormeaux et al., 2016). As Lewa-Borana is a wildlife conservancy, vervets experience little to no conflict with humans (Dupuis-Desormeaux et al., 2018). Throughout the study period, our two study groups had regular access to food handouts and could easily access garbage pits where they foraged food scraps (e.g., corn, cooked rice, local fruits, etc.).

2.2 Data Collection

Our team collected scan data on five randomly selected vervet monkeys at 15-minute intervals from February 2020 to August 2022 to record their general behaviour (e.g., moving, resting, grooming, copulating, etc.) as well as any interactions and the identity of their nearest neighbour (>5 meters) (Altmann, 1974). This was supplemented with *ad libitum* data collection of all agonistic interactions for adult and subadult males (>4 years) (Henzi, 1982; Struhsaker, 1967a). Focal follows were conducted on adult and subadult males at Lewa-Borana (Marwell &

Boma groups) from April 25th to August 17th, 2022. Previous studies on wild vervet monkeys in Kenya indicate that the months chosen for our focal follows fall within their natural mating season (Andelman, 1987; Isbell & Jaffe, 2013; Struhsaker, 1967a; Whitten, 1983). During focal follows, the date, time, and all behavioural observations (see Appendix for ethogram) were recorded. Focal individuals were chosen at random, ensuring there had been at least one different individual followed before repeating observations on an individual. In cases where a male emigrated from a study group to an unknown group (e.g., OLE from Marwell), data collection on that male ceased and the dispersal date was recorded. All data collection occurred between the hours of 7:00 a.m. and 6:00 p.m.

All adult and subadult males and females were individually identified due to variation in fur markings, colouration, tail appearance and/or scar damage. Interactant identities were recorded in all social behaviours. If individual identification of social interactants was not possible, the interactant was classified by sex and age-class (e.g., adult male/female, subadult male/female, juvenile male/female, infant, extra-group individual (with sex and age-class if possible to determine), unknown). When the exact age of a male focal individual was unknown (primarily those in Boma group since many natal males were born into the group prior to the start of the study), we considered males to be subadult males when they began mating attempts, and they became adults when they emigrated from their natal group. Subadult males were included in this study because they are capable of fertilizing and competing for females (Cheney et al., 1988).

2.3 Data Analysis

Behavioural data for each predictor variable was extracted from focal data only (April to August 2022). Each predictor variable (with the exception of Hinde's index) was transformed into a rate by dividing the behaviour by the total number of hours spent observing an individual male. Rate of mating effort, copulation rate, rate of female mating presentations, rate of female mating refusals, and rate of female mating refusals per mating effort were expressed in events per hour while rate of female-male grooming, rate of male-female grooming, and rate of female proximity were expressed in seconds per hour. Mating effort was defined as a sum of all copulations, mounts, and mating refusals per individual male. Hinde's index (-1 to +1) determines which member of a pair of male-female dyads is responsible for maintaining proximity to each other and measures the percentage of approaches initiated by the male minus the percentage of leaves initiated by the male. A negative value occurs when the female maintains proximity to the male and a positive value occurs when the male maintains proximity to the female (Hinde & Atkison, 1970). We calculated the individual Hinde's index for each male as the average Hinde's index of all intrasexual dyads for that male. Female proximity was calculated by summarizing the time (seconds) each male spent in proximity (< 2 meters) to one or more females.

2.3.1 Dominance Hierarchies

To construct a male dominance hierarchy for each group, we extracted all dyadic male-male agonistic interactions (e.g., supplant, avoid, head-bob, bite, stare-attack; Henzi, 1982; Struhsaker, 1967) (see Appendix for ethogram) from the scan, *ad libitum,* and focal data. The winner (i.e., individual directing aggressive behaviour) and loser (i.e., individual directing submissive behaviour) were recorded for each agonistic bout and in the case of no clear winner, the bout was recorded as a draw. Agonistic bouts were defined as any agonistic interactions between a given male-male dyad within 15 minutes of each other.

We calculated Elo-ratings (function: extract_elo, package: Elo-rating; Neumann & Kulik, 2020) which measure dominance ranks based on sequences of interactions. This rating system is particularly useful as ratings can be obtained at any point in time throughout a study period and are independent of group size. Additionally, the system is not interrupted by demographic changes such as births, deaths, and immigrations. For example, when a new individual enters a group, the Elo-rating process continues, and the new individual is added into the rating system after a few initial interactions. This is especially useful for assessing dominance rank in groups with fluid demography (Neumann et al., 2011).

To calculate male dominance rank, we assigned an initial Elo score of 1000 to all individuals (Foerster et al., 2016; Neumann et al., 2011; Neumann & Kulik, 2020). Immigrant males were also assigned an Elo score of 1000 and five interactions for each new male were necessary before determining the male's actual rank (Newton-Fisher, 2017). We calculated an optimized *k* for each group (function: optimizek, package: Elo-rating; Neumann & Kulik, 2020) by testing a range of k values from 4-200 at a resolution of 491 and calculating the log likelihoods for each value (Schwegel et al., 2022). We standardized the optimized *k* across each field site (Marwell: k = 78.4, Boma: k = 112.8) by calculating the difference between the log likelihood of each tested *k* value and the optimized *k* value for each group and selected the integer *k* value with the lowest standard deviation as the optimized *k* across the field site (k = 90.4)

We calculated individual average Elo scores by extracting Elo scores (function: extract_elo, package: Elo-rating; Neumann & Kulik, 2020) on each day of the field season to calculate the average Elo score throughout the field season for each individual male. These averages were then transformed into the corresponding ordinal rank (an integer expressing the individual's position in the dominance hierarchy (i.e., 1 = highest rank) (Levy et al., 2020) to obtain each individual's average ordinal rank throughout the field season. Ordinal rank was chosen as it is the best measure for density-dependent competition (e.g., access to fertile females) (Levy et al., 2020).

2.4 Statistical Analysis

All statistical analysis were conducted using the statistical programming software R (version 4.1.1) (R Core Team, 2020) with the significance level set to $\alpha \leq 0.05$.

To test for correlation among response variables, we conducted Pearson's correlations (function: cor.test, package: stats) on all predictor variables. To examine the role of male dominance rank on sociosexual behaviours and intersexual affiliation (Hypotheses 1 & 2, Table 1 & 2) we created a linear model (function: lm, package: lme4; Bates et al., 2015) for each of our nine response variables (rate of mating effort (count/hour), copulation rate (count/hour), rate of received mating presentations (count/hour), rate of received mating refusals (count/hour), rate of received mating refusals per effort (count/hour), rate of female directed grooming (sec/hour), rate of female received grooming (sec/hour), Hinde's index (-1 to 1), rate of female proximity (sec/hour) with male rank (average, ordinal), age-class (subadult, adult), minimum male tenure length (months), group identity (Marwell, Boma), and the interaction between male rank and age class, as well as the interaction between male rank and minimum male tenure length as fixed effects for each model. Each linear model was weighted by individual total focal time (seconds) to account for variation in the time spent observing each male. We started each linear model by checking for multicollinearity among predictor variables by removing the interaction variables and computing variance inflation factors (VIFs) (function: check_colinearity, package: performance; Lüdecke et al., 2021) and found no multicollinearity (i.e., all VIF < 3; James et al., 2013; Mason, 1987). We checked for outliers (function: check_outliers, package: performance; Lüdecke et al., 2021) and in the cases where they were found, we removed them from the model to run the model with and without outliers. We checked for normality of the standardized residuals (function: check_normaility, package: performance; Lüdecke et al., 2021) and found no significant deviation from normal distribution ($p > 0.05$). Finally, we performed automated model selection (function: dredge, package: MuMIn; Bartoń, 2023) to choose the best predictors for each response variable and identified the best model based on the one with the lowest Akaike Information Criterion corrected for small sample size (AICc). Models within 2 AICc of each other were considered to be equally valid and in such cases, the top model was chosen as the model with the highest adjusted R^2 value (Dormann et al., 2018).

2.4.1 Dominance Hierarchy Characteristics

We calculated hierarchy linearity (function: h.index, package: Elo-rating; Neumann & Kulik, 2020) using Landau's modified *h'* index which is suitable for measuring the strength of linearity present in a set of dominance relationships when there are unknown or tied dominance relationships. The index ranges from 0 to 1 with higher indices representing more linear hierarchies (de Vries, 1995), the general consensus is that any value equal to or higher than 0.8 is indictive of strong linearity (Bergstrom & Fedigan, 2010; Isbell et al., 2002; Wikberg et al., 2013). We tested whether the observed linearity differed significantly from the expected steepness (function: h.index, package: Elo-rating; Neumann & Kulik, 2020) after 1000 interactions. The expected steepness can be calculated as *h'* = 3/(N+1), where N is the number of individuals in the dominance hierarchy (de Vries, 1995).

Hierarchy steepness was calculated (function: steepness, package: Elo-rating; Neumann & Kulik, 2020) using the dyadic dominance index (D_{ij}) calculated from a normalized David's Score. The dyadic dominance index measures individual overall success while correcting for the number of competitive interactions between dyads. For example, in dyad AB, if A defeats B in four out of five interactions, the probability of A defeating B is P_{AB}=0.8, whereas for dyad CD, if C defeats D in eighty out of one hundred interactions, the probability of C defeating D is also P_{CD}=0.8. The dyadic dominance index corrects for this by creating a steepness value that takes the number of interactions between dyads into account, thereby, allowing the comparison of matrices containing different interaction frequencies (de Vries et al., 2006). Furthermore, a normalized David's score obtains a steepness measure that varies between 0 and 1 and is independent of the number of individuals in a group (while the steepness measure when using a David's score (David, 1987, 1988) would vary between 0 and N, where N= the number of individuals in a group). Therefore, normalizing the David's score allows steepness comparisons between different-sized groups (de Vries et al., 2006). We tested whether the observed steepness differed significantly from the expected steepness (function: steepness, package: Elo-rating; Neumann & Kulik, 2020) under the null hypothesis that, for every dyad, the chance of winning or losing is equally likely between individuals (de Vries et al., 2006).

The mean directional consistency was measured by calculating the mean directional consistency index (DCI) of all dyadic interactions (function: DCindex, package: Elo-rating;

Neumann & Kulik, 2020). This index ranges from 0 to 1, with DCI = 1 representing complete directional consistency (or unidirectionality) between individuals and DCI = 0 representing an even tie (or bidirectionality) between individuals (van Hooff & Wensing, 1987). Strong hierarchies can be defined as those reaching a minimum mean DCI of 0.95 (Young & Isbell, 2002).

We measured the hierarchy stability of each group (function: stab.elo, package: Elo-rating; Neumann & Kulik, 2020) through *S* values based on Elo-ratings. This function measures the ratio of rank changes per individuals present over a given period and is independent of group size. *S* values can range from 0 to 1 with *S* = 1 representing high rank stability or a fixed rank order throughout the study period and *S* = 0 representing total instability or rank order reversing every other day (McDonald & Shizuka, 2013).

3.0 Results

We recorded a total of 305 hours of focal follows (Marwell: 159 hours, Boma: 146 hours), 482 male-male agonistic bouts (Boma: 162 bouts, Marwell: 320 bouts), and 820 intersexual social interactions (Boma: 272 interactions, Marwell: 548 interactions) throughout the 4-month field season (April 25 to August 17, 2022). Over the field season, matings were predominantly initiated by males with females resisting male mating attempts in approximately 33% of all sexual interactions observed.

The male study subjects of Boma group (N = 6) consisted of two adult males who had immigrated from outside groups before the field season and four natal, subadult males. One adult male (TRT) immigrated into the group at least 5 months before the field season and the second (VEN) was already a group member when research began in February 2020 (about 27 months before the field season). At the start of the field season, the average minimum male tenure length for Boma group was 21.3 months ± 8.6. Throughout the field season, Boma consisted of 12 adult females and nine infants who were born within three months of the field season as well as one infant who was born during the field season (on April 6, 2022). The alpha male in Boma group (VEN) remained highest ranking throughout the field season (Figure 2)

The study subjects in Marwell group (N = 7) were all adult males who had immigrated from outside groups. One individual (DUG) joined from an unknown group about one month before the study period, on March 17, 2022, while GRG and DRG left their natal group (Boma) and joined Marwell together on April 8, 2022 (weeks before the field season). BRT joined Marwell about 7 months before the field season and the three other adult males (OLE, KUB and TAD) were already group members when research began in February 2020 (about 27 months before the field season). At the start of the field season, the average minimum male tenure length for Marwell group was 11.8 months ± 13.2. Marwell experienced one adult male dispersal throughout the study period (OLE on July 20, 2022) to an unknown outside group. Throughout the field season, Marwell consisted of 13 adult females, one of which who died on June 29, 2022. There were six infants born within three months of the field season. The alpha male in Marwell group (OLE) maintained highest rank for several months and then rapidly transitioned to fifth ranking after being overtaken by GRG (Figure 3). Around this time, BRT experienced rank increase from fourth highest to second highest rank (Figure 3).

3.1 Relationships Between Response Variables

We carried out Pearson’s rank correlations on all response variables (Table 3). Rate of male mating effort was positively correlated with copulation rate (r = 0.796, p = 0.0011) and rate of female mating refusals (r = 0.796, p = 0.0011). Rate of female mating presentations was positively correlated with copulation rate (r = 0.773, p = 0.002) and negatively correlated with rate of female mating refusals per mating effort (r = -0.659, p = 0.0143) and rate of female directed grooming (r = -0.613, p = 0.0258). All other correlations were not significant.

Table 3. Pearson's correlation coefficients (r) and associated p-values (p) of all response variables: rate of mating effort (ME), copulation rate (CO), rate of female mating presentations (MP), rate of female mating refusals (MR), rate of female mating refusals per mating effort (MR/ME), rate of female directed grooming (DGR), rate of female received grooming (RGR), Hinde's index (HD) and rate of female proximity (FP).

		ME	CO	MP	MR	MR/ ME	DGR	RGR	HI
ME	r								
	p								
CO	r	0.796							
	p	0.0011*							
MP	r	0.471	0.773						
	p	0.105	0.002*						
MR	r	0.796	0.328	-0.0348					
	p	0.0011*	0.274	0.910					
MR/ ME	r	-0.052	-0.418	-0.659	0.472				
	p	0.866	0.155	0.0143*	0.103				
DGR	r	0.101	-0.222	-0.613	0.318	0.406			
	p	0.742	0.466	0.0258*	0.288	0.168			
RGR	r	0.505	0.338	0.041	0.417	0.0451	0.491		
	p	0.078	0.259	0.894	0.156	0.884	0.088		
HI	r	-0.079	-0.211	-0.085	0.242	0.509	-0.189	0.144	
	p	0.795	0.489	0.782	0.427	0.075	0.537	0.638	
FP	r	0.489	0.382	0.436	0.217	-0.487	-0.017	-0.0174	-0.196
	p	0.089	0.197	0.135	0.474	0.091	0.955	0.955	0.521

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

3.2 Rate of Mating Effort

The average rate of male mating effort was 0.62 ± 0.38 attempts per hour (range: 0.12 – 1.36). The single top model for rate of male mating effort included male rank and group identity as predictor variables (Table 4) where higher-ranking males put forth more mating effort relative to lower-ranking males (-0.077 ± 0.027, t = -2.878, p = 0.016) and Marwell group invested more time in mating effort relative to Boma group (0.619 ± 0.101, t = 6.131, p < 0.001).

When the outlier individuals COC (subadult male in Boma), TRT and VEN (adult males in Boma) were removed, there was complete separation of the variable age class by group identity so analysis without outliers was re-run while also removing the predictor variables age class and the interaction between age class and average ordinal rank. With outliers removed, results were qualitatively similar. The single top model still included male rank and group identity (Table 5) where higher-ranking males still put forth more mating effort relative to lower-ranking males (-0.111 ± 0.026, t = - 4.264, p = 0.004) and Marwell group still invested more time in mating effort relative to Boma group (0.590 ± 0.101, t = 5.871, p < 0.001).

3.3 Copulation Rate

The average rate of copulations was 0.23 ± 0.20 copulations per hour (range: 0 – 0.66). There were two top models within 2 AICc, with the best model including male tenure length, group identity, and male rank (Table 4). Males with shorter tenure lengths were statistically more likely to copulate than males with longer tenure lengths (-0.008 ± 0.002, t = -3.162, p = 0.012) and the males in Marwell group had a significantly higher rate of copulations than the males in Boma group (0.237 ± 0.060, t = 3.977, p < 0.001). Additionally, there was a trend for higher-ranking males to receive more copulations relative to lower-ranking males (-0.029 ± 0.014, t = -1.992, p = 0.078).

3.4 Rate of Mating Presentations

The average rate of mating presentations received by males was 0.22 ± 0.24 mating presentations per hour (range: 0 – 0.71). There were two top models within 2 AICc, with the best model including male rank and male tenure length (Table 4). There was a trend towards higher-ranking males receiving more mating presentations relative to lower-ranking males (-0.033 ± 0.016, t = -2.044, p = 0.068) and males with shorter tenures were statistically more likely to receive mating presentations than males with longer tenures (-0.019 ± 0.003, t = -6.954, p < 0.001).

When the outlier individual GRG was removed, results were qualitatively similar. The single top model still included male rank and male tenure length, but also included the interaction between male rank and male tenure length (Table 5). The trend for higher-ranking males being more likely to receive mating presentations than lower-ranking males became statistically significant (-0.162 ± 0.028, t = -5.875, p < 0.001). Males with shorter tenures were still statistically more likely to receive mating presentations than males with longer tenures (-0.044 ± 0.005, t = -8.084, p < 0.001). The interaction between male rank and male tenure length became a predictor of received mating presentations with males with higher rank and shorter tenure lengths receiving more mating presentations than males with lower rank and longer tenure lengths (0.004816 ± 0.00107, t= 4.505, p < 0.001).

3.5 Rate of Mating Refusals

The average rate of mating refusals received by males was 0.22 ± 0.19 mating refusals per hour (range: 0 – 0.63). There were four top models within 2 AICc, with the best model including group identity, male rank, and age class as predictor variables (Table 4). The males in Marwell group received a higher number of mating refusals relative to the males in Boma group (0.331 ± 0.103, t = 3.23, p = 0.01). Contrary to our predictions, higher-ranking males received more mating refusals relative to lower-ranking males (-0.054 ± 0.019, t = -2.827, p = 0.02).

Additionally, there was a trend towards adult males receiving a lower number of mating refusals relative to subadult males (-0.195 ± 0.109, t = -1.792, p = 0.107).

When the outlier GRG was removed, the single top model including group identity and male tenure length (Table 5) with the males in Marwell group receiving a higher number of mating refusals relative to the males in Boma group (0.179 ± 0.058, t = 3.114, p = 0.012) and males with longer tenures receiving a higher number of mating refusals relative to males with shorter tenures (0.009 ± 0.003, t = 3.244, p = 0.01).

3.6 Rate of Mating Refusals per Mating Effort

The average rate of mating refusals per mating effort received by males was 0.36 ± 0.2 mating refusals per effort per hour (range: 0 – 0.67). There were five top models within 2 AICc, with the best model including age class, male tenure length, and group identity (Table 4). As predicted, adult males received a significantly lower number of mating refusals per effort relative to subadult males (-0.329 ± 0.110, t = -2.981, p = 0.015). Males with longer tenures received a significantly higher number of mating refusals per effort relative to males with shorter tenures (0.008 ± 0.003, t = 2.399, p = 0.04). Additionally, there was a trend towards the males in Marwell group receiving more mating refusals per effort relative to the males in Boma group (0.212 ± 0.098, t = 2.175, p = 0.058).

When the outlier GRG was removed, results were qualitatively similar, with no changes to the best model predictor variables (Table 5). Adult males still received a significantly lower number of mating refusals per effort relative to subadult males (-0.295 ± 0.071, t = -4.167, p = 0.003) and males with longer tenures still received a significantly higher number of mating refusals per effort relative to males with shorter tenures (0.012 ± 0.002, t = 4.882, p = 0.001). The trend towards the males in Marwell group receiving more mating refusals per effort relative to the males in Boma group became significant (0.171 ± 0.063, t = 2.712, p = 0.027).

3.7 Rate of Female Directed Grooming

The average rate of males grooming females was 34.1 ± 31.4 seconds per hour (range: 3.8 – 91.5). Males groomed females in 29% of all intersexual grooming interactions recorded during the field season. When considering the total amount of time males spent engaged in grooming behaviour, 65% was spent self-grooming, 24% was spent grooming females, and 11% was spent grooming other males. The single top model for rate of males grooming females included group identity and male tenure length (Table 4) with the males Marwell group spending significantly more time grooming females than the males Boma group (37.802 ± 11.032, t = 3.427, p = 0.006). Additionally, males with longer tenure lengths spent significantly more time grooming females than males with shorter tenure lengths (2.353 ± 0.479, t = 4.91, p < 0.001).

When the outlier COC was removed, results were qualitatively similar, with no changes to the best model predictor variables (Table 5). The males in Marwell group still spent significantly more time grooming females than the males in Boma group (37.195 ± 11.954, t = 3.111, p = 0.012) and males with longer tenures still spent significantly more time grooming females than males with shorter tenures (2.364 ± 0.507, t = 4.666, p = 0.001).

3.8 Rate of Male Directed Grooming

The average rate of females grooming males was 82.5 ± 54.6 seconds per hour (range: 25.0 – 202.4). Females groomed males in 71% of all intersexual grooming interactions recorded during the field season. There were two top models within 2 AICc, with the best model including group identity and male tenure length (Table 4). The males in Marwell group received a significantly higher rate of grooming from females relative to the males in Boma group (85.353 ± 24.266, t = 3.517, p = 0.006) and there was a trend towards males with longer tenure lengths receiving a higher rate of female grooming relative to males with shorter tenure lengths (2.091 ± 1.054, t = 1.983, p = 0.075).

When the outlier GRG was removed, results were qualitatively similar, with no changes to the best model predictor variables (Table 5). The males in Marwell group still received a significantly higher rate of grooming from females relative to the males in Boma group (84.937 ± 26.353, t = 3.223, p = 0.01) and there was still a trend towards males with longer tenure lengths receiving a higher rate of female grooming relative to males with shorter tenure lengths (2.098 ± 1.117, t = 1.878, p = 0.093).

3.9 Hinde’s Index

The average Hinde’s index was 0.151 ± 0.163 (range: -0.129 – 0.428) indicating that on average, males are responsible for maintaining proximity to females in male-female dyads. There were three top models within 2 AICc, with the best model including age class alone (Table 4). There was a non-significant trend towards adults having a lower Hinde’s index relative to subadult males (0.169 ± 0.087, t = 1.941, p = 0.078). The average Hinde’s index for adult males was 0.099 ± 0.152 and the average Hinde’s index for subadult males was 0.269 ± 0.134.

3.10 Rate of Female Proximity

The average rate of males being in proximity to one or more females was 345.3 ± 158.5 seconds per hour (range: 190.8 – 669.7). The single top model included age class alone (Table 4) where adult males spend more time in proximity to one or more females relative to subadult males (199.4 ± 77.59, $t = 2.57$, $p = 0.026$). On average, adult males spend 0.12% of their time within 2 meters of one or more females while subadult males spend 0.06% of their time within 2 meters of one or more females.

When the outlier individuals TRT and VEN (two adult males in Boma group) were removed, there was complete separation of the variable age class by group identity so analysis without outliers was re-run while also removing the predictor variables age class and the interaction between age class and average ordinal rank. With outliers removed, there were two top models within 2 AICc, with the best model including male rank and group identity (Table 5) where higher-ranking males spend significantly more time in proximity to one or more females relative to lower-ranking males (-31.18 ± 12.21, $t = -2.553$, $p = 0.034$) and males the males in Marwell group spend significantly more time in proximity to one or more females relative to the males in Boma group (196.19 ± 46.1, $t = 4.256$, $p = 0.003$).

Table 4. Results of Dredge model selection for all response variables, run in R. Predictor variables for all models include male rank, minimum tenure length, age-class, group identity, and all possible interactions. Top models for each response variable are within Δ2AICc of lowest score; best model selected from top models using highest adjusted R^2 value (in bold).

Response Variable	Predictor Variables	AICc	ΔAICc	Adjusted R^2	Outliers
Rate of Male Mating Effort	**Male Rank + Group Identity**	**1.9**	**0.0**	**0.767**	Case 8 (COC) + Case 10 (VEN) + Case 13 (TRT)

Rate of Received Copulations	Group Identity + Minimum Tenure Length	-10.9	0.0	0.709	None
	Male Rank + Group Identity + Minimum Tenure Length	**-10.1**	**0.82**	**0.775**	
Rate of Received Mating Presentations	**Male Rank + Minimum Tenure Length**	**-11.2**	**0.0**	**0.797**	Case 4 (GRG)
	Minimum Tenure Length	-11	0.21	0.739	
Rate of Received Mating Refusals	Male Rank + Group Identity	-4.6	0.0	0.413	Case 4 (GRG)
	Group Identity	-3.1	1.44	0.168	
	Null model	-3.1	1.5	N/A	
	Male Rank + Group Identity + Age Class	**-3**	**1.6**	**0.520**	
Rate of Received Mating Refusals per Mating Effort	Minimum Tenure Length	-4.8	0.0	0.395	Case 4 (GRG)
	Age Class	-4.4	0.37	0.378	
	Age Class + Minimum Tenure Length	-4	0.8	0.493	
	Age Class + Minimum Tenure Length + Group Identity	**-3.9**	**0.88**	**0.631**	
	Age Class + Group Identity	-3	1.74	0.455	
Rate of Female Directed Grooming	**Group Identity + Minimum Tenure Length**	**121.6**	**0.0**	**0.669**	Case 8 (COC)
Rate of Female Received Grooming	Group Identity	142.1	0.0	0.329	Case 4 (GRG)
	Group Identity + Minimum Tenure Length	**142.1**	**0.02**	**0.470**	
Hinde's Index	**Age Class**	**-6.6**	**0.0**	**0.187**	None
	Null model	-6.2	0.36	N/A	
	Group Identity	-6	0.58	0.150	
Rate of Female Proximity	Age Class	170	0.0	0.318	Case 10 (VEN) + Case 13 (TRT)

Table 5. Results of Dredge model selection for all response variables with outliers removed, run in R. Predictor variables for all models (except rate of female proximity) include male rank, minimum tenure length, age-class, group identity, and all possible interactions. Top models for

each response variable are within Δ2AICc of lowest score; best model selected from top models using highest adjusted R^2 value (in bold).

Response Variable	Predictor Variables	AICc	ΔAICc	Adjusted R^2
Rate of Male Mating Effort	**Male Rank + Group Identity**	**1.8**	**0.0**	**0.817**
Rate of Received Mating Presentations	**Male Rank + Minimum Tenure Length + Male Rank:Minimum Tenure Length**	**-18.8**	**0.0**	**0.937**
Rate of Received Mating Refusals	**Minimum Tenure Length + Group Identity**	**-12.6**	**0.0**	**0.540**
Rate of Received Mating Refusals per Mating Effort	**Minimum Tenure Length + Group Identity + Age Class**	**-12**	**0.0**	**0.859**
	Minimum Tenure Length + Age Class	-10.5	1.54	0.760
Rate of Female Directed Grooming	Minimum Tenure Length + Group Identity	114.9	0.0	0.664
Rate of Female Received Grooming	Group Identity	131.7	0.0	0.306
	Minimum Tenure Length + Group Identity	**133.4**	**1.69**	**0.446**
Rate of Female Proximity	**Male Rank + Group Identity**	**137.1**	**0.0**	**0.678**
	Group Identity	138.4	1.32	0.48

3.11 Dominance Hierarchy Characteristics

Table 6 summarizes the sociometric variables for each group. The measure of linearity for Boma group's male dominance hierarchy over the field season was moderately linear ($h' = 0.7429$; $0.5 \geq h' \geq 0.8$; Bergstrom & Fedigan, 2010; Isbell et al., 2002; Wikberg et al., 2013) and not significantly different (right-tailed p = 0.112) from the expected h' value of 0.4265. The observed steepness measure was $D_{ij} = 0.6747$ while the expected steepness was $D_{ij} = 0.346$ (right-tailed p = 0.002), indicating that the degree of steepness for Boma group's dominance hierarchy was significant. The mean directional consistency index for Boma group's dominance hierarchy over the field season was DCI = 0.7875, indicating strong unidirectionality (van Hooff & Wensing, 1987). The stability measure for Boma group was $S = 0.9854$, indicating high rank stability throughout the study period (McDonald & Shizuka, 2013). To visualize the stability of ranking, Figure 2 shows the evolution of the Elo-score across the field season for Boma group.

The degree of linearity for Marwell group's male dominance hierarchy over the field season was moderately linear ($h' = 0.7679$) (Bergstrom & Fedigan, 2010; Isbell et al., 2002; Wikberg et al., 2013). Marwell group's observed linearity measure differed significantly (right-tailed $p = 0.04$) from the expected h' value of 0.3799. Marwell group's observed steepness measure was $D_{ij} = 0.6127$ while the expected steepness was $D_{ij} = 0.328$ (right-tailed $p = 0.002$), indicating that the degree of steepness for Marwell group's dominance hierarchy was significant. The mean directional consistency index for Marwell group's dominance hierarchy over the field season was DCI = 0.6159 while the stability measure was $S = 0.9833$, indicating high rank stability throughout the study period (McDonald & Shizuka, 2013). To visualize the stability of ranking, Figure 3 shows the evolution of the Elo-score across the field season for Marwell group.

Table 6. Sociometric variables of male dominance hierarchy in the two groups of vervet monkeys.

Group	N	Stability (S)	Mean Directional Consistency Index (DCI)	Observed Steepness (D_{ij})	Expected Steepness (D_{ij})	Observed Linearity (h')	Expected Linearity (h')
Boma	6	0.9854	0.7875	0.6747	0.346	0.7429	0.4265*
Marwell	7	0.9833	0.6159	0.6127	0.328*	0.7679	0.3799*
	Mean	0.9844	0.7017	0.6437	0.337	0.7554	0.4032
	Sd	0.001	0.121	0.044	0.013	0.018	0.033

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

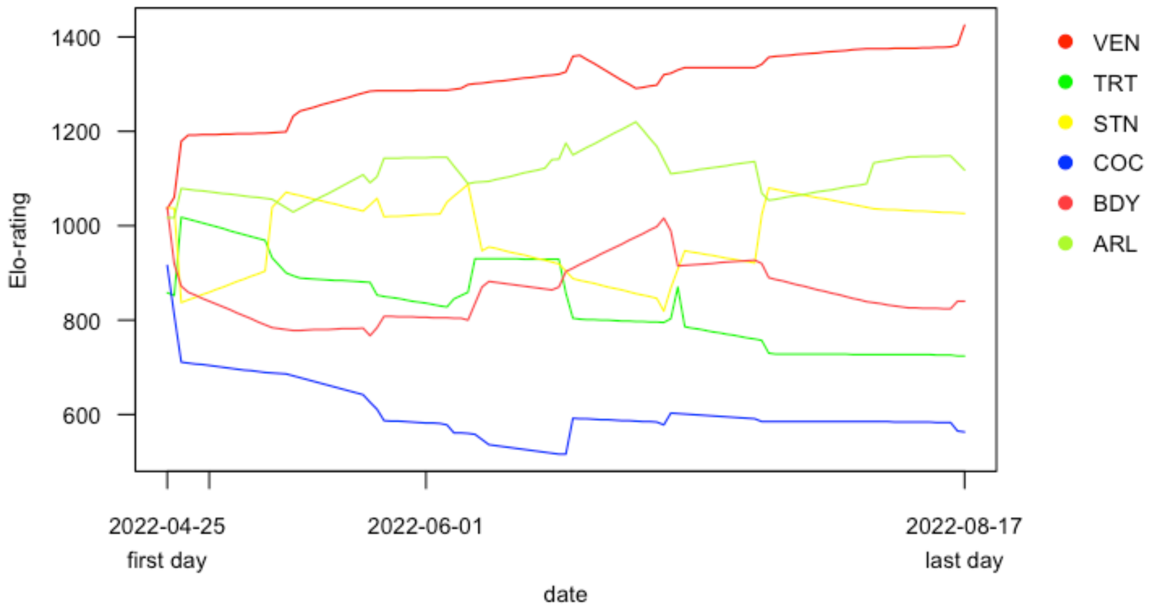


Figure 2. Evolution of individual male Elo-scores for Boma group from 25 April to 17 August 2022. Larger numbers indicate greater dominance. Each colour represents one individual.

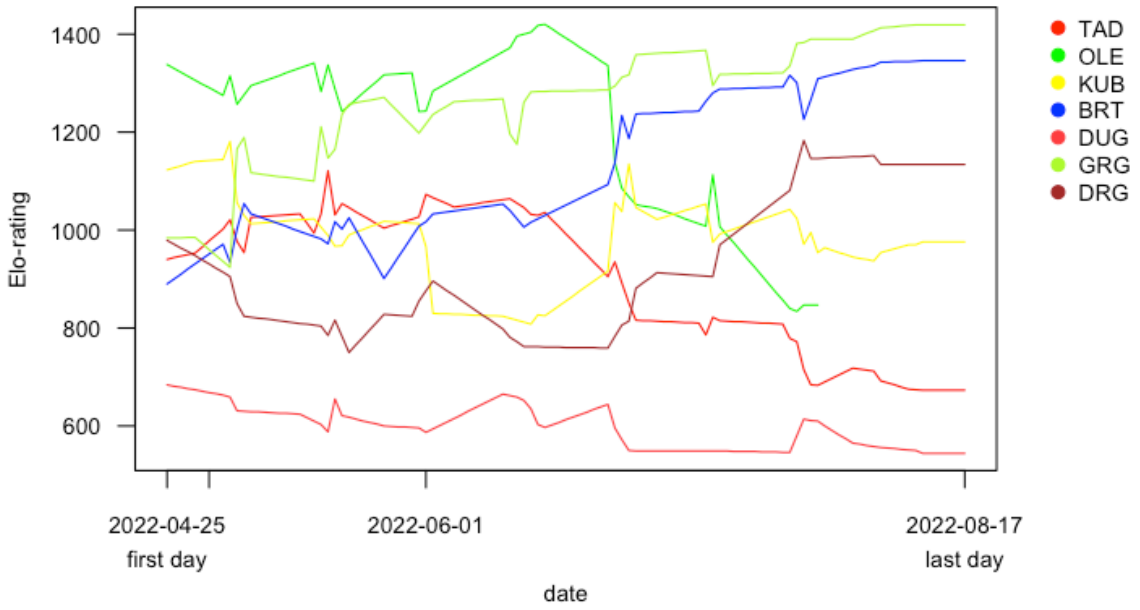


Figure 3. Evolution of individual male Elo-scores for Marwell group from 25 April to 17 August 2022. Larger numbers indicate greater dominance. Each colour represents one individual.

4.0 Discussion

We examined the relationship between male age, dominance rank, and tenure length on male mating effort and female mate choice. We generally found that adult, high-ranking male vervet monkeys who have recently immigrated into their social group tended to put forth more mating effort and copulated more frequently; these males were also generally preferred by females. That said, female preference for novel males likely dampened the positive relationship between male dominance rank and copulation rate. We also found that despite different group compositions, as well as demographic and rank changes, the male dominance hierarchies for both of our study groups were strikingly similar, with both groups having high stability indices and moderate linearity, with only modest differences between groups in steepness and directional consistency.

4.1 Sociosexual and Affiliative Behaviour

Dominant males may attempt to copulate more often than subordinate males because they are better able to monopolize access to females (Altmann, 1962) and are preferred by females (Altmann, 1962; Cowlishaw & Dunbar, 1991; Georgiev et al., 2015; Small, 1989) giving them more opportunities to do so. Mate-guarding reflects male mating effort in many primate species that live in multimale, multifemale groups (Altmann & Alberts, 2003), but in primate species such as the vervet monkey, where females exhibit concealed ovulation and sexual dimorphism is less marked, mate-guarding is rarely observed (Muller & Wrangham, 2004; van Schaik et al., 2004). Therefore, our study examined copulation attempts (i.e., sum of all copulations, mounts, and mating refusals per individual male) as an indicator of mating effort. In line with our prediction (hypothesis 1, prediction 1a), we found that higher-ranking male vervets put forth more mating effort than lower-ranking males. Our results are also consistent with findings from other studies of multi-male multi-female primates. For example, in rhesus macaques, dominance was positively related to mate-guarding (Berard et al., 1994; Higham et al., 2011) and paternity success, with sires engaging in longer mate-guarding episodes than non-sires (Berard et al., 1994). Likewise, an 8-year study on mandrills (*Mandrillus sphinx*) found a strong correlation between male dominance rank and mating effort, with alpha males accounting for 94% of mate-guarding (Setchell et al., 2005).

Our prediction (hypothesis 1, prediction 1b) that higher-ranking males will engage in more copulations than lower-ranking males was also partially supported by the trend that higher-ranking males copulate at higher rates than lower-ranking males. When outliers were removed, we also found that higher-ranking males spent more time in proximity to females than lower-ranking males. A captive study on vervets found that, after the experimental removal of the alpha male, subordinate males initiated more affiliative behaviour and increased the amount of time spent in proximity to females (Keddy Hector & Raleigh, 1992). Thus, dominant males may inhibit the intersexual behaviour of subordinate males and monopolize access to females through proximity maintenance. The observed trend between male rank and mating success was likely influenced by other socioecological circumstances (e.g., female choice, breeding seasonality) that affect the degree to which alpha males can monopolize access to mates (Emlen & Oring, 1977; Gartland et al., 2021; Majolo et al., 2012; van Hooff & van Schaik, 1994). For example, although our results show that females prefer to mate with high ranking males over subordinate males, they also show mate preference for new immigrant males over males with longer tenures. Additionally, wild vervet monkeys exhibit moderate to high breeding seasonality (Schwegel et al., 2022) which is expected to reduce the efficacy of dominance as a male mating strategy as male monopolization of females becomes increasingly difficult with an increase in the number of synchronously fertile females (de Jong et al., 2012; Emlen & Oring, 1977).

The observed positive trend between male rank and mating success was likely due to dominant males monopolizing access to females over subordinate males (hypothesis 1, prediction 1a and 1c) as shown above, as well as female mate preference for dominant males over subordinate males (hypothesis 1, prediction 1c-e).

We found a positive trend for higher-ranking males to receive higher rates of mating presentations from females relative to lower-ranking males. That said, higher-ranking males also received higher rates of mating refusals relative to lower-ranking males. We suggest that these seemingly contradictory results reflect a "try more, fail more" approach; in other words, the larger mating efforts of higher-ranking males (as seen in our study) relative to lower-ranking males are also associated with higher rates of mating refusals. We did a *post hoc* test examining mating refusals per mating effort as an outcome variable and found that male dominance rank was not a predictor.

Although higher ranking males received more female mating presentations than subordinate males, our prediction (hypothesis 2, prediction 1a-1b) that females would prefer to affiliate with higher-ranking males was not supported since male rank was not a predictor of rates of intersexual grooming nor Hinde's index. Thus, although female's show sexual preference for dominant males over subordinate males, male rank did not play an important role in the formation of intersexual social bonds within our study.

Our study presented strong evidence for female mate preference for novel males in vervet monkeys. We found that males with shorter tenure lengths received more copulations, more mating presentations, fewer mating refusals, and lower mating refusals per mating effort than males with longer tenure lengths (hypothesis 1, prediction 2a-d). Thus, females may be choosing to mate with newer males as a means to avoid inbreeding depression and increase genetic variation among their offspring (Bengtsson, 1978; Kokko & Ots, 2006; Szulkin et al., 2013; Waser et al., 1986; Small, 1989). This is analogous to the findings that immigrant males receive more mating presentations from females in Japanese macaques (Huffman, 1991), rhesus macaques (Lindburg, 1983; Manson, 1995), and baboons (Packer, 1979a, b). Males with longer tenure lengths had significantly lower copulation rates than novel males. Although our study and the literature provide evidence that this is influenced by female choice (Berard, 1999; Henzi & Lawes, 1987; Huffman, 1992; Packer, 1979a, b; Smuts, 1985), there is suggestion that the negative relationship between male tenure length and copulation frequency may also be influenced by male mate choice for unrelated females. Females should exhibit stronger mate choice than males (Trivers, 1972), but males are still expected to avoid inbreeding through exerting mate choice and dispersing from their natal groups (Tennenhouse, 2014; Pusey & Packer, 1987; Moore, 1993). Several studies on group-living primates have found that when resident males have tenures that exceed the age at which their female offspring become fertile, they often avoid breeding with them (Godoy et al., 2016; Griffin et al., 2003; Muniz et al., 2006; Vigilant et al., 2015). Although we suspect that male mate prefernce for unrelated females is also driving the negative relationship between male tenure length and copulation rate, our study was unable to test this hypothesis as we don’t have access to genetic data and our research has only been ongoing since February 2020. Thus, although resident males may have daughters within our study groups, we cannot verify this. It would be interesting to test this hypothesis for future studies with the use of genetic data.

The high degree of female mate choice for novel males seen in our study likely muted the relationship between male dominance rank and copulation success. Similar occurrences have been seen in rhesus macaques, where a shift in female preference over time resulted in a lower reproductive skew (Berard, 1999). Here, the longer a male held highest rank, the more females preferred to mate with new immigrant males, resulting in a decline in copulation success for high-ranking males (Berard, 1999). Similarly, in wild capuchin monkeys, the alpha male's probability of producing offspring decreased as his tenure increased (Wikberg et al., 2016). Likewise, in a study of captive vervet monkeys, Weingrill et al. (2011) found that the tenure length of the alpha male was the only variable that affected alpha male copulation and paternity success. Analogous to our study, Weingrill et al. (2011) found a negative relationship between tenure length and mating success where the alpha male's copulation frequency decreased by 22% each year throughout a three-year study despite remaining top ranking throughout the entirety of the study. Although male tenure length was an important predictor in many of our top models, minimum male tenure length was not a precise indication of actual tenure length as several males were already present in our study groups at the start of data analysis in February 2020. These males were assigned the minimum tenure length of 29 months which is not entirely accurate. Overall, our study supports the hypothesis that tenure length is also an important predictor of mating success within wild populations of vervet monkeys.

Contrary to our prediction (hypothesis 2, prediction 2a), we found that males with longer tenure lengths have higher rates of intersexual grooming than males with shorter tenure lengths. Although males may form friendships with females to increase mating opportunities (Gumert, 2007; Hemelrijk et al., 1992; Norscia et al., 2009; for review see Van Schaik & Paul, 1996), our study found that male tenure length correlates positively with intersexual grooming but negatively with mating success, indicating that grooming may not be related to sociosexual behaviour. In support of this, we found a negative correlation between rate of received mating presentations and rate of male grooming of females indicating that females present sexually more often to males who do not spend time grooming them. Thus, we suggest that females prefer to form social bonds (as seen through intersexual grooming rates) with males with long tenures as they are familiar and their behaviour is predictable while showing mating preference for novel males to increase genetic diversity and/or avoid inbreeding depression.

The positive relationship between intersexual grooming rates and tenure length may also be a product of reciprocal grooming (i.e., males with longer tenures are grooming females at a higher rate than males with shorter tenures and females are returning the favour). Females have been documented grooming reciprocally in multiple primates species, including vervets (Barrett et al., 1999; Henazi & Barrett, 1999; Muroyama, 1994; Silk et al., 1999). In a meta-analysis of 22 primates species Schino & Aureli (2008) found that females primates preferentially groom group members that groom them most. Additionally, Barrett et al. (1999) and Manson et al., (2004) found that female primates time-match grooming given and received during grooming sessions. Within our study, females spent more than double the amount of time grooming males than males spent grooming females. Thus, although grooming reciprocation could play a role in the rate of females grooming males seen in our study, it likely was not a central factor. Our study was not set up to test this specific hypothesis. Future studies should examine each male-female grooming dyad and account for dominance rank, tenure length and age of both sexes to better understand the mechanisms behind intersexual grooming.

Males may groom females for several additional reasons such as a form of mating effort and/or to increase their rank. Our study found an inverse relationship between male tenure length and mating success. Males with long tenures may therefore invest more effort in making themselves attractive to females as a means of increasing their mating opportunities (Van Schaik & Paul, 1996). This has been observed in wild baboons (*Papio anubis*) where older males, with long tenures, change their reproductive tactics and begin caring for females in order to gain access to them (Silk et al., 2020). Since the females within our study showed mate preference for novel males, males with longer tenures may be grooming females at a higher rate than males with shorter tenures to form relationships with females as an attempt to increase their mating opportunities.

Primates can also exchange grooming for rank-related benefits (for review see Schino & Aureli, 2008) and there is evidence that male vervets use grooming to increase their rank. Young et al. (2017) found that in wild vervets, males who groomed well-connected females, were more likely to increase their rank. Likewise, in a captive study of vervets, experimental removal of the alpha male resulted in subordinate males rapidly increasing their affiliative behaviour towards females through grooming (Keddy Hecktor & Raleigh, 1992). Suggesting that removal of the alpha male resulted in subordinate males engaging in behaviour that may enhance their likelihood of attaining high rank (Keddy Hecktor & Raleigh, 1992). Therefore, vervets may use grooming to increase their rank which should in turn, increase their mating success. To explore this hypothesis, future studies should examine the dominance rank of both sexes, predicting that males who groom high-ranking females will benefit from rank increases over time.

Our prediction (hypothesis 1, prediction 3a) that adult males will exhibit greater mating effort than subadult males was not supported, as age-class was not a predictor of mating effort. However, we found partial support for our prediction (3b-3e, Table 1) that adult males will copulate more and/or be preferred by females; adult males received a lower number of mating refusals and mating refusals per effort relative to subadult males. Although age-class was not a predictor of mating effort and copulation rate, one of our groups (Marwell) was composed entirely of adult males whereas the other group (Boma) had a mix of adult and subadult males. We did find that the males in Marwell group put forth more mating effort and had higher rates of copulation than the males in Boma group. This is consistent with our predictions as some of the variation associated with male age-class was likely accounted for by the variation seen in group identity. Higher mating success and female preference for immigrant adult males over natal subadult males is consistent with our suggestion that male and female reproductive objectives should aim to increase genetic diversity and avoid inbreeding depression (Kokko & Ots, 2006; Pusey & Packer, 1987; Small, 1989; Tennenhouse, 2014; Waser et al., 1986).

Our study did not support our predictions (hypothesis 2, prediction 3a-3c) that females will spend more time engaged in affiliative interactions with natal subadult males over immigrant adult males. Instead, we found that subadult males have a higher Hinde’s index and spend less time in proximity to females than adult males. The higher Hinde’s index for subadult males indicates that they must put forth more effort to maintain proximity to females than adult males. Thus, females tolerate proximity to adult males over subadult males. Additionally, on average, adult males spend twice as much time in proximity to females than subadult males. We also found that Marwell group engaged in higher rates of intersexual grooming than Boma group. This could further support our predictions due to the compete separation of age-class by group identity seen in our study (discussed above).

Vervet monkeys live in multi-male multi–female groups, with male-biased dispersal (Cheney & Seyfarth, 1983; Isbell et al., 1991; Struhsaker, 1967b). In general, individuals of the philopatric sex are expected to form stronger social bonds with natal group members given their permanent association, while members of the dispersing sex are expected to form looser social bonds with kin of the opposite sex (Clutton-Brock & Lukas, 2012; Di Fiore, 2003; Widdig et al., 2016). Macaques (spp.) also live multi-male male–female groups, with male-biased dispersal (Gouzoules & Gouzoules, 1987; Schülke & Ostner, 2012). In several macaque species, juvenile males begin to form looser bonds with the females in their natal groups after the first year of life, with their bonds continuing to decrease as males reach sexual maturity (Hershberger et al., 2009; Lonsdorf, 2017; for review see Amici et al., 2019). Instead, immature males are more likely to form strong social bonds with age-related male peers in their group (Kulik et al., 2015b; for review see Amici et al., 2019). For example, Japanese macaques decrease the variety of social behaviours exchanged with their mothers after the first year of their life and affiliate more with male age peers, especially through social play (Nakamichi, 1989). Likewise, a longitudinal study in rhesus macaques found that natal males spend more time in proximity to females in the first two years of their lives, but then preferentially interact with other males (Kulik et al., 2015b). These preferential social bonds with male kin may reduce the cost of dispersal as many male dispersing primates, including vervets, exhibit parallel dispersal with age-mates or may migrate into groups containing related male kin (rhesus macaques: Albers & Widdig, 2013; crab-eating macaques: Gerber et al., 2016; white-faced capuchins, *Cebus capucinus*: Jack & Fedigan, 2004a, b; vervet monkeys: Cheney & Seyfarth, 1983). A few weeks before the start of the field season, two males engaged in parallel dispersal from their presumed natal group (Boma) and immigrated together in our other study group (Marwell). This observation is consistent with the idea that in male-biased dispersing species, subadult males are expected to reduce their social bonds with the females in their groups and preferentially interact with males as they reach sexual maturity.

In female-philopatric species, adult females are also expected to reduce affiliative interactions towards natal males as they mature. Maternal aggression towards maturing male offspring is common and has a strong negative impact on social bonding (Hinde & Simpson, 1975; Nakamichi, 1989; Worlein et al., 1988). Other female group members also direct more aggression towards natal males as they age (Kulik et al., 2015a). Females might exhibit aggression towards natal males to inhibit social bonding between sons and maternal family so that natal males search for alternate bonding partners (Kulik et al., 2016), become independent earlier (Bardi & Huffman, 2002) and/or disperse earlier from their natal groups (Kulik et al., 2016). In rhesus macaques, the time of natal dispersal can be predicted by mother-son relationships when sons are between two to three years of age (Colvin, 1986). Thus, females weakening their social bonds towards natal males as they mature may contribute to promote dispersal and avoid inbreeding.

We found that the males in Marwell group put forth more mating effort, had higher rates of copulations, and received more mating refusals and mating refusals per effort than the males in Boma group. Additionally, we found that the males in Marwell group engaged in more affiliative interactions with females than the males in Boma group (i.e., higher rates of intersexual grooming and higher rates of female proximity). Overall, Marwell group engaged in more than twice the number of intersexual social interactions than Boma group.

As mentioned above, the differences observed between our study groups could be due to the complete separation of age-class by group identity present in our study. That is, Marwell group (entirely adult males) engaged in more social interactions than Boma group (2 adult males, 4 subadult males) because of female preference for sociosexual and affiliative interactions with adult males over subadult males (discussed above). Additionally, at the start of the field season, the average minimum male tenure length for Boma group was almost double the length of the average minimum male tenure length for Marwell group. Thus, female preference for novel males (discussed above) may account for the differences in sociosexual rates seen between our groups.

Other statistical ways to test group identity are by including it in the models as a random variable or by testing each group separately. We could not test group as a random variable as there was complete separation between the groups by age-class, thus, the best alternative for future analysis would be to test each group separately. We were unable to test the effect of group composition in the current study due to the small sample size (N = 2 groups) and because the total number of adult males and females did not differ greatly between our two study groups (Marwell: males: N=7, females: N=13 and Boma: males N=6; females: N=12). To test the effect of group composition on sociosexual behaviour in vervet monkeys, future studies should compare across a larger number of groups, or across time for the same groups.

4.2 Dominance Hierarchy Characteristics

The stability index was exceptionally high for both groups (Boma: $S = 0.9854$, Marwell: $S = 0.9833$). Stable hierarchies appear to be common throughout the animal kingdom. In a meta-analysis of 40 published datasets in a variety of taxa, McDonald and Shizuka (2013) found that all dominance hierarchies tend to be temporally stable (mean stability *S* = 0.81). The particularly strong stability indexes seen within our study groups may be linked to the small number of males in each group; Estevez et al (2007) suggest a negative relationship between group size and stability, if animals in larger groups are unable to recognize all group members (Estevez et al., 2007). That said, it is also possible that the stability index is not particularly useful for primate studies. During the current study period, Marwell group experienced a higher number of rank changes than Boma group as seen in more frequent line crossings for Marwell group in the evolution of Elo-scores for each group (Fig. 2 & 3). The higher proportion of rank changes experienced by the males in Marwell group compared to Boma group is not reflected in the difference in the stability index between groups ($\Delta S = 0.0021$). Thus, this measurement may not be the best practice for quantifying hierarchy stability in the current study. Elo-plots, which show the evolution of individual Elo-scores across time, might therefore be a better tool for visualizing group stability across time. The drawback to Elo-plots is that they cannot be statistically compared across groups or studies.

Both groups had significant and moderately linear male dominance hierarchies (Bergstrom & Fedigan, 2010; Isbell et al., 2002; Wikberg et al., 2013). The moderately strong hierarchy linearity seen in our population could be linked to the small number of adult/subadult males in each group. Hierarchy linearity is expected to be weaker in larger groups as one male is less likely to be dominant over all other males in larger groups (Mesterton-Gibbons & Dugatkin, 1995).

Marwell group's male dominance hierarchy was slightly less stable, directionally consistent, and steep than Boma group's (Table 6). This is likely due to the presence of three new males immigrating into Marwell group at the beginning of the field season. Changes to group composition, through the immigration of new males can lead to hierarchy instability (Neumann et al., 2011). While Boma group's alpha male (VEN) remained highest ranking throughout the field season, the alpha male in Marwell group (OLE) maintained highest rank for several months and then rapidly transitioned to fifth ranking before dispersing to an outside group. OLE was overtaken by GRG, an immigrant male who joined Marwell group two weeks before the field season and subsequently achieved highest rank. Neumann et al. (2011) found that in a population of crested macaques, hierarchies were less stable after the immigration of males that achieved high rank while the immigration of low-ranking males had no such effect on stability. Thus, the immigration of GRG, who subsequently achieved highest rank, likely resulted in Marwell group experiencing lower stability than Boma group.

The stronger directional consistency index and steepness seen in Boma group over Marwell group indicates that between individuals, differences in competitive ability were stronger and dominant individuals were more likely to win competitive encounters in Boma group than in Marwell group (van Hooff & Wensing, 1987). Thus, counter attacks on aggressive behaviour were more likely in Marwell group. This is further supported by the finding that Marwell group engaged in nearly double the number of male-male agonistic interactions than Boma group throughout the field season. The limited amount of male-male agonistic bouts seen in Boma group compared to Marwell group could be due to the high proportion of subadult males present in Boma group. This is because, in male-biased dispersing species, subadult males are likely to form affiliative social bonds with age-related male group members, especially in species that exhibit parallel dispersal (discussed above) (Albers & Widdig, 2013; Cheney & Seyfarth, 1983; Kulik et al., 2015a; Nakamichi, 1989).

The slight differences in hierarchy characteristics between groups would suggest that dominance as a male mating strategy would be slightly favoured in Boma group over Marwell group and we may expect to see a stronger relationship between male rank and copulation success in Boma group over Marwell group. This is because dominant males are predicted to win more agonistic interactions in stable, steep, and linear hierarchies with strong directional consistencies, like in Boma group, than in hierarchies with weaker expression, as seen in Marwell group. Hence, the reproductive benefits associated with dominance rank should be higher in hierarchies with stronger expression (Vehrencamp, 1983). To quantitatively test this, a larger number of study groups is needed. Future studies should compare the relationship between male dominance hierarchy characteristics and the correlation coefficient between male rank and mating success across a larger number of groups and/or across time, populations, or species.

5.0 Significance

In primates, the relationship between male dominance rank and mating success has been found to vary both within and across species (for reviews see Cowlishaw & Dunbar, 1991; Ellis, 1995; Majolo et al., 2012). Similarly, studies on vervet monkeys have produced conflicting results between captive (Keddy Hector, 1986; Weingrill et al., 2011) and wild populations (Cheney et al., 1988), as well as between the same populations over consecutive years (Freeman, 2012; Freeman et al., 2016; Minkner et al., 2018). These findings indicate that the ability for male primates to monopolize access to mates is influenced by several unique socioecological factors that can be species dependent, population dependent, and time dependent.

This study contributes to the relatively limited literature studying the relationship between male mating effort and female mate choice in vervet monkeys while highlighting various factors that affect the potential for dominant males to monopolize access to females. To the best of our knowledge, this is the first study that quantifies the characteristics of male dominance hierarchies for vervet monkeys. These novel findings provide insight into the efficacy of dominance as a mating strategy and the factors that influence female monopolization potential in primates. Furthermore, reporting of these characteristics can be used for direct comparison across studies which is integral for understanding the equivocal relationship between male dominance and mating success in group-living species.

6.0 Appendix

6.1 Ethogram

LETTER 1: Type of data to be entered
Self (S) – focal, self- or generally-directed behaviour
Contact (C) – focal in physical contact = 0m
Proximity (P) –focal within 2 meters of interactant
Direct (D) – focal gives, or directs, the behaviour
Receive (R) – focal receives the behaviour
Mutual (M) – mutual behaviour
OOO – out of sight

LETTERS 2&3: Behaviour Codes
SELF or GENERALLY DIRECTED (S)
Rest (RE), state – individual is sitting in a relaxed (i.e., non-vigilant) manner; may also be lying on side or straddling a tree branch (Struhsaker 1967a)
Scan (SC), state – individual is looking around, turning its head, in the farther visual distance >2meters; often occurs as a standing pause during a "move" (included visual foraging only during summer 2016 project); differs from "rest" because the animal is usually not sitting or lying down.
Visual Forage (VF), state – individual is slowly moving or standing still while looking around in foreground <2m (on the ground, in tree or shrub branches, grasses); differs from "Move" because "Visual Forage" is often includes locational displacement less < 1 meter.
Move (MO), state – walking or galloping, occasionally including a hop, and may be preceded or interrupted by vigilance (Struhsaker, 1967a); locational displacement greater than 1 meter and excludes positional changes/adjustments with locational displacement of less than 1 meter (Schoof).

- Move between (MB) – moving between trees
- Move within (MW) – moving within a tree
- Move on ground (MG) – moving on the ground

Vigilant (VG), event – standing erect on hindlimbs staring in one directing or glancing in several directions (Struhsaker, 1967a); if in tree, the actor stands quadrupedally or sits with chest forward and stares or glances (Schoof)
Self-Groom (SG), state - an individual combs through its own pelage using fingers and/or mouth, and may place foreign particles in mouth (Schoof 2016, included scratching)
Scratch (SK), event – includes scratching (*sensu* "self-cleaning" in Struhsaker 1967a).
Feed (FE), state – individual is manipulating and/or ingesting food.

- When possible, the observer should note the food species and part in the "comments"
- Food parts include: Ripe Fruit (RF), Unripe Fruit (UF), Unknown Fruit (FR), Flower (FL), Young Leaf (YL), Mature Leaf (ML), Leaf Bud (LB), Young Leaf Petiole (YLP), Mature Leaf Petiole (MLP), Bark, Dead Wood, Pine Needles, Seeds, Seed pods, Pith, Soil, Tuber/Root/Potato

Drink (DR), state – individual is ingesting water from a ground or tree source (natural or man-made), normally involves lowering head towards standing water from water holes or rain pools;

individuals may also lick water from hands, fingers, tree branches, or pelage of others (Struhsaker 1967a).

Yawn (YW), event – Mouth open all the way, briefly, in the vertical rather than horizontal plane; head may go back a bit. Lips may cover teeth or roll back, exposing top and bottom canines.

Other (OT), state/event – any behaviour not described in the ethogram; use "comments" section to describe behaviour

Out of sight (OO), state – focal animal is out of sight of the observer, usually resulting from substantial visual obstruction such as a building or dense vegetation, or because the focal animal has been "lost".

SOCIOSEXUAL (S,P, C, G or R; occasionally M)

Hip grab (HG), event – actor will stand behind female and grab at her hips pulling her in as if to mount but does not mount.

Inspect (IN), state – actor visually inspects, touches, licks or smells the genital region of the recipient; this may include looking from a short distance (<1ft), manipulating with hands or mouth, touching with face and includes various forms of "muzzling" as described by Struhsaker (1967a). Self licking or manipulating (males genitals) is S,P or C

Present (PR), event – female actor stands quadrupedally and orients her hindquarters towards the male recipient, sometimes glancing over shoulder; female may stop to present if followed by a male or male grabs hindquarters of a sitting female (i.e., behaviour of "estrous female" as described in Struhsaker 1967a).

- Note: a male focal animal can therefore Receive a Present (RPR) from a female Interactant.

Mount (MT), state – actor holds mountee hips with its hands, and legs with its feet (i.e., foot clasping); mount with no thrusting; may be associated with grooming and individuals may alternate between role of actor and recipient; note: mount may be incomplete, with grasping of only one body part Struhsaker 1967a)

Thrusting mount (TM), state – actor mounts (see above) recipient with pelvic thrusts; thrusts may be relatively rapid and short and/or relatively slow and long (Struhsaker 1967a); may be followed by a pause before dismount. (Field assistants call this copulation or mating (CO).

- In the comments" section, observer should attempt to (1) note whether the thrusts are rapid/short or slow/long, (2) count the **number of thrusts**, (3) note if the presence/absence of a "**pause**" before dismount, and (4) note the presence/absence of **ejaculate** on the male and female's genitals.

Mating refusal (MR), event –female actor who is being grabbed by male remains sitting, lies down, crouches low, or walks away; note that female may also hit, lunge, or make "anti-copulatory squeal-scream" vocalizations (i.e., behaviour of "anestrous female" as described in Struhsaker 1967a).

Penile erection (PE), event – actor has a conspicuously erect red penis; may occur during 1) grooming when recipient is male, 2) intragroup agonism, usually by the aggressor (Struhsaker 1976a)

AFFILIATIVE (G or R; occasionally M)

Approach (AP), state – One monkey moves into contact or within 2 meters of a second monkey (Jack 1998).

Leave (LE), state – One monkey moves out proximity (2 meters) of another monkey (Jack 1998).

***Breast feed (BF)** – actor suckles from one or both nipples simultaneously (Struhsaker 1967a); this is a behaviour directed by an infant (sometimes a young juvenile) to a female recipient; a.k.a., nursing or suckling.

Carry (CA) – actor has another individual, usually an infant, clinging to its ventral surface or sitting/straddling on its back while engaged in locational movement.

Entwine tails (ET; Mutual behaviour) – two individuals sitting in close proximity on a branch criss-cross their tails (Struhsaker 1967a)

Groom (GR), state – actor combs through the fur of recipient using fingers and/or mouth, and may place foreign particles in mouth; may be accompanied by lipsmacking or teeth chattering (Struhsaker 1967a).

Groom solicit (GS), event – actor presents a specific body part to recipient for grooming (Struhsaker 1967a)

Ignore (IG), event – actor presents a groom solicit that is not acted on by the recipient. (Event)

Hug (HU), event – actor wraps their arms around the recipient while sitting dorso-ventrally or ventro-ventrally (recipient-actor) and may be associated with grooming; a.k.a. embrace (Struhsaker 1967a).

Play (PL; D, R, or M behaviour; or S for rare self-play), state – Play behaviours are quite variable and encompass a large number of behaviours described elsewhere (e.g., grab, chase, wrestle, mount, groom, embrace, hop, etc…)

- in play, these behaviours – such as chase or groom – are "alternated with one another in rapid sequence" and "may be the major distinctions between play and non-play encounters, rather than uniquely different behavior patterns" (Struhsaker 1967a: 33)
- intergroup play between juveniles and juvenile males of different groups may occur (Struhsaker 1967a).

***Wean (WE)** – female actor refuses breast-feeding attempt, or nips and/or pushes away a suckling infant (Struhsaker 1967a); this is a behaviour directed by a female to an infant or young juvenile.

Mouth to mouth (MM) , event– actor approaches recipient and the two put their mouth close together touching (or nearly).

AGONISTIC

In "comments", note the stimulus or context prior to the agonistic event(s), such as copulation/mount, male, infant, grooming, food, space, or unclear; do not leave blank (i.e., if you didn't notice anything, write "unclear").

Aggressive/Dominance Behaviours (G or R; occasionally M)

Bite (BI), event – as described, usually accompanied by grabbing (Struhsaker 1967a)

Bob (BB), event – Jerking or bobbing of head or entire body in up and down motion (on sagittal plane); for body includes torso bobbing from quadrupedal to bipedal position – often associated with eyelid flash (*sensu* "jerking" in Struhsaker 1967a)

Branch-shaking (BS), event – Actor deliberately bounces once or twice on a branch, sometimes associated with racing through trees creating noticeable noise, normally associated with intergroup encounters (Struhsaker 1967b, Henzi 1982)

Broadside (BD), event – Actor stands perpendicular to receiver, pauses, and then moves on; actor's tail may be raised. Note: Receiver is usually sitting (Henzi 1982; *sensu* "sideward-display" in Struhsaker 1967a)

Chase (CH), **state**– Actor moves rapidly toward the recipient, who runs away (*sensu* "chase-and-attack" in Struhsaker 1967a); recipient frequently looks back at actor while running away, and often emits submissive vocalizations

- note: some chases may be "false" (sensu "false-chase" in Struhsaker 1967a), wherein the actor gallops slowly and hesitatingly towards the recipient that is never caught → actor generally subordinate to the recipient

Coalitionary Display (CD) – any agonistic interaction involving three or more monkeys; the initial aggressor(s) is the "actor(s)", while the initial victim(s) is the "recipient(s)"; additional details on the behaviours involved should be noted in the "comment" section.

Eyelid flash (EF), event – actor exposes lighter coloured eyelids by retracting brow while maintaining eye contact or staring at the recipient (Struhsaker 1967a); may also be submissive ("defensive") in nature if actor is crouching (Struhsaker 1967a)

Hit (HI), event – actor hits, or slaps, the recipient with its hand (Struhsaker 1967a)

Lunge (LU), event – Actor leaps or jumps towards the recipient. Forward lurching of the chest.

Penile Display (PD), event– Male actor displays red and erect penis while standing bipedally or sitting upright with his hands on the recipient, whose face is directed towards the actor's genitals (Struhsaker 1967a).

Red-white-and-blue display (RB), state – Male actor displays the red perianus, white pelage between anus and scrotum, and blue scrotum to the recipient; male encircles or paces next to recipient with tail lifted, or briefly stands on his hindlimbs while oriented towards the recipient, thereby exposing genitals; actors include only adult, subadult, and older juvenile males (Struhsaker 1967a; Henzi 1982). Note: Receiver is usually sitting and vocalizing. Like a male presenting/ may involved movement around receiving individual.

Solicit Assistance (SA) – aggressor or victim of aggressive behaviour solicits assistance from others by "head flagging", glancing back and forth between opponent and individual assistance is being solicited from, or vocalizing (e.g., chuttering)

Supplant (SU), event –the actor moves towards the recipient and occupies the space, eats the food, takes copulatory position, or assumes the grooming position of the recipient; the recipient or "supplantee" generally moves away, sometimes engaging in submissive behaviours such as lip-smacking or submissive vocalizations (Struhsaker, 1967a); a.k.a. displacement.

- Note: indicate in "comments" what the actor removed: food, grooming, or space (note that because "space" is generally taken when removing food or grooming from the recipient, "space" should only be used if neither food nor grooming were removed from the supplantee)

Submissive (G or R; occasionally M)

Avoid (AV), **event**– at the approach of another individual (i.e., the recipient of the avoidance behaviour), the actor spontaneously vacates and moves away without any threat or aggression from the other individual; the recipient may just be passing by and does not occupy the space vacated by the actor (i.e., the individual doing the "avoiding")

- note: if the space (or food/grooming partner) is then occupied by the approaching individual, this behaviour should be coded as a supplant directed by the approaching individual.

Cowering (CW), event – Actor lowers head/body by crouching towards the ground and avoids eye contact with recipient; actor may be moving away from recipient; usually associated with submissive vocalizations/lipsmacking (Henzi 1982; sensu "crouching" in Struhsaker 1967a)
Fear grimace (FG), event – actor opens mouth about halfway and exposes teeth by retracting lips on horizontal plane (resembles a "smile); often accompanied by submissive vocalizations and staring at the recipient (*sensu* "grimacing" in Struhsaker 1967a).

<u>VOCALIZATIONS</u> (G or R; occasionally M)
Alarm call (AC), event – Alarm calls are often multi-syllabic barks can be emitted in response to a real or perceived threat, most notably for "other vervet group", snakes, eagles (i.e., *rraup*), leopards (i.e., *chirp*), & dogs and humans at Nabugabo (http://www.psych.upenn.edu/~seyfarth/Baboon%20research/vervet%20vox.htm)

Bark (BK), event – low-pitched and gruff uni-syllabic exhaled vocalization emitted by males during intergroup encounters and occasionally during intragroup agonism; given towards other vervet monkeys who are fighting, it is emitted to stop the fighting (Struhsaker, 1967b).
***Chutter (CT), event** – low-pitched, monotonal and staccato vocalization emitted by females and juveniles to express aggression and solicit assistance; mouth is closed and the teeth are covered (Struhsaker, 1967b).
Submissive vocalizations (SV), event – lipsmacking, teeth-chattering, purring (Struhsaker 1967b, Henzi 1982), and also includes:

- ***Woof woof (WW)****:* This call is non-tonal, deep, and has a guttural sound (Struhsaker, 1967) emitted with closed or slightly-open mouth to indicate submission (Struhsaker, 1967b).
- ***Wa (WA)****:* This call is a continuous tonal exhalation that occurs with a grimace and indicates submission (Struhsaker, 1967b); may be combined with as "Woof-wa" vocalization.
- ***Rraugh (RR)****:* For this call the mouth is closed or partially opened and the teeth are covered (Struhsaker, 1967b). This call is emitted by yearlings when they approach older members of the group, and is a signal of nonaggression (Struhsaker, 1967b); includes both the long and short rraugh, and the aarr-rraugh.
- ***Lipsmack (LS):*** Moving the lips together quickly, opening and closing the mouth repeatedly.

***Squeal-Scream (SS):** high-pitched, piercing calls usually are emitted by females and juveniles that are seeking help from threats by an aggressor, and may be anti-copulatory (Struhsaker, 1967b).

<u>INFANT INTERACTIONS (C:Contact; R:Receive or D:Direct)</u>
*When applicable, instantaneous samples of focal animal's infant should be recorded at 0, 5 10, and 15 mintues of focal follow.
Ventral contact (VC;), event –actor initiates contact between torso of infant with the ventrum of mother (Bardi et al. 2004).
End ventral contact (EC), event –Actor separates torso of infant from the ventum of mother (Bardi et al. 2004)
Breast Feed (BF), event – infant's mouth is in contact with one or both nipples simultaneously (Struhsaker 1967a)

End Breastfeed (EB), event – infant that was in nipple contact stops voluntarily (i.e., not "weaning")
Weaning (WN), event – infant that was in nipple contact is forced to stop breastfeeding by the action of the focal
Restrain (RS), event – Focal keeps infant from breaking contact (Bardi et al. 2004)
Reject (RJ), event – Focal prevents attempted contact by infant (Bardi et al. 2001)

INTERACTANT(S)

For identified monkeys, write their name or code in the Interactants (or NN) column;
For unidentified monkeys, use the following two or three letter codes; if there are multiple individuals of the same age/sex category, add number identifiers. For example, AM1, AM2

AM – Adult male
AF – Adult female without infant
AFI – Adult female with infant
AD – Adult, unsexed
SM – Subadult male
SF – Subadult female
SB – Subadult, unsexed
JM – Juvenile Male
JF – Juvenile Female
JV – Juvenile, unsexed
INF – infant (always unsexed)
XX – Unidentified vervet
ZZ – other species (if known, indicate the species in the "comments"; e.g., snake, bird, dog, cow)
OO – observer
OH – other human

- If there are multiple interactants, use a comma to separate their IDs

ADDITIONAL NOTES:

Copulatory harassment of a male or a mating pair has been observed, but the behaviours comprised in copulatory harassment include other behaviours described herein (e.g., biting, lunging, grabbing, etc…). As such, if copulatory harassment is observed, this should be noted in the "comments" of the associated behaviour.
***behaviours** identified with an asterisk (*) are not usually performed by adult or subadult males; e.g., Breast feed, Wean, Chutter and Squeal-Scream.

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