Should I stay or should I go? Hormonal and demographic correlates of natal dispersal in a population of wild vervet monkeys.

by

AREND R. VAN BLERK

thesis presented for the degree of

MASTER OF SCIENCE

in the Department of Biological Sciences

UNIVERSITY OF CAPE TOWN

MARCH 2021

Supervisor: Prof. M.J. O'Riain, University of Cape Town, South Africa.

Co-supervisor: Prof. R. Bshary, University of Neuchâtel, Switzerland.

PLAGIARISM DECLARATION

I know the meaning of plagiarism and declare that all of the work in the dissertation, save for that which is properly acknowledged, is my own.

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14 MARCH 2021

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ACKNOWLEDGEMENTS

I would like to thank Professor Justin O’Riain for supervising this thesis, for generously funding my studies and for giving me the opportunity to return to UCT.

Thank you to Professor Redouan Bshary for his insight and comments throughout this study and for giving me the opportunity to visit the University of Neuchâtel and funding the analyses of the samples.

Thank you to everyone from the Inkawu Vervet Project, in particular Professor Erica van de Waal, for giving me the opportunity to work on my MSc while at IVP and for allowing me access to the IVP database. Also to the students and volunteers who collected the data and the samples, especially Severyne, Alysson, Alison and Charlotte who dedicated many hours to preparing the samples at the field station. You guys were amazing!

Thank you to Dr Zegni Triki for training me in the lab and for your comments, support and friendship.

Thank you Dr Gàetan Glauser and Dr Armelle Vallar for running the samples through the HPLC and for making sense of it all.

To everyone at the Eco-Ethology Lab, thank you for your friendship and for making my time there as memorable as you did. It would not have been the same without you.

To my family and friends, thank you all for your love and support.

A very special thank you to my wife, Dr Jennifer Botting, for her continued support and unconditional love and for putting up with me throughout this time. I would not have been able to do this without you and your support throughout my MSc means the world to me.

I would like to thank everyone from the Mawana Game Reserve for allowing us to work on their beautiful reserve and also for their support and friendship.

ABSTRACT

Natal dispersal is an important maturational milestone in the life of many primates and is associated with changes in the physical and social environment. To integrate into an unrelated group, an individual must abandon its known environment and face various challenges which can often be costly. Male dispersal is most common among Old World monkeys, but is poorly studied due to the difficulty of following dispersing individuals. Even fewer studies have attempted to explore the hormonal correlates of dispersal owing to the difficulties of obtaining sufficient faecal samples of the same individuals before, during and after a successful dispersal. In this study, I aimed to better understand the hormonal correlates (i.e. testosterone and cortisol) of dispersal in free ranging, habituated male vervets leaving their natal groups (natal dispersal). I collected faecal samples from 10 males and assessed the effects of age, rank, natal group size, adult sex ratio and number of same sex peers, to investigate potential influences on the triggers for natal male dispersal. My results show that standardised rank, but not testosterone levels, was significantly lower in the three months following a successful primary dispersal than before the animals left their natal group. Natal males from larger groups had significantly higher testosterone levels than those from smaller groups and dispersed significantly later than males from smaller groups. Cortisol levels were rarely above the minimum detection level, suggesting dispersal in vervets is not a stressful behaviour, possibly because of high levels of familiarity with individuals in troops into which males had immigrated. Limitations included the difficulty of following known individuals into habituated study troops, which resulted in a relatively small sample size of successfully dispersing males. Furthermore, a lack of adequate faecal samples at key points in the life history of individuals reduced resolution on pre- and post- dispersal hormonal correlates. Further studies will require a larger proportion of the study population to be habituated and regularly followed to allow for a more rigorous assessment of dispersal success and hormonal correlates. This study advances the limited knowledge we have on the potential drivers of male dispersal in vervets and primates more generally.

1. INTRODUCTION

1.1. Dispersal in mammals

Philopatry is a common phenomenon among mammals and refers to social structures wherein one of the two sexes remains in the natal group for their entire life, while the other sex disperses. The literature refers to dispersal in various ways depending on the species and the topic of the research (Greenwood, 1980) and some argue that a single definition cannot include all the different varieties of dispersal we observe in nature (Holekamp et al., 1984). In this study, I will assume the definition of Strier (2016), in which dispersal is defined as:

"*emigration from a social group; can involve emigration from a natal group or, in secondary dispersal, emigration from another group into which the individual has previously immigrated*".

This definition is best suited for this study as it focusses on the movement of individuals from one social group to another, and particularly because it also makes the important distinction between natal and secondary dispersal. Natal dispersal refers to an individual's first dispersal event in which it disperses from its natal group and either attempts to immigrate into another group or establish a new group. Secondary dispersal refers to all dispersal events that follow natal dispersal. Natal dispersal usually occurs around the time that an individual reaches sexual maturity (Howard, 1960).

Among mammals, males are more often the dispersing sex, while females are more often the philopatric sex and remain in their natal groups (Greenwood. 1980). This is, however, not always the case and there are species in which the roles are reversed, and females are the dispersing sex (Crocket, 1984: Red Howler Monkeys; Nagy et al., 2007: Sac-winged bats; Munshi-South, 2008: Large Treeshrew; Muehlenbein and Watts, 2010: Chimpanzees;) and others in which both sexes disperse (Packer and Pusey, 1987). Among Old World Monkeys, male dispersal is the most common form of dispersal (Packer, 1979 and Alberts and Altmann, 1995: baboons Cheney and Seyfarth, 1983: Vervet Monkeys), but female dispersal does also occur (Marsh,1979: Red Colobus Monkeys).

1.2. Costs and benefits of dispersal

Dispersal plays an important role on an individual level, but also on a population- and species level. However, there is some disagreement among scientists as to its ultimate function. Many researchers seem to agree that dispersal likely evolved as a mechanism to avoid inbreeding (Greenwood, 1980; Dobson, 1982, Cheney and Seyfarth, 1983). ‘Inbreeding Depression’ is a reduction in the viability and fertility of offspring resulting from the mating of close kin (Packer, 1979). Inbreeding has been related to decreased heterozygosity, increased levels of sperm deformation, as well as decreased levels of testosterone in male lions (Packer and Pusey, 1987). In one baboon population, a 40% reduction in offspring viability was shown for a male that bred in his natal troop (Packer, 1979). Despite these results others suggest that there may be simpler ways of avoiding inbreeding than through dispersal (Moore and Ali, 1984) and in some species of vertebrates inbreeding does not seem to impose a fitness cost (Rood, 1987: Dwarf mongoose; Bulger and Hamilton, 1988: Chacma baboons).

1.2.1. Potential costs of dispersal

Dispersal can be a perilous endeavour and is associated with many risks and challenges to the individual. The increased risk of mortality is likely the greatest risk a dispersing individual faces as it has such a decisive effect on an individual’s future reproductive prospects. This risk can come in many forms including predation (Garrett and Franklin, 1988; Isbell et al., 1990), aggression from unfamiliar conspecifics (Henzi and Lucas, 1980; Dittus, 1986; van Noordwijk and van Schaik, 2001; Marty et al., 2017), and factors related to unfamiliarity with the new environment (Waser and Jones, 1983; Packer and Pusey, 1987; Isbell et al., 1990). Higher mortality rates among dispersing individuals have been documented in multiple species and mortality rates as high as 38% have been estimated in dispersing capuchins (Janson et al., 2012), while mortality rates of about 13% have been documented in dispersing male baboons (Alberts and Altmann, 1995). Although aggression among males is common throughout the year, among seasonal breeders, aggression levels have been shown to increase during the mating season along with an increase in the intensity of the behaviours (Henzi and Lucas, 1980; Marty et al., 2017). Dispersal has been shown to coincide with the peak mating season (Henzi and Lucas, 1980; Young et al., 2019). Recently dispersed individuals attempting to integrate into a troop have also been shown to bear the brunt of agonistic interactions (Henzi and Lucas, 1980). This has also been documented in non-seasonal breeders; male olive baboons have been documented to chase away males attempting to immigrate and the newcomers were frequently seen with severe wounds (Packer, 1979).

A tendency to disperse to neighbouring groups has been shown in various primate species (Cheney and Seyfarth, 1983; van Noordwijk and van Schaik, 2001) and it is generally thought that dispersing over short distances will decrease the risks associated with dispersal (Bengtsson, 1978). In these cases, the traveling distance is minimal and individuals might not experience significant environmental change over the short dispersal distance. When dispersing alone, as is often the case in secondary dispersers like vervet monkeys (Cheney and Seyfarth, 1983), dispersing over a short distance will also decrease the time an individual will spend by itself. However, when the dispersal distance increases, as was the case for a male vervet, (Henzi and Lucas 1980), and a Japanese macaque (Norikoshi et al., 1975), the dispersing individual might be exposed to a completely new and unfamiliar environment and spend a considerable time alone. An individual might also have to endure dispersing over unsuitable habitat in an attempt to reach or find a more suitable one (Dobson, 2013). Dispersing individuals deplete their energy stores (Dufty and Belthoff, 2001) as they have been shown to forage less efficiently (Clutton-Brock, 2016) dedicating more time to vigilance behaviours (Bachman, 1993; Nunes and Holenkamp, 1996). Dispersing male meerkats have been shown to progressively lose weight and experience increased parasite loads when they disperse (Clutton-Brock, 2016). Moving into an unknown environment will bear various costs as individuals will lose access to known resources (Pusey and Packer, 1987).

Dispersing individuals will also experience significant social change and challenges. A dispersing individual will abandon its place in the hierarchy as well as its relationships when it disperses. When integrating with a new group, males of many primate species start at the bottom of the hierarchy (Strier, 2016), and will have little to no social support upon arrival at the new group. This lack of social support along with the individual's low rank makes an individual vulnerable to attack from other group members, with very little opportunity to defend itself.

A more indirect cost of dispersal is evident in gregarious species in which dispersing individuals spend an extended period of time alone; in these cases, dispersing individuals lose mating opportunities and have heightened predation risk (Alberts and Altmann, 1995).

Infanticide is another risk which males need to consider when dispersing. Although it does not directly affect the individual, it does affect his reproductive success through a loss of inclusive fitness. In the event of forced evictions common in lions and capuchins (Packer and Pusey, 1987; Jack and Fedigan, 2004a), the forcefully evicted male(s) does not have a choice, but when dispersal is voluntary, individuals need to decide between potentially losing their offspring in their current group to infanticide, or dispersing and attaining new mating opportunities. In the event of a takeover, lions that have dominance over two separate prides are often seen to abandon the pride with older cubs in favour of the pride with the younger cubs (Packer and Pusey, 1987). It is thought that older cubs stand a greater chance of escaping the infanticidal behaviour of the new male(s) and that the deposed male can increase his inclusive fitness by rather dedicating his time to the protection of the younger cubs in the other pride (Packer and Pusey, 1987).

Clearly the risks and challenges of dispersal are high but despite this, dispersal is a common phenomenon among mammals suggesting the advantage outweigh the potential costs.

1.2.2. Benefits of dispersal

Juvenile males often do not have mating opportunities until after they have participated in natal dispersal (Greenwood, 1980; van Noordwijk, 1985; Pusey and Packer, 1987) and females have been shown to actively reject advances from closely related males as well as unrelated natal males with whom they are familiar (Taylor and Sussman, 1985; Sauther, 1991). Dispersal allows males to attain access to receptive, unrelated females (Bengtsson, 1978; Greenwood, 1980; Shields, 1987), which greatly increases their reproductive prospects (Henzi and Lucas, 1980). Lindburg (1969) found that, in Rhesus monkeys, most dispersing males copulated with females of their newly joined groups.

Dispersal also allows individuals to escape from breeding competition with resident males and allows them to find and integrate into groups in which they would have better reproductive prospects (Clutton-Brock, 2016). Dispersal in male white-faced capuchins has been shown to be driven by intragroup competition (Jack and Fedigan, 2004b) with males often dispersing to groups that have higher female-to-male ratios. This tendency to disperse to groups with higher female to male ratios has also been documented in many other primate species (Pusey and Packer, 1987). In white-faced capuchins, dispersing males also typically attain higher ranks after dispersal which is closely related to reproductive success in this species (Jack and Fedigan, 2004b). In vervet monkeys, dominant males deter subordinate males from mating with females, even when females initiate the mating activity (Henzi and Lucas, 1980). By dispersing, these subordinate males have the opportunity to obtain a higher rank that is also associated with greater mating success (Cheney, 1983). This relationship between high rank and reproductive success has also been described in long-tailed macaques (van Noordwijk, 1985) in which the dominant male was the father of between 60% and 90% of infants, although see Minkner et al. (2018) for mixed evidence of dominance –based reproductive bias in male vervets.

A more indirect benefit of dispersal is the potential for inclusive fitness. The concept of inclusive fitness suggests that the overall fitness of an individual is not only determined by its own survival and reproductive success, but also by the survival and reproductive success of related individuals (Strier, 2016; Molles, 2015). Perrin and Mazalov (1999) argue that competition among related individuals will reduce inclusive fitness. By dispersing an individual will decrease competition with its relatives and subsequently create a more favourable environment for the remaining relatives, increasing its own fitness through the survival and reproduction of its relatives.

1.3. Strategies for Dispersal

Various "strategies" for dispersal have been proposed that may minimise the potential costs to the dispersing individual or increase the chances of integrating with the new group. Peer dispersal (also referred to as parallel dispersal) is probably the most common and well-studied of the dispersal strategies. Peer dispersal occurs when an individual disperses alongside peers or disperses to a group that contains peers. Peer dispersal has been documented in various species, including vervet monkeys (Cheney and Seyfart,1983), long-tailed macaques (van Noordwijk and van Schaik, 2001) and white-faced capuchins (Jack and Fedigan, 2004a). By dispersing with peers, a male will arrive at a new group with existing allies which could either defend an individual during an attack or decrease the chances of an attack occurring (Cheney and Seyfarth, 1983; Cheney, 1983; Ijsseldijk, 1989; van Noordwijk and van Schaik, 2001). It has also been suggested that that the presence of peers might deter unrelated competitors from attempting to integrate with the group (van Noordwijk and van Schaik, 2001). Jack and Fedigan (2004a) suggests that peer dispersal is likely to increase survivorship among natal dispersers, while also increasing inclusive fitness benefits. Peer dispersal rates in white-faced capuchins have been reported to be as high as 82% (Jack and Fedigan, 2004a) with individuals remaining in their natal troop until the maturation of potential dispersal partners (Cheney and Seyfarth, 1983; mentioned in Jack et al., 2012).

Jack et al. (2014) argues that a delay in the attainment of adult body size could help natal dispersers integrate groups with very little aggression. Between group encounters in white-faced capuchins are usually quite aggressive, but Jack and Fedigan (2004a) noted that young males sometimes stay behind with another group after an encounter and interact affiliatively with members of the group and sometimes even permanently join group. They suggest that smaller, juvenile males with low levels of testosterone are less of a threat to resident adult males than other fully grown adult males allowing juveniles to integrate with little aggression (Jack et al., 2014). Similar results have also been found in long-tailed macaques where young males have also been found to disperse before attaining full adult body size, subsequently undergoing a growth spurt to develop full adult features (van Noordwijk and van Schaik, 2001).

Among some primate species, males have also shown clear behavioural differences during their immigration period. Van Noordwijk and van Schaik (1985) describe two types of immigrating males among long-tailed macaques and identified some differences between the two types. They were termed Unobtrusive and Bluff immigrants. Bluff immigrants displayed high levels of aggression and attempted to take the dominant position immediately upon entering the group, while unobtrusive males were submissive to other individuals in the group and typically assumed a rank lower than the median of the group (van Noordwijk and van Schaik, 1985). Alberts et al. (1992) documented a similar event in yellow baboons where a single male that entered a group was more aggressive than any of the other males and obtained high dominance rank within one week of entering the group. Although these strategies clearly have serious potential costs associated with them (like injury through increased fighting), the payoff is also high as is demonstrated by the attainment of high rank, which is related to reproductive success (Alberts et al., 1992).

1.4. Dispersal in vervet monkeys

Females are the philopatric sex in vervet monkeys and males disperse from their natal groups (natal dispersal) at around 5 years of age, around the time they reach sexual maturity (Cheney and Seyfarth, 1983). During their lives, male vervet monkeys will disperse multiple times after their initial dispersal from their natal group (secondary and tertiary dispersal). Most dispersal events occur around the mating season (Henzi and Lucas, 1980; Cheney and Seyfarth, 1983; Young et al., 2019) when females become reproductively active (Cheney and Seyfarth, 1983). Many of these migrations occur a couple of weeks before the mating season and it is thought that by dispersing a few weeks before the mating season, males allow themselves time to integrate the new group before the start of the mating season, which will increase their chances of reproducing (Young et al., 2019). During the mating season, the rate and intensity of aggressive interactions increase and newly immigrated males bear the brunt of these aggressive interactions (Henzi and Lucas, 1980). It has been suggested that males can decrease the levels of aggression they will receive in a new group by dispersing to a group which already contains individuals from his previous group (Cheney and Seyfarth, 1983). By doing this, males could already have allies in the new group which can assist during aggressive interactions. Although most secondary dispersers are subordinate individuals, males generally do not disperse due to aggression received from higher-ranking males (Cheney and Seyfarth, 1983). The exception to this rule appears to occur in the event of a male losing his dominant rank. When a dominant male loses his rank, the newly dominant male will constantly harass the recently displaced male until the displaced male departs from the troop (Henzi and Lucas, 1980).

It is often assumed that males disperse due to a sexual attraction to females (Cheney and Seyfarth, 1983). However, previous studies have found that natal males do not always disperse to groups with the highest number of females or to groups with the most female-skewed sex ratios (Cheney, 1983), indicating that other factors are likely at play. It has also been suggested that individuals should disperse to higher quality areas, but this may not be the case for vervet monkeys; vervets in the Amboseli population in Kenya have been recorded transferring to ecologically poorer areas (Cheney and Seyfarth, 1983).

Among vervet monkey natal dispersers, there is a tendency to disperse to neighbouring groups, to groups that contains known individuals from the natal group as well as to disperse alongside peers (peer dispersal). This tendency has not been recorded among secondary dispersers (Cheney and Seyfarth, 1983). By dispersing to neighbouring groups, vervets minimize the distance they travel and potentially the risks associated with it, like predation (Cheney and Seyfarth, 1983). Male vervets can also monitor the group before dispersing, for example during between-group encounters, allowing them to choose the best time to disperse. Both male and female vervet monkeys can distinguish between the vocalisations of individuals in neighbouring groups (Cheney and Seyfarth, 1982) and it is thus possible that individuals in a neighbouring group may already be familiar with an immigrating male; this could potentially make immigration easier for that male. Interestingly, dispersal seems to affect the level of aggression of between group encounters in vervet monkeys; when vervet groups exchanged males in the past, the aggression during a between group encounter was less and the groups showed more affiliative behaviours (Cheney and Seyfarth, 1982).

In some ways successfully dispersing is a male’s first step towards reproductive success, but it is in no means the only factor which determines whether a male will reproduce successfully. Although the relationship is not perfectly clear, studies have shown that higher ranking male vervets have a higher reproductive success than lower ranking males (Minkner et al., 2018; Cheney, 1983). Apart from successfully dispersing and integrating into a new group, a male will thus have to also rise in rank to improve his chances of reproducing successfully.

1.5. Proximate triggers of dispersal

Whilst there are clearly both benefits and costs to dispersal, the mechanisms that cause individuals to leave their current groups remains unclear. Proximate triggers of dispersal are events, or conditions, that precede a dispersal event and are thought to initiate or cause the event. Stenseth et al. (1992) distinguished between two types of triggers: extrinsic and intrinsic triggers. Extrinsic triggers refer to external factors that could have caused an individual to disperse, such as changes in the organism’s environment or loss of dominance, while intrinsic triggers refer to internal factors such as hormones or genetics. As discussed previously, there is an important distinction to be made between natal dispersal, when individuals leave their birth group, and secondary dispersal, when individuals migrate between two non-birth groups. Reaching sexual maturity, and thus often natal dispersal, is often strongly correlated with age. It is therefore possible that a single individual can be triggered to disperse by a completely different set of factors depending on which stage of its life history the individual is in at the time of the dispersal event.

1.5.1. Extrinsic triggers of dispersal

Extrinsic triggers of dispersal are usually pressures from the individual's environment and include both the physical-and social environment. The immigration of males into a new group can often be a socially disruptive event. Evidence from multiple species has indicated that resident males often disperse after the arrival of a new male(s) in a group (Jack et al., 2012: white-faced capuchins; Hanby and Bygott, 1987: lions; Sugiyama, 1967: gray langurs). These dispersal events can be due to forced evictions that are associated with high levels of aggression, but they can also be voluntary. Jack et al. (2012) found that of five predictor variables in their model, the occurrence of a group takeover was the only variable to accurately predict the dispersal of males in white-faced capuchins. The majority of dispersal events (both natal and secondary dispersal events) were not due to forced evictions (Jack and Fedigan, 2004a; Jack and Fedigan, 2004b), although forced evictions were also observed. Alpha male white-faced capuchins have also been shown to be much less likely to disperse voluntarily than subordinate males (Jack and Fedigan, 2004b), which is likely attributed to the much higher reproductive success alpha males experience (Jack and Fedigan, 2003). In lions, the dispersal of sub adult males is strongly correlated with the arrival of a new unrelated male in the pride (Hanby and Bygott, 1987). Sub adult males are actively evicted by the new males and evicted individuals are often seen with injuries, indicating the high intensity of aggressive interactions (Pusey and Packer, 1987). Similar trends have also been reported in gray langurs (Sugiyama, 1967). In rhesus macaques, the instability of the male dominance hierarchy has been show to attract, in particular, young dispersing males, while older males that were resident in the group dispersed from the group (van Noordwijk and van Schaik, 2001).

The loss of dominance rank has also been shown to often be followed by the departure of the displaced individual(s). Henzi and Lucas (1980) studied inter-troop movements in wild vervet monkeys and found that dominant males that were recently deposed, migrate once they lose their dominance in a group. The newly dominant male also shows increased aggression towards the recently deposed male in the form of harassment and displacement. Individuals might also be able to sense their likelihood of attaining a high rank in a group and if they are not very likely to attain high rank, they will disperse. Henzi and Lucas (1980) also reported that when two adult vervets immigrated into a group together and one attained dominance status, the other individual dispersed, despite not receiving any signs of aggression from the other male. Similar observations have also been reported in long-tailed macaques (van Noordwijk and van Schaik, 2001). Reproductive success has been shown to be closely linked to high dominance rank in some species (van Noordwijk and van Schaik, 2001; Jack & Fedigan, 2003), so when a dominant individual is displaced, it greatly effects future reproductive opportunities. This relationship is however not as obvious in vervets likely due to a males' limited potential to monopolise mating opportunities due to the codominance of females in this species (Minkner et al., 2018).

Finally, in species in which dispersal is closely associated with the mating season, sexual attraction to extra-group individuals seems to be a likely trigger of dispersal (vervet monkeys, Cheney and Seyfarth, 1983; Young et al., 2019; Rhesus Monkeys, Lindburg, 1969, ringtailed lemurs, Sussman, 1992). Some species show a tendency for males to disperse to groups with a higher female-to-male ratio (Jack and Fedigan, 2004b), but this tendency has not been found in vervet monkeys or long-tailed macaques (Cheney, 1983; van Noordwijk and van Schaik, 2001). From this, it would seem that gaining access to unrelated females or unfamiliar females is more important that gaining access to a larger number of females (Pusey and Packer, 1987).

Interestingly, apart from an attraction to reproductively active females, some male primates have also shown a preference to associate with extra-group males as well as males from their own group that are attempting to disperse (Pusey and Packer, 1987). In Japanese macaques, Matsumara (1993) described the relationship between young male macaques of neighbouring troops. Affiliative interactions between all male groups frequently occurred and it was suggested that associating with young males of the other group first could facilitate integration into the group (Matusmara, 1993). As discussed above, peer migration (or parallel migration) has been documented in multiple species (vervets: Cheney and Seyfarth, 1983; Capuchins, Jack and Fedigan., 2004a; Japanese macaques: Kawanaka, 1973, Long-tailed macaques: van Noordwijk and van Schaik, 2001) and it has been suggested that the dispersal of peers could prompt dispersal in other individuals (Pusey and Packer, 1987). Young vervet males have been shown to frequently disperse alongside their older brothers and also disperse to groups that contain familiar males (Cheney and Seyfarth, 1983).

1.5.2. Intrinsic triggers of dispersal

The potential role of hormonal as well as genetic influences upon dispersal have been suggested due to the extensive occurrence of dispersal throughout the animal kingdom, as well as its close association to specific developmental stages (Stenseth et al., 1992). Two main intrinsic factors have been suggested; 1) the ontogenetic switch and 2) testosterone. The ontogenetic switch hypothesis suggests that dispersal will occur when an individual reaches a specific body mass or when a certain amount of energy is stored as fat (Holekamp, 1986). According to this theory, dispersing individuals will be heavier or show a different pattern of weight gain compared to non-dispersers of the same age. The results from Holekamp (1986) supported this theory with dispersing male Belding's Ground Squirrels (*S. Beldingi*) being heavier than non-dispersers of the same age. However, the author did observe dispersers and non-dispersers of the same body mass and consequently suggested that body mass alone could not account for the dispersal pattern. Holekamp (1986) suggested that instead some parameter closely related to body mass, like percentage of body mass represented as fat, could perhaps account for the initiation of dispersal behaviour.

In a follow up study, Nunes and Holekamp (1996) manipulated the body mass of multiple Belding's Ground Squirrels by supplementing their diets with additional food and monitoring the effects on body mass, body fat and dispersal behaviour. They found that provisioned males were heavier at an earlier age and dispersed earlier than control males. Body fat percentage was found to differ between dispersing males and non-dispersing males of the same age and dispersed males showed greater body fat percentages suggesting that dispersal is mediated by body fat or some variable that is closely associated with body fat such as circulating oxidisable metabolic fuels (Wade and Schneider, 1992). These results were replicated in a similar study by Nunes et al. (1999) (also on Belding's ground squirrels) providing additional support for the theory. O'Riain et al. (1996) found support of the existence of a dispersive morph among captive colonies of naked-mole rats. Apart from the behavioural and physiological differences displayed by dispersers when compared to other colony members, the researchers also identified a distinct morphological difference;

dispersing individuals had significantly higher body fat percentages compared to individuals of similar age and mass and the researchers suggest that these fat reserves may act as a "nutritional safeguard" which could sustain the individuals during the dispersal period.

These studies provide convincing results for the ontogentic switch theory among rodent species, but whether these results can be generalized to other, non-rodent species remains unclear. Woodroffe et al. (1995) found evidence for a larger body length in dispersing vs non-dispersing European badgers, but the authors made no mention of other factors that could accompany increased body length (such as increased body mass or body fat). It does however not seem unfathomable that dispersal can be mediated by the availability of energy stores in other species too. The timing of energetically expensive events has been shown to be influenced by the availability of metabolic fuel as well as body mass and body fat content (Barnes, 1984). It is not too difficult to imagine that dispersal can be seen as such an energetically expensive event and that the timing of dispersal can consequently be affected by the availability of energy reserves (or the lack thereof) as an individual might have to rely on these to successfully disperse. Various behavioural changes have been associated with dispersal, that include increased activity levels as well as increased exploratory behaviour among dispersers (Holekamp, 1986; Ritchison et al., 1992). Dispersing individuals have also been shown to receive increased levels of aggression from conspecifics when trying to integrate with a new group (Henzi and Lucas, 1980; Holekamp, 1986; Pusey and Packer, 1987). The combination of these factors suggests that dispersal will be an energetically expensive event as individuals will have increased activity levels, while having less time to forage as they will spend more time being vigilant and consequently decrease their energy intake (Nunes and Holekamp, 1996; Bachman, 1993).

In addition to factors such as body mass, it has been suggested that hormones may play a key role in dispersal. The activational role of androgens (such as testosterone) in dispersal was first suggested by Phoenix (1959). During this study, researchers injected pregnant female guinea pigs with testosterone propionate and then studied the offspring of these females during adulthood. They concluded that these hormones have an organising effect on the neural tissues that mediate mating behaviour during the embryonic and foetal phases and that they play an activational role during adulthood. During the foetal and embryonic phases, the presence of these hormones causes the genital tissues to differentiate between masculine or feminine development, while during adulthood, these hormones are secreted and causes mating behaviour to be expressed (or activated) within the individual.

As these androgens are suggested to play an activational role, we would expect their secretion prior to the onset of sexual behaviour. If we relate this to dispersal, we would expect increased levels of testosterone around the time of dispersal or in the period leading up to dispersal. Although Phoenix et al. (1959)'s results support this hypothesis, many subsequent studies have failed to find similar supportive evidence (Holekamp et al., 1984; Nunes et al., 1999: Belding's Ground Squirrels; Holekamp and Smale, 1998: Spotted Hyenas and Strier and Ziegler, 2000: Muriqui Monkeys, Akinyi et al., 2017: baboons) although see (Young et al., 2019: vervet monkeys; Taitt and Krebs, 1982: Townsend's voles) for further support.

Holekamp et al. (1984) studied the effects of hormones on natal dispersal in Belding's ground Squirrels, during which they tested the *Activational Hypothesis*. In this study some male and female ground squirrels were gonadectomized (testes or ovaries removed), while some were operated on, but had no gonads removed (sham-operated). The behaviour of treated individuals was then compared to the behaviour of untreated individuals during dispersal. Castration did not significantly decrease the probability of dispersal in males, but most castrated males did migrate significantly later than untreated males. Interestingly, sham-operated males also tended to disperse at a later age. Testosterone levels were also found to be very low during the dispersal period. The results of this study therefore reject the *Activational Hypothesis* as we would have expected castration to affect the probability of dispersal.

However, in contrast, Taitt and Krebs (1982) found that testosterone implants increased immigration among female voles while also increasing their home range size. Importantly for the current study, Young et al. (2019) studied dispersal triggers in male vervet monkeys and found preliminary support for testicular androgens (such as testosterone) being the proximate physiological trigger for male dispersal. Their results show that a rise in dispersal probability is closely linked to a rise in testicular androgen levels. They also found a strong positive correlation between male dispersal and female reproductive activity, with the peak in male dispersal preceding the peaks in mating activity and conception of females by approximately 4 weeks. It is suggested that this allows males the time to integrate from the periphery of the new group into the centre (Young et al., 2019), which can sometimes take up to a month (Cheney and Seyfarth, 1983). They do however acknowledge the fact that there is still uncertainty to whether the rise in androgens triggers dispersal or whether they are a result of males no longer being supressed by females (Holekamp and Smale, 1998). It should also be borne in mind that the results were preliminary, and a comprehensive in-depth analysis was not performed.

1.6. Why study testosterone and cortisol in relation to dispersal?

Jack et al. (2012) suggested that in species in which natal dispersal occurs within a narrow age range, it is likely that changing hormonal levels (often associated with the onset of sexual maturity) act as a proximate trigger for dispersal. In species in which the age at natal dispersal is more flexible and shows more variability, it is likely that a combination of physiological and social factors triggers an individual to disperse.

Testosterone and cortisol are steroid hormones that are produced in the gonads and adrenal cortex respectively (Nelson and Kriegsfeld, 2017). Steroid hormones are small lipophilic molecules and are classified as sex- or adrenal steroids depending on the organs in which they are produced (Adkins-Regan, 2005; Nelson and Kriegsfeld, 2017). The role of testosterone in the onset of male sexual activity (as well as other life history events) and cortisol's role in the mediation of stressful events identify them as hormones of high interest when studying dispersal.

It is often argued that dispersal is a stressful event in the life of any animal as dispersers will be exposed to a range of potential stressors that can include changes and unfamiliarity with the environment, increased aggression from conspecifics and increased predation risk (see section 3.2.2, Potential costs of dispersal). Experiencing a stressful event increases the activity of the hypothalamic-pituitary-adrenocortical (HPA) axis that causes an increase in the production and release of glucocorticoids (Creel, 2001). Elevations in glucocorticoids (such as cortisol) mobilise energy sources, particularly glucose, from non-carbohydrate sources, such as proteins, which allows the organism to utilise this energy to resolve the stressful situation (Creel, 2001; Campbell and Reece, 2008). Studying changes in cortisol levels in relation to life history events (such as dispersal) provides us with valuable information regarding the stressfulness of these events and how individuals or a species experience it.

Natal dispersal is a major maturational milestone among many mammals, as individuals often do not have the opportunity to reproduce until after they have participated in natal dispersal (Greenwood, 1980). This is also a dispersing individual's first opportunity to attain an adult dominance rank, which will have major consequences on its future reproductive success (Cheney, 1983; van Noordwijk, 1985). As was discussed in section 1.5.2. (*Intrinsic Triggers of dispersal*), researchers have suggested that testosterone might activate dispersal in some species, but testosterone has also been linked to various other physiological and behavioural changes such as spermatogenesis, the onset of sexual behaviour and the development of secondary sexual characteristics, all of which are closely associated with dispersal (Holekamp and Smale, 1998; Campbell and Reece, 2008; Eisenegger et al., 2011).

Studies examining the hormonal correlates of dispersal have been conducted in various species of birds and mammals. The methods between the studies have, however, differed which makes comparing the results challenging. One of the reasons for this variation is the difficulty in following dispersing individuals (Akinyi et al., 2017). So, while some studies have been able to compare the same individuals before and after dispersal (Holekamp and Smale, 1998), other studies have had to rely on comparisons between residents and immigrants (Reyer et al., 1986; Woodroffe et al., 1995) which does not allow for taking individual differences into account. The results have also not remained consistent, sometimes indicating positive relationships (Reyer et al., 1986; Holekamp and Smale, 1998; Woodroffe et al., 1995; French and Schaffner, 1995; Beehner et al., 2006), while other studies have found no relationships (Strier and Ziegler, 2000; Beehner et al., 2006; Akinyi et al., 2017).

Reyer et al. (1986) relied on comparisons between individuals in different life history stage, rather than comparing the same individuals across different life history stages. In Pied Kingfishers (*Ceryle rudis*), Reyer et al. (1986) found that immigrant males (secondary helpers) had higher testosterone levels than natal males (primary helpers). There are however two types of adult males, secondary helpers and breeders. When comparing secondary helpers to breeders, there was not a significant difference in testosterone levels between the two, suggesting that the increase in testosterone between primary and secondary helpers is due to dispersal status, rather than sexual activity.

A positive relationship between dispersal and testosterone has also been described in mammals. Holekamp and Smale (1998) studied the relationship between blood plasma-testosterone and cortisol levels and dispersal in male spotted hyenas (*Crocuta crocuta*). They had the opportunity to test this relationship between resident and dispersed individuals, but also to test it in the same individuals before and after dispersal. After controlling for maturational variables, they found that blood plasma-testosterone levels were significantly higher in immigrant (dispersed) males than in sexually mature natal (resident) males. Plasma cortisol levels on the other hand were not significantly different between natal and immigrant males. When comparing the same individuals before and after dispersal, they found that testosterone levels increased after individuals dispersed. Nunes et al. (1999) studied the relationship between blood plasma testosterone and dispersal in Belding's Ground Squirrels (*Spermophilus beldingi*). They were unable to detect freely circulating testosterone in juveniles during the age classes when dispersal occurred. They did however find that adult males had significantly higher circulating blood plasma-testosterone levels than juvenile males. Woodroffe et al. (1995) studied dispersal in a population of European Badgers (*Meles meles*) and found that immigrant males had higher testosterone levels than individuals that did not disperse.

The disinhibitory effect of dispersal on the suppression of male testosterone secretion before dispersal was proposed by Holekamp and Smale (1998). In this theory, the authors propose that the "persistent exposure to female kin in the natal area inhibits testosterone secretion in adult natal male hyenas and that dispersal disinhibits testosterone secretion". According to this theory, natal dispersers will experience an increase in testosterone levels after dispersing from their natal groups. Their theory was supported by their own results as well as earlier (French and Schaffner, 1995: black tufted-ear marmosets) and later studies (Beehner et al., 2006: Chacma Baboons). An issue with the Holekamp and Smale study, however, is that they only studied a single clan of spotted hyena. The immigrant males were thus unknown before arrival in the study group and the authors were consequently unable to determine whether or not these males were natal or secondary dispersers. This can cause potential issues with their theory. If all the immigrant males in their study happened to be natal dispersers (or at least the majority), then the theory is supported by strong results. But if these immigrant males were secondary dispersers, the results could be flawed and factors other than dispersal could be playing a role in the increased testosterone levels seen in immigrant males. If the testosterone secretion was inhibited by residence in their natal clan, we would expect an increase in testosterone immediately or soon after dispersal. In the case of secondary dispersers, a long period could have elapsed in which the individuals could have immigrated or in which other factors could have caused this increase in testosterone levels.

1.7. Hormonal correlates of dispersal in primates

Despite various studies in non-primate species finding positive relationships between dispersal and testosterone, primates have showed varying trends in this regard. The genus *Papio* is a particularly well-studied primate genus with regards to the hormonal correlates of dispersal and multiple studies have been published exploring these factors. Akinyi et al. (2017) studied the relationship between dispersal and faecal testosterone (fT) and faecal glucocorticoid (fGC) levels in yellow baboons that sometimes interbreed with olive baboons. fT and fGC levels from faecal samples collected up to one month after dispersal were compared to faecal samples collected two to six months after natal dispersal. They found no significant difference in fT levels between the two categories, but rather found that fT was significantly related to age and seasonality, showing an increase with age, while also being higher in the wet season than the dry season. They found no relationship between fGC levels and dispersal. Akinyi et al. (2017) suggests that in male baboons, the physiological effects of dispersal are either very short lived, an idea supported by other literature (Marty et al., 2017) or that male baboons are very well adapted to handling the associated challenges of dispersal. An additional consideration is the fact that many of the individuals in this study dispersed to neighbouring troops. This means that some of the associated costs of dispersal could be removed due to shorter dispersal distances as well as a degree of familiarity with the territory due to the overlap of neighbouring troops (Akinyi et al., 2017).

Beehner et al. (2006) studied the relationship between dispersal and faecal testosterone levels in male chacma baboons (*Papio ursinus*). When all the samples of the dispersed males were pooled together, dispersing males showed higher mean testosterone levels than non-dispersing males. However, in reality there were two “types” of male dispersers in the study; young males that recently left their natal group and older males that left and re-entered the study group multiple times. When these types of males were considered independently from one another, the results changed. In the older males, the dispersing males still had higher testosterone levels than the non-dispersing males, but in the younger males there was no significant difference between dispersers and non-dispersers. This means that no direct connection could be drawn between testosterone and dispersal in young males, as all young males had high levels of testosterone, regardless of whether they have dispersed. Consequently, the authors could not draw any clear conclusions about the roles of testosterone in natal dispersal. Rather the relationship between testosterone and dispersal was evident in older migrating males. It is important to note however that the sample size in this study was small (all males, n=13; old males, n=7; young males, n=6), which begs the question as to the statistical power of these findings. Nonetheless, despite the small sample size and the similar sample size of the old and the young males, the result for the older males is still significant. Both young and old males had higher testosterone levels in the month following dispersal compared to the month preceding dispersal.

In the same population of chacma baboons, Bergman et al. (2005) studied the relationship between faecal glucocorticoids (fGCs) and dispersal. Both males that immigrated or emigrated had significantly higher fGC levels than males that did not take part in either event. A comparison was then done between the month immediately following immigration of a male and subsequent months to determine the effect of immigration on fGC levels. It was found that fGC levels were significantly higher in the month following immigration than in the other months. A similar technique was used to study the effects of emigration and samples from the month preceding emigration were compared to the samples preceding that month, but there was no significant difference found between these categories.

Albert et al. (1992) had the opportunity to study the immigration of an unusually aggressive male into one of their study groups of a population of yellow baboons (*Papio cynocephalus*). They found that this immigrating male had high basal cortisol levels (in the highest quartile of all individuals) and that his testosterone levels were much higher than the average of adult males, being almost double that of the second highest value. This male also attained a high rank very quickly and became the dominant male within his first week upon entering the group. Alberts et al. (1992) argue that these high testosterone levels are likely a result of the high aggression, and not the cause of it, as previous research has shown that the manipulation of testosterone does not necessarily cause similar changes in aggression (Dixson, 1980; Rose, 1985 as cited by Alberts et al., 1992).

In addition to baboons, the hormonal correlates of dispersal have also been studied in some macaque species. Marty et al. (2017) studied the effects of dispersal and immigration on faecal glucocorticoid metabolite (fGCM) levels in male crested macaques (*Macaca nigra*). The transition between groups seemed to have no effect on fGCM levels, but there was an increase in fGCM levels the first few days following immigration into the new group. This variation in fGCM levels, however, only lasted for the first week after immigration and by the second week following immigration the fGCM levels returned to baseline levels. Individual factors that could predict fGCM levels in response to immigration were also evaluated and it was found that the best predictors of fGCM levels in immigrant males were time since arrival and number of males in the target group (males other than the immigrating male). The number of days after immigration and number of males in the target group, were both found to be significant predictors of fGCM levels whereas rank achieved, aggression received, and proximity to other males did not significantly influence fGCM levels in immigrating males. The highest fGCM levels were recorded in the first two days following immigration after which there was a marked decline over the following days.

Finally, van Schaik et al. (1991) studied the relationship between urinary testosterone and dispersal in a population of Long-tailed Macaques (*Macaca fascicularis*) and found that natal males had significantly lower testosterone levels than immigrant males.

1.7.1. Studies of testosterone and cortisol in vervet monkeys

As discussed in the previous section, with regards to the activational hypothesis, Young et al. (2019) published the first study that examined the relationship between faecal androgen metabolites (fAM) and dispersal in vervet monkeys, finding that fAM levels increased as the probability of dispersal increased. This study was preliminary and did not include in-depth analyses but is still important as it is the first of its kind performed on the species.

Importantly, Young and colleagues were also the first to validate the relationship between stress and the associated changes in cortisol levels in vervet monkeys, which is critical when studying dispersal. Young et al. (2017) studied fGCM in both captive and wild vervet monkeys. The captive study was concerned with the validation of the study protocol and determining the most appropriate EIA (enzyme immunoassay) for the study. They found that the cortisol assay was the most appropriate for studying fGCM concentrations in faecal samples, but also that the peak was only seen between 25 and 33 hours after the stressful event, which in this case was an adrenocorticotrophic hormone (ACTH) stimulation test. This means that there is a delay of between 25 and 33 hours between the production of the GC's due to the stressful event and the excretion of the faeces that contain them, a period of approximately between 24 to 36 hours. They also found that individuals took between 43 and 74 hours to return to baseline levels (between two and three days).

In the second part of this study, the researchers attempted to validate their findings by studying the physiological stress response in what the authors perceived to be a stressful event in wild vervet monkeys, a rank change between the two highest ranking females in the group. Researchers noticed that a rank change was taking place between the alpha and beta females and predicted that this could be a stressful event for the two participating individuals as well as the rest of the group members. The alpha female's cortisol levels increased by 215% (from 80.1ng/g to 172.49ng/g) four days after the stressful event, while the beta female's cortisol levels changed by 217 % (from 54.0ng/g to 117.2ng/g) five days after the event. This study therefore provides important preliminary information about the fluctuation in cortisol levels in vervet monkeys.

1.8. Costs of prolonged elevation in cortisol or testosterone levels

The benefits of increased steroid hormone levels, such as testosterone and cortisol, is demonstrated through their respective roles in reproduction, rank attainment and energy mobilisation. But research has also demonstrated various detrimental effects of prolonged elevated levels of these hormones which can negatively affect an individual's survival. These include increased metabolic rates (Welle et al., 1992), increased risk of prostate cancer, production of oxygen radicals and immunosuppression along with its associated consequences such as increased parasite load (Muehlenbein et al., 2004 Decristophoris, Hardenberg and McElligott, 2007).

Many studies across a variety of mammals have documented the immunosuppressive effects of increased steroid hormone levels. Muehlenbein and Watts (2010) studied the relationship between cortisol and testosterone levels in relation to parasite load and rank in male chimpanzees. They found that both testosterone and cortisol were positively correlated with intestinal parasite richness, meaning that the higher the concentration of testosterone or cortisol were, the more unique species of parasites (in this study protozoans and helminth species) could be identified. They also found a positive relationship between dominance and helminth richness, but interestingly, not protozoan richness.

Although the results were not statistically significant, Sapolsky and Spencer (1997) found a slight positive relationship between cortisol levels and IGF-1 (Insulin-like Growth Factor 1) in a population of olive baboons. IGF-1 is an anabolic hormone that is associated (among other things) with wound healing and immune stimulation, suggesting that increased cortisol levels might be related to the suppression of the immune system.

Alberts et al. (1992) also identified an immuno-suppressive effect of increased cortisol levels in baboons. Researchers found that the immigration of a particularly aggressive male baboon was associated with increased levels of cortisol among group members. The increased cortisol levels among the group members was found to be associated with a decrease in lymphocyte count among the baboons.

Increases in basal metabolic rate (BMR) associated with increased testosterone levels have been reported in humans. Welle et al. (1992) reported an increase in BMR in men that received testosterone enanthate injections. An increase in BMR in humans might not necessarily be a significant cost as we often readily have access to food, but for wild, foraging animals, this might not be the case. Animals that inhabit areas that experience strong seasonal rainfall and consequently seasonal food availability could be negatively affected by an increase in BMR due to an increase in energy expenditure that is not supported by an increase in food availability.

Finally, increased levels of testosterone have also been associated with certain behavioural changes, which can negatively affect an individual’s survival. Free-living male lizards have been shown to display increased levels of aggression with increasing levels of testosterone (Moore and Marler, 1987), while their survivorship has been shown to decrease with increased levels of aggression (Marler and Moore, 1988). In this case the behavioural change associated with increased testosterone levels has had a detrimental effect on the survivorship of an individual. In a captive population of Talapoin monkeys, Dixson and Herbert (1977) found that gonadectomised male Talapoin monkeys showed increased levels of aggression after receiving testosterone treatment. Although the researchers did not test for a relationship between survivorship and increased aggression in Talapoin monkeys one could extrapolate a similar relationship as was seen in the lizards by Marler and Moore (1988), as increased aggression in primates have been linked to increased severity of wounds and injuries (*see section 1.2.1. Potential costs of dispersal*).

1.9. Factors influencing hormonal fluctuations

Changes in hormone levels in relation to a single factor (in our case dispersal) are difficult to study as a variety of factors can simultaneously influence hormonal fluctuations. Although the following section is by no means a comprehensive summary of all the factors that influence hormone levels, it should adequately demonstrate the various considerations to keep in mind when attempting to study hormonal changes.

Testosterone has been shown to be positively related to dominance rank in various primate species including chacma baboons (Beehner et al., 2006), chimpanzees (Muehlenbein et al., 2004) and white-faced capuchins (Jack and Fedigan, 2004a), but results from a study on vervet monkeys, did not provide significant findings although a general positive trend was observed (Steklis et al., 1985). Although the majority of dispersing male primates will assume a low rank upon immigration into a new group (Strier, 2016), some male primates have been shown to attain high ranks almost immediately upon immigrating into a new group. Alberts et al. (1992) studied the immigration of a male baboon into a new group and found that this male attained dominance rank within one week of integrating into the new group. This particular individual also displayed the highest testosterone and cortisol levels of all males in the group. The direction of rank change has also been shown to greatly influence testosterone levels. Beehner et al. (2006) found that in a population of male chacma baboons, males moving up the dominance hierarchy had significantly higher testosterone levels than males moving down the dominance hierarchy. These can be important factors to consider in dispersal depending on what the dispersing individual’s rank was prior to dispersal. As was mentioned earlier, males usually assume a low rank upon integrating into a new group. If a high-ranking male disperses, it is thus likely that he will assume a low-ranking position in the new group. This change in rank from high to low can greatly influence hormonal levels, but it might affect a lower ranking male's levels less. Contrastingly, if a male takes the "bluff immigrant approach" (see section 1.3. Strategies for dispersal) and is successful, a high-ranking male might not experience much rank change (as it would be moving from a high to a high ranking position) but a low ranking male would move up in rank in the new group.

Sapolsky and Spencer (1997) found that in a population of olive baboons, individuals in the lower half of the hierarchy had higher glucocorticoid concentrations than individuals in the upper half of the hierarchy, a pattern which was repeated across the population. The authors suggested that the increased glucocorticoid concentrations in lower ranking individuals are due to the physical and psychological stresses associated with a lower social rank.

Seasonality has also been shown to influence hormone levels. Akinyi et al. (2017) found that in yellow baboons fGC levels were higher in the dry season compared to the wet season, but that fT levels were reversed and were higher in the wet season than the dry season. A study of White-faced capuchins partially supported these results; the authors found the same trend for fGCs but found increased faecal androgen levels in the dry season (the opposite of Akinyi et al., 2017). The authors, however, suggest that this is largely due to the increased rates of between group encounters in the dry season (Schoof and Jack, 2013). Pappano and Beehner (2014) found increased fT levels in male Geladas in the wet season, while Bergman et al. (2005) found no relationship between fGC levels and seasonality in chacma baboons. Among species in which males are strict seasonal dispersers, this will not necessarily be a problem as all dispersing individuals should disperse within a narrow period and there should not be much seasonal overlap. But in species in which males disperse throughout the year, seasonality could be a very important factor to consider. Closely related to seasonality, faecal hormones have also been shown to be affected by diet. Dantzer et al. (2011) found that changes in the diets of red squirrels were associated with changes in both faecal androgen and faecal cortisol levels. The authors suggest that increased consumption of dietary fibre could increase the transition time of materials allowing these materials to be reabsorb hormone metabolites in the gut. This can be particularly evident in areas that experience great differences in rainfall between the wet and the dry season and consequently marked seasonal changes in vegetation.

It is also likely that life history stage may affect hormone levels in individuals; previous research has found a relationship between testosterone and age in chacma baboons (Beehner et al. 2006), wherein testosterone levels peaked around the age of 100 to 120 months after which it steadily declined. Jack et al. (2014) studied the relationship between faecal hormones (testosterone, dihydrotestosterone and glucocorticoids) and life history stages of wild, male white-faced capuchin monkeys (*Cebus capucinus*). They found that life history is a significant predictor of fT (faecal testosterone) levels and that fT levels increased with progressing life history stage and age (from infant to Adult). Jack et al. (2014) considered alpha males and deposed alpha males as separate life history stages from subordinate males and found that fT levels increased throughout these stages until an alpha male was deposed in which case fT levels significantly decreased. Although the fT profiles of subadult and subordinate males were very similar, the fT levels of the alpha males were more than 11 times higher than that of subordinate males supporting the idea that fT levels respond to a males' change in dominance status. Jack et al. (2014) suggests that the increased levels of testosterone is associated with the development and maintenance of the distinctive morphological characteristics exhibited by alpha males. Life history was, however, not found to be a good predictor of fGC and fDHT (faecal dihydrotestosterone) levels.

1.10. Research Aims

Previous studies on the relationship between steroid hormones and dispersal in primates have yielded mixed results (as discussed above) and further studies in this area are required. This study aimed to explore the variation in faecal testosterone and cortisol levels in relation to dispersal, group size and rank in male vervet monkeys participating in natal dispersal.

I hypothesised that natal dispersal would coincide with changes in hormone levels in male vervet monkeys. I predicted that faecal cortisol levels would increase after dispersal, considering that dispersal is likely to be a stressful event, particularly for natal males (Marty et al., 2017), but that cortisol levels will return to baseline levels within a few days of the dispersal event (Akinyi et al., 2017). I also predicted that faecal testosterone levels would increase after natal dispersal as dispersing individuals mature and fully develop into adult males (Akinyi et al., 2017; Holekamp and Smale, 1998).

In addition to examining the relationship between these intrinsic factors and dispersal in male vervets, this dissertation aimed to explore the relationship between age at natal dispersal and various extrinsic factors, including:

- i) Natal group size
- ii) Adult sex ratio in natal troop.
- iii) The number of same sexed peers in the natal troop.

By examining both intrinsic and extrinsic factors potentially associated with dispersal, I aim to improve our understanding of the proximate triggers of dispersal in male vervet monkeys and to contextualise this within the literature for dispersal in primates.

2. METHODOLOGY

2.1. Study area

The Inkawu Vervet Project (IVP) is based on the privately-owned Mawana Game Reserve in Kwazulu Natal, South Africa (S -28.00522, E 31.20593). The reserve is approximately 10 000 ha in extent, while the study area (Figure 1) is approximately 950ha, situated in the north-eastern corner of the reserve. The properties bordering the Mawana Game Reserve are a combination of communal land, private game reserves and commercial farms cultivating oranges, maize and nuts.

The area experiences predominantly summer rainfall in the form of afternoon thundershowers with little to no rain during the winter months. The Hlonyane River flows through the reserve from West to East and is a perennial source of water for animals on the reserve. A drought in 2016 and 2017 saw the river dry up for extended periods of time with only a few pools of stagnant water remaining. Various dams are also spread throughout the reserve which, under normal conditions, contain a relatively stable water level, but these also dried up during the drought. Temperatures vary greatly between seasons and can rise above 40˚C in summer and drop below 0˚C in winter.

The research area is generally gently sloped, but a low rising mountain range is present in the South Eastern corner and in areas where the slopes are steeper, multiple large gullies have formed due to erosion. Poor historical land use practices, including overgrazing have allowed bush encroachment in many areas. These areas are generally dominated by sicklebush (*Dichrostachys cinerea)* and *Vachellia* species. Woody vegetation in the study area is largely dominated by *Vachellia* species*,* mainly scented-pod acacia (*Vachellia nilotica)* and umbrella thorn *(Vachelia tortillis*)*,* sicklebush *(Dichrostachys cinerea),* red ivorywood *(Berchemia zeyheri)* and buffalo thorn *(Ziziphus mucronata)*. A variety of animal species are present on the farm and include larger mammals such as elephant, giraffe, kudu, impala, wildebeest, zebra and blesbok (see appendices for detailed species list). Martial eagles, leopards and pythons are known to predate on vervets (Cheney and Seyfarth, 1990). As all three of these predators have been observed on Mawana Game Reserve it is highly likely that they are the main predators of vervets on the reserve. On rare occasions researchers have observed vervets getting killed by dogs that are trained by humans for bushmeat harvesting.

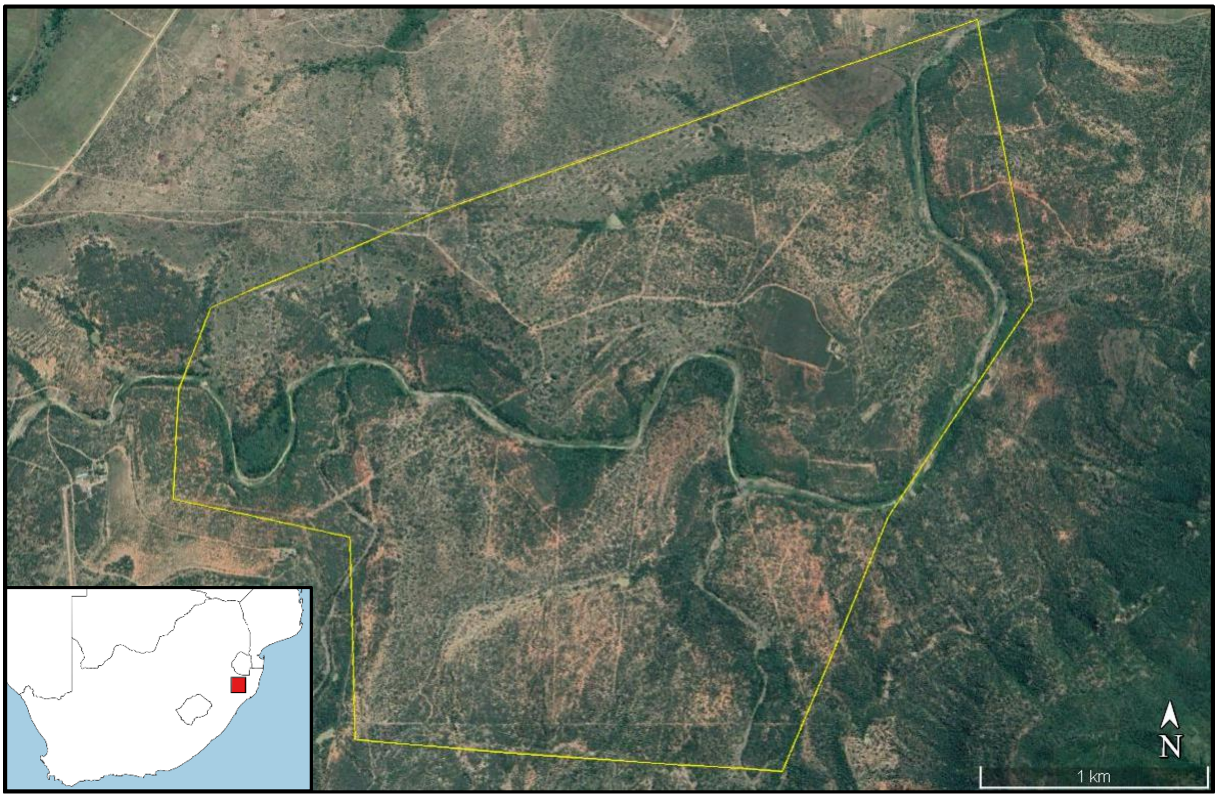


Figure 1: Map of the research area (yellow border) within the Mawana Game Reserve, Kwazulu Natal, South Africa (Google Earth, 18 March 2019, -28.005289, 31.206061).

2.2. Study animals

Behavioural data on three wild vervet groups (Ankhase [AK], Baie Dankie [BD] and Noha[NH]) have been collected since 2010. Data collection on three other troops including, Lemon Tree (LT, January 2011), Kubu (KB, June 2011) and Crossing (CR, January 2014) commenced later. Data collection included aspects of life history (all births and deaths, male dispersal into or out of study groups), physiology (faecal hormones), kinship (genetic relatedness) and behavioural observations (scans and focals). Data were collected by both postgraduate students and volunteers that were trained in the appropriate data collection protocols. Observers were trained to recognise individual monkeys and completed an identification test as well as inter-observer tests prior to data collection to ensure data accuracy between observers. The data used in this study form part of a long term life history project and the data was not specifically collected for the purpose of this study. Rather I was granted access to the data and samples that form part of this long term project. Non-invasive methods (observational and faecal sample collection) were used to collect the aforementioned data. The Inkawu Vervet Project has permission from Ezemvelo KZN wildlife as well as the owners of the Mawana Game Reserve to conduct research with the study population of vervet monkeys. The methods used in this study were subjected to strict ethical standards and have been approved by the University of Neuchâtel.

2.3. Faecal sample collection, extraction, shipment and purification

2.3.1. Faecal sample collection

Faecal samples were collected opportunistically from January 2015 to February 2018 for individuals in three troops (Ankhase, Baie Dankie and Noha) of wild vervet monkeys. Other researchers and I opportunistically collected faecal samples from individuals in each of the three study troops during the first two hours of morning observations, which commenced at sunrise. Sampling included individuals of all ages (with priority given to adults) with the aim of collecting one sample from each individual at least once per month. Data collection occurred routinely from Monday to Saturday including public holidays. Each sample included the monkey’s identity, and any uncertainty prevented an observed sample from being collected.

The collection procedure was as follows:

1) Identify defecating monkey.
2) Put on a pair of gloves.
3) Take a transparent bag, put it over one hand and collect faecal sample with bag.
4) Pull bag over sample so sample is inside bag and mix the sample in the bag by massaging it with fingertips.
5) When properly mixed, take Pasteur pipette and aim to remove one gram of faeces from the bag and place it in a 15ml centrifuge tube with a screw cap lid. Close centrifuge tube with screw cap lid.
6) Take permanent marker and write the following information on the centrifuge tube:
    - Name, age and sex of individual
    - Group
    - Time of collection
    - Date of collection
    - Collector's ID.
7) Place the centrifuge tube in a cooler box, ensuring that it is positioned against the ice pack and close the cooler box.
8) Discard excess faeces and dispose of used materials in waste receptacle at the field station.

Samples were collected from each observer at the end of the two-hour post-sunrise session and placed inside a cooler box with fresh ice packs. Once at the field station, the samples were weighed and placed in an electric freezer at -18°C.

2.3.2. Hormone extraction at the field station

Samples were removed from the freezer and allowed to thaw (approximately 10 min) after which the following steps were followed:

1) 5ml of 80% methanol per gram of sample was added to each sample (thus for every 0.2g of sample, 1ml of methanol was added).
2) Samples were then shaken by hand for ten minutes. If the sample was not completely mixed, it was shaken until mixed.

3) Mixed samples were placed in a refrigerated centrifuge for 10 minutes at 5000RPM at 4°C.
4) 2 x 1ml of supernatant was then transferred from the 15ml centrifuge tube to two labelled 1.5ml micro-centrifuge tubes.
5) Micro centrifuge tubes were then placed in the freezer at -18°C until shipment.

2.3.3. Shipment to Switzerland

Samples were transferred to a cryogenic container (Taylor Wharton, CP500, dry shipper) containing absorbed liquid nitrogen. Once filled, the temperature within the cryogenic container is approximately -180°C and has a 7-day working time. Samples were then loaded and transported by air to the University of Neuchatel in Switzerland, where the samples were stored in a -80°C freezer. All samples arrived and were moved to the -80°C freezer within the 7-day working time as specified by the manufacturer.

2.3.4. Sample selection

A total of 2231 faecal samples from 103 individuals were collected. Of these, a subsample of 86 samples from 12 individuals were selected for the analyses. Sample selection was based on sex (we only looked at males) life history records and included all samples which were obtained from individuals that dispersed during the study period and conformed to at least two of the following four ‘dispersal’ categories:

- Category 1: samples collected 14 - 10 months before an individual’s dispersal.
- Category 2: samples collected 3 to 0 months before an individual’s dispersal.
- Category 3: samples collected 0 to 3 months after an individual’s immigration.
- Category 4: samples collected 10 – 14 months after an individual’s immigration.

Categories 1 and 4 serve as control categories as three months before and after immigration should be long enough to assume that testosterone levels in these samples were not affected by dispersal, as has been suggested by previous studies in baboons and macaques (Bergman et al., 2005; Marty et al., 2017). Categories 2 and 3 were selected to create a hormonal profile of a dispersing individual before and after dispersal (complete dataset under Appendices).

When examining the data, I noticed that of the 12 males in the analysis, one (Cancun) was a secondary disperser, while the other 11 were natal dispersers. Consequently, Cancun was excluded from all the analyses (n= 5 samples). Another individual Hibe (an individual from AK group) stayed with BD for a day and then returned to his natal group (AK). He then disappeared from AK two days later. Taking his behaviour from the previous few days into account, it is highly likely that he dispersed to a non-study group, but I am unable to confirm this. Hibe (n=3 samples) was thus removed from the analyses too.

2.3.5. Sample purification for HPLC (High Pressure Liquid Chromatography) and MSMS (Tandem Mass Spectrometry)

A pilot study conducted at the Inkawu Vervet Project (IVP) in 2014 and 2015, established the protocol for the purification of faecal from vervet monkey faecal samples (Kernen, 2015). The full protocol is available under the Appendices section.

2.4. Determining rank

Rank was determined using the EloRating Package in R statistical software. Dyadic conflicts were recorded ad libitum throughout the study period and the aggressor (winner) and the victim (loser) of each dyadic interaction was entered into a matrix for each day (See Table 1 for a list of relevant behaviours).

A winner-loser matrix along with a presence-absence matrix was constructed to determine the EloRating of individuals on specific days. The EloRating for all the individuals present on a specific day is expressed as a series of numbers where the highest EloRating represents the highest rank and the lowest EloRating the lowest rank. To calculate the ordinal rank for a specific individual on a specific day, I examined the EloRating for that specific day and determined the number of individuals present on that specific day, as well as our individual's rank (for example, Unwabo was ranked number 16 out of 39 individuals on the 14th of May 2015). This rank was referred to as the individual's Ordinal Rank. On that specific day, Unwabo's ordinal rank was 16. The Ordinal rank was then used to determine the Standardised rank according to the following formula as per Robbins (2005):

$$\text{Standardised Rank} = \frac{(N-R)}{(N-1)}$$

N = number of individuals in group

R = ordinal rank

The Standardised Rank is expressed as a value between 0 and 1, with 0 being the lowest rank and 1 being the highest rank (See Appendix B).

Table 1: List of behaviours, their codes and a description of each behaviour

Behaviour (code)	**Aggressor/ Victim**	**Description**
Stare (St)	Aggressor	Individual raises eyelids so white skin below the eyebrow is visible and stares at another individual(s), often moving head forwards
Attack (At)	Aggressor	Forward motion of the body towards another individual(s)
Approach (Ap)	Aggressor	Individual approaches another individual (slower than in attack)
Grab (Gb)	Aggressor	Grabbing a part of another individual's body with hand
Take Place (Tp)	Aggressor	Individual takes the place recently occupied by another individual
Bite (Bi)	Aggressor	Individual bites another individual on body
Hit (hi)	Aggressor	Individual hits another individual on body using hand(s)
Chase (Ch)	Aggressor	Individual runs after another individual who is fleeing
Aggressive Call (Ac)	Aggressor	Individual makes a vocalisation during a conflict
Steal Food (Sf)	Aggressor	Individual takes food from another individual
Hand on Head (hh)	Aggressor	Individual places hand on top of another individual's head
Avoid (Av)	Victim	Individual turns head or moves body away from the aggressor, or stops previous behaviour
Jump Aside (Ja)	Victim	Individual jumps aside to avoid something or someone
Crawl (Cr)	Victim	Individual moves top half of body to floor whilst facing an aggressor
Leave (Le)	Victim	Individual walks away from an aggressor
Retreat (Rt)	Victim	Individual quickly moves away from another individual (but not pursued, as in chase)
Flee (Fl)	Victim	Individual runs away from an aggressor as they are chased
Scream	Victim	Individual screams (high-pitch vocalisation) towards an aggressor

2.5. Sample exclusion and outliers

2.5.1. Testosterone

The limit of quantification for testosterone is 0.3ng/ml and the detection limit is 0.1ng/ml. Of the original 86 samples analysed, 84 produced testosterone concentrations higher than 0.1ng/ml leading to the exclusion of just two samples. Both samples were from the same individual Hlokolozo (Category 1, sample number 1534 and 1565) which, because he still had samples in three of the four categories, allowed his inclusion in the statistical analyses. In total therefore I had to exclude 10 samples from three individuals (Cancun = 5 samples, Hibe = 3 samples and Hlokolozo = 2 samples); also see section *4.3.4. Sample Selection for Hormone Extraction*). The final analyses were thus performed on 76 samples from 10 individuals.

The data from the mass spectrometer gave concentrations in ng/ml. So before running the statistical analysis, the data was converted from ng/ml to ng/g using the following formula:

Concentration (ng/g) = $\left(\frac{\text{Calculated Concentration(ng.ml)}}{0.08}\right) \text{x } 0.15$

Upon visual inspection of the data there were some clear outliers, in particular sample 693 from Mvula (18.71ng/g). I calculated the mean, the four quartiles, Interquartile Range (IQR) and the Lower and Upper Fences of the data set using Microsoft Excel 2016 to provide objective criteria for outlier removal (see Table 2). Accepting the Upper Fence of 5.94 ng/g, resulted in the exclusion of four data points from the analysis.

Table 2: Summary of outlier information

Mean	2.39
Quartile 1	0.96
Quartile 2	1.60
Quartile 3	2.95
Quartile 4	18.17
IQR	1.99
Lower Fence	-2.02
Upper Fence	5.94

Table 3: The identified outliers with their associated category and testosterone concentration.

Sample Number	Individual	Category	Concentration (ng/g)
693	Mvula	2	18.17
714	Kies	2	8.29
1474	Hwahwaza	2	8.29
2256	Hwahwaza	4	7.84

2.5.2. Cortisol

The limit of quantification for cortisol is 1.0ng/ml and the detection limit of cortisol is 0.4ng/ml. Of the 86 samples analysed only 15 had concentrations above the detection limit resulting in the exclusion of 71 samples below the detection limit. This small sample size precluded statistical analyses using cortisol samples.

Table 4: The number of samples in each dispersal category and number of samples above detection limit within that category as well as which individuals the samples were from.

Dispersal category	Number of samples	Number of samples with concentrations above detection limit	Percentage %	Individuals with samples above detection limit
Category 1	13	2	0.15	Ububibi and Hwahwaza
Category 2	24	7	0.29	Kies, Mvula, Ububibi, Cancun, Hwahwaza and Ububibi
Category 3	34	3	0.09	Hibe, Dwergie and Hlokolozo
Category 4	15	3	0.20	Mvula, Wolfie and Hwahwaza

2.6. Statistical analyses

All statistical analyses were performed using the Statistical Software, R (version 3.5.1 – Feather Spray) and Microsoft Excel 2016.

2.6.1. Peer migration

To be considered a peer migration, two individuals from the same natal group had to disperse from that natal group and then immigrate into the same group within two weeks of one another. Only individuals of which the departure date from natal group, immigration date into new group and immigration group were know, were included.

2.6.2. Age at natal dispersal

Age at natal dispersal was determined by subtracting date of birth from date of dispersal from natal group. Only individuals for which the date of birth, the date of natal dispersal, and the dispersal group were known, were used in the analysis. Many other individuals likely dispersed to non-study groups, but as we cannot say with absolute confidence that they dispersed and were not predated, they were not included in the analysis.

2.6.2.1. Adult sex ratio in natal group and age at natal dispersal

I calculated the adult sex ratio for natal dispersers in their natal group on the day that they dispersed. This was done by counting all adult males and females in the group and then dividing the number of adult males by the number of adult females.

$$(\text{adult sex ratio} = \frac{\text{number of adult males}}{\text{number of adult females}})$$

A Shapiro-Wilk test indicated that the variable “dispersal age in years” was non-normally distributed ($W = 0.763$, $p = 0.003$). Due to the non-normal nature of the data, a Spearman’s ranks correlation test was performed to further explore the relationship between age of dispersal and adult sex ratio.

2.6.2.2. Number of same sexed peers in natal group and age at natal dispersal

I counted the number of same sexed peers in a natal disperser's group and compared it to the age at which that individual dispersed. Only male peers that were born in the same year as the individual were used in the analysis. Unfortunately, the sample size was relatively small and unevenly distributed, with multiple individuals dispersing from the same group, on the same year, with the same number of same sexed peers. A Shapiro-Wilk test indicated that the variable "dispersal age in years" was non-normally distributed (W = 0.763, p = 0.003). After log transformation, the data was still non-normally distributed (W = 0.782, p = 0.004). Due to the non-normal distribution of the data, I ran a Spearman's rank correlation on the relationship between age at dispersal and number of same sex peers in natal group.

2.6.2.3. Natal group size and age at natal dispersal

I calculated the natal group size for each natal disperser on the day that they dispersed from their natal group. The data were primarily distributed into two clusters, forming a cluster with small group sizes and another with large group sizes (see Figure 2 under section 3.2.1). Therefore, I decided to divide the group size data into two non-overlapping categories: small (group size 16-22, n =6) and large (group size 33-44, n = 7). The data in the variable "age at natal dispersal" were non-normally distributed (Shapiro-Wilk test, W= 0.763, p-value = 0.003), so I used a Wilcoxon Rank Sum Test to compare age at dispersal between these two groups.

2.6.3. Testosterone and natal dispersal

I used Generalised Linear Mixed Models (GLMMs, Bates et al., 2014) to explore the relationship between testosterone and natal dispersal for individual males in different groups. Small sample size led to running GLMMs with the outliers included as well as the largest outlier excluded resulting in two separate GLMMs; Test 1 – all outliers included, Test 2 – largest outlier removed. For each analysis, I performed a Shapiro-Wilk normality test which revealed that the data for each test were not normally distributed (Test 1: W = 0.665, p-value = 7.177e-12; Test 2: W = 0.840, p-value = 1.658e-07). Due to the non-normal distribution of the data, I log transformed the data, after which the data followed a normal distribution (Test 1: W = 0.977, p-value=0.203; Test 2: W = 0.967, p-value = 0.054). Where the GLMM revealed significant differences, I used a posthoc Tukey test to further investigate the results. I originally aimed to run a GLMM with all outliers excluded, but as the data lost significance after the second test, it did not permit further investigation.

2.6.4. Testosterone concentration and standardised rank

I calculated the standardised rank of each individual on the day that a faecal sample from that individual was collected. As the testosterone concentration was calculated for the faecal samples, I was able to compare the standardised rank of an individual to the testosterone concentration of his faecal sample on the same day. Since EloRating requires a relatively large number of interactions between individuals to calculate rank, I was unable to calculate the standardised rank for 13 of my samples. This is because when an individual has recently immigrated into a group, there are often an insufficient number of interactions recorded between that particular individual and other group members. The Shapiro-Wilk test showed that the data was non-normally distributed (W = 0.840, p-value = <0.001). Due to the non-normal distribution of the data, I log transformed the data. The Shapiro-Wilk Test showed that the data was normally distributed after the log transformation (W = 0.967, p-value = 0.054). A GLMM with a Gaussian distribution was performed to test the relationship, with individual set as a random intercept to account for the fact that a different number of samples was collected for each individual.

2.6.5. Standardised rank and dispersal category

As above, I calculated the standardised rank of an individual on every day that a faecal sample for that individual was collected and used a GLMM to test whether dispersal category affected individual rank. I was unable to calculate standardised rank for 13 of the samples. The Shapiro-Wilk test showed that our data was normally distributed (w= 0.962, p-value = 0.057). A GLMM (with Gaussian distribution) was performed to test the relationship, with individual set as a random variable to account for the fact that a different number of samples was collected for each individual.

2.6.6. Natal group size and pre-dispersal testosterone concentration

GLMMs were used to determine whether pre-dispersal testosterone concentrations were related to natal group size. For each faecal sample that was collected, I calculated the size of the individual's natal group on that day. As I focussed on pre-dispersal testosterone concentrations, I only considered samples from categories one and two in the analysis. The Shapiro-Wilk test showed that our data was non-normally distributed (w = 0.891, p-value = 0.002). Due to the non-normal distribution of the data, I log transformed the data. The Shapiro-Wilk test showed that the data was normally distributed after log-transformation (w = 0.094, p-value = 0.088). A GLMM (with Gaussian distribution) was performed to test the relationship, with individual set as a random intercept to account for the fact that a different number of samples was collected for each individual.

3. RESULTS

3.1 Peer migration

A total of 45 males were born in the studied population from 2011 to 2013. Of these 45 males, 10 dispersed with peers (peer dispersal), while 3 remained in their natal group after peers of the same age had emigrated. These three males (Rooikat, Vakie and Hola) all disappeared from their natal group approximately 8 months later, although we can only confirm that one (Rooikat) dispersed. Of the remaining 32 males, 12 died before dispersing from their natal group, two dispersed by themselves to study groups, one formed part of a splinter group (the splinter group was not studied) and the remaining 17 natal males' fates were unknown. Nine of the 17 males with unknown fates, likely participated in peer dispersal due to the close timing of their disappearance with other individuals, but we cannot be sure as they did not disperse to other study groups. Individuals did not necessarily disperse at the same time (although some did), but within a week or two and to the same group.

3.2. Age at natal dispersal

The average age of natal dispersal in our population was 4.71 years, with a minimum age of 4.40 years and a maximum age of 5.40 years (n = 14, sd = 0.31 years).

Table 5: Life history data for the 14 male vervet monkeys which were used for determining age at natal dispersal in our study troops. Data include the birth date, natal troop, date of emigration, troop into which each individual immigrated, the date of immigration and the age in both days and years of each successful dispersal.

Individual	Date of birth	Birth group	Date of departure from natal group	Immigration group	Date of immigration	Age (days) at dispersal	Age (years) at dispersal
Hwahwaza	2011/09/16	AK	2016/06/04	BD	2016/06/08	1723	4.72
Ububhibhi	2011/11/21	AK	2016/05/24	BD	2016/05/28	1646	4.51
Unwabo	2012/10/22	AK	2017/05/03	BD	2017/05/04	1654	4.53
Nyoni	2012/10/22	AK	2017/05/16	BD	2017/05/16	1667	4.57
Rheban	2012/10/27	NH	2017/12/05	BD	2017/12/05	1865	5.11
Hlokoloza	2012/12/23	AK	2017/05/23	BD	2017/05/24	1613	4.41
Avon	2013/11/11	KB	2018/04/06	NH	2018/05/14	1607	4.40
Spook	2011/10/18	BD	2016/06/16	CR	2016/06/23	1703	4.67
Poeding	2011/11/11	BD	2016/06/11	CR	2016/06/15	1674	4.59
Ogies	2011/11/02	BD	2016/06/03	CR	2016/06/10	1675	4.59
Noktober	2011/10/26	BD	2016/06/11	CR	2016/06/15	1690	4.63
Rooikat	2011/12/05	BD	2017/04/27	CR	2017/05/10	1970	5.40
Akkedis	2011/11/07	BD	2016/05/28	CR	2016/06/10	1664	4.56
Vincent	2011/10/01	LT	2016/12/22	BD	2017/02/13	1909	5.23

3.2.1. Natal group size and age at natal dispersal

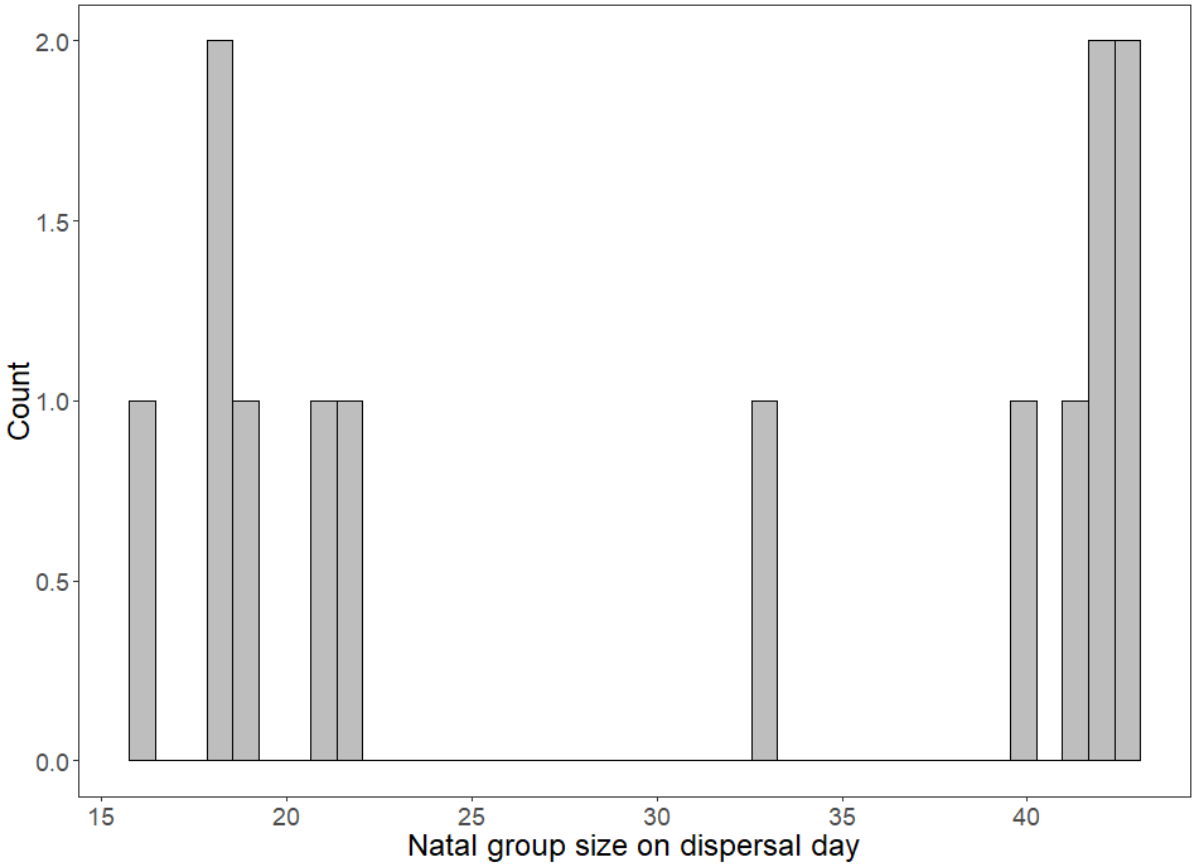


Figure 2: Histogram showing distribution of natal dispersers at different group sizes. The samples formed two clear clusters of small and large groups, with the group size of 33 included with the larger cluster for analysis.

A Wilcoxon Rank Sum test revealed that individuals in the larger natal groups (Category 2, 33-44 individuals) dispersed significantly later than individuals in the smaller natal groups (Category 1, 16-22 individuals) (W = 6, p-value = 0.038, Figure 3).

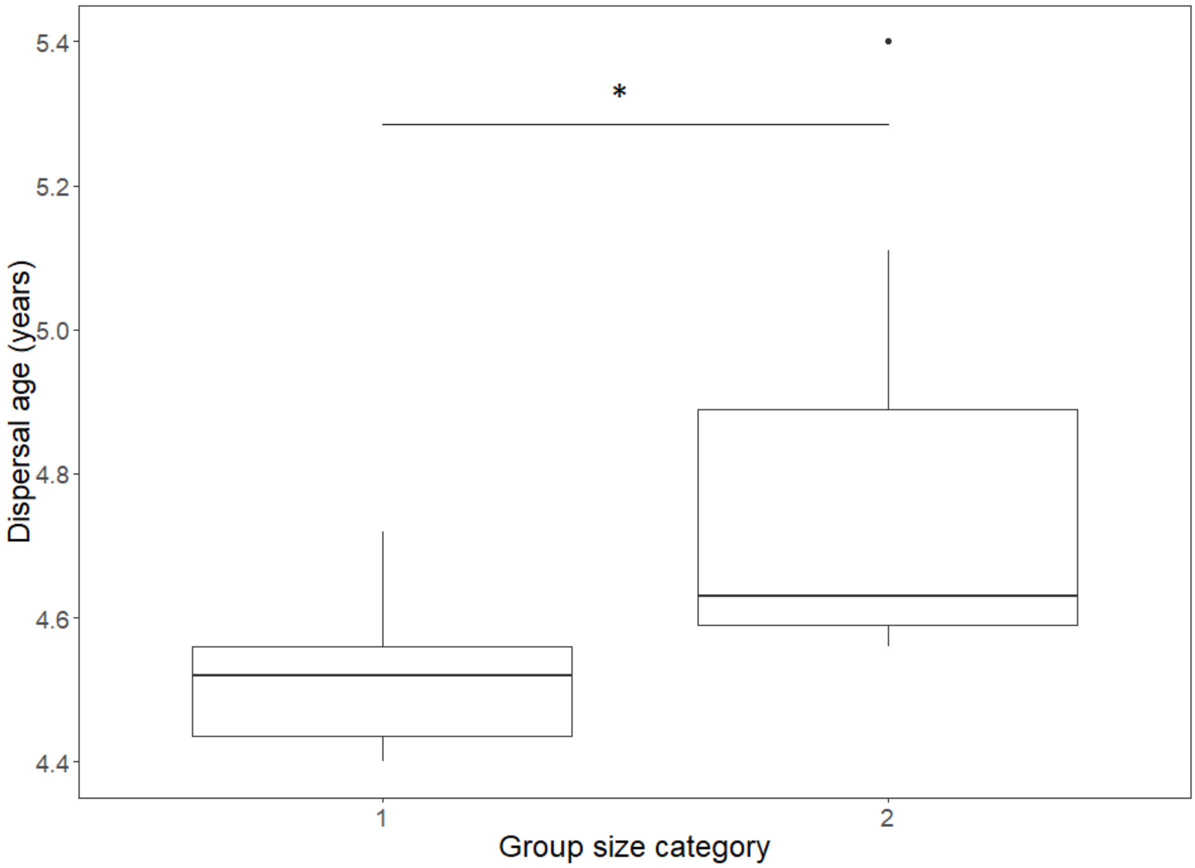


Figure 3: Box and whisker plot showing median (4.590) and interquartile range (0.140) of age at natal dispersal (years) by group size category. Group size category 1 = 16-22 individuals; Group size category 2 = 33-44 individuals. Individuals in Group size category 2 dispersed significantly later than individuals in group size category 1 (W = 6, p-value = 0.038).

3.2.2. Adult sex ratio in natal group and age at natal dispersal

A Spearman’s rank correlation indicated no significant correlation between adult sex ratio in natal group and age at dispersal from natal group (S=363.470, p-value = 0.996, rho = 0.001, see Figure 4).

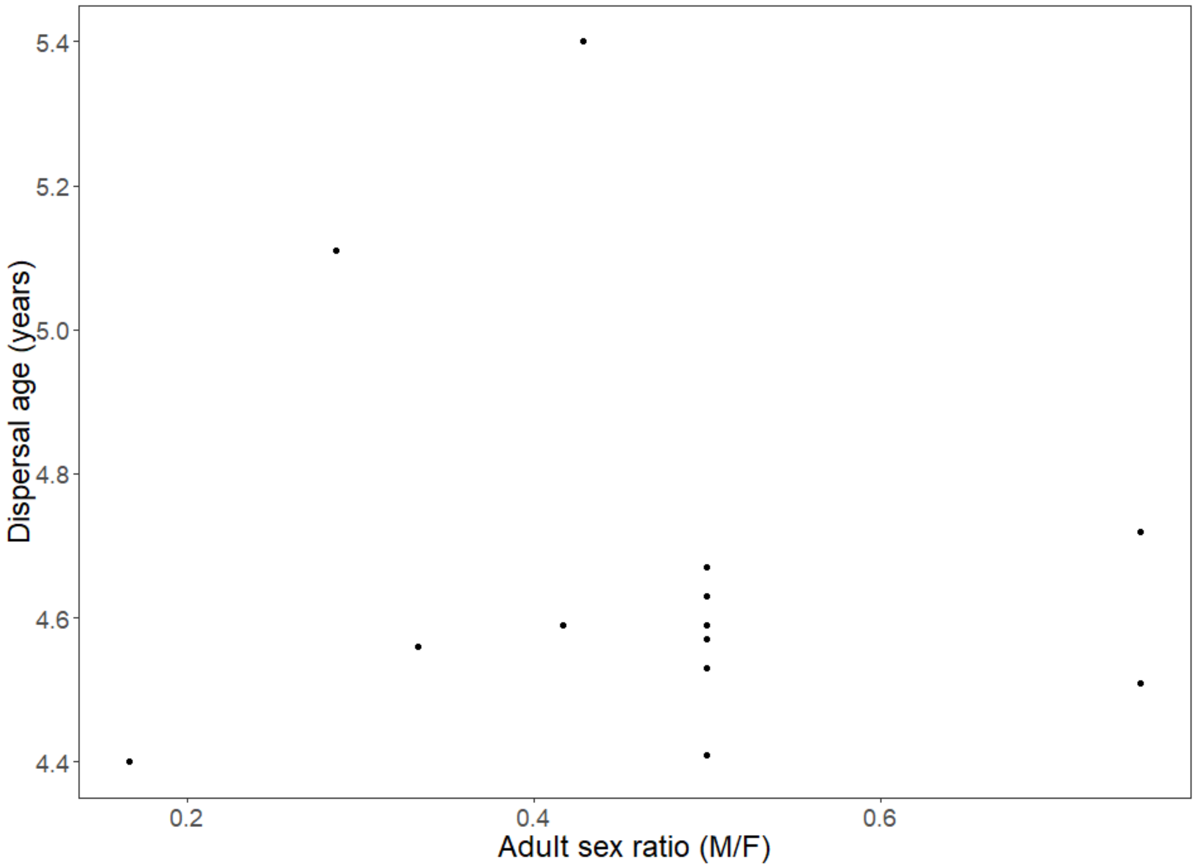


Figure 4: Graph showing non-significant relationship between age at natal dispersal (years) and adult sex ratio in natal group.

3.2.3 Number of same sexed peers in natal group and age at natal dispersal

A Spearman's Rank correlation found no significant relationship between the number of same sexed peers in the natal group and age at natal dispersal (S = 285.090, p = 0.477, rho = 0.217, see Figure 5).

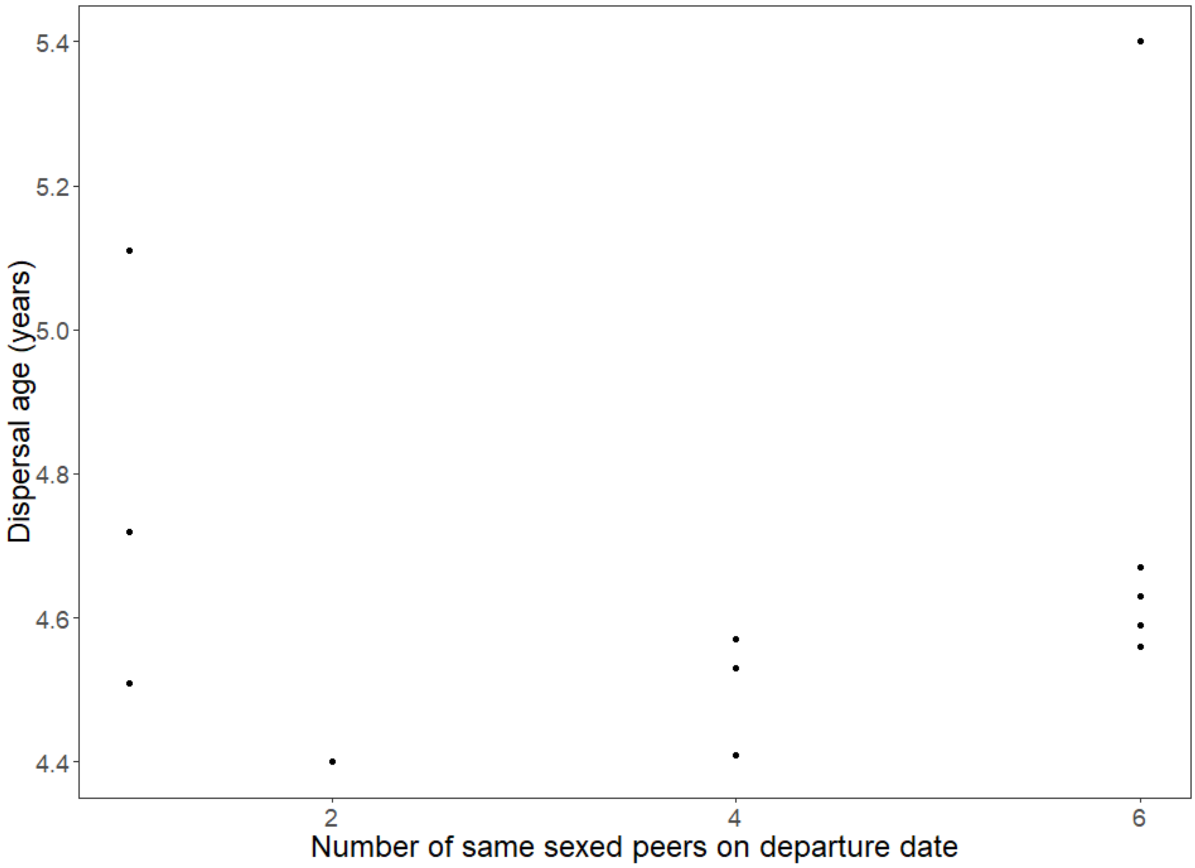


Figure 5: Graph showing non-significant relationship between number of same sexed peers in natal group on date of departure and age at natal dispersal (years).

3.3. Testosterone and natal dispersal

Test 1 – All outliers included

When all outliers were included, Category had a significant effect on testosterone levels in male vervets with Category 3 (0-3 months post-dispersal) being the only significant covariate (Table 6). A posthoc Tukey test (Table 7) revealed that Category 3 had significantly ($p < 0.05$) lower levels of testosterone compared to Category 2 (0-3 months before dispersal, Figure 6).

Table 6: Results of the GLMM comparing the testosterone concentrations between the four categories of 1 to 4. Category 1 = 14 to 10 months before dispersal, Category 2 = 3 to 0 months before dispersal, category 3 = 0 to 3 months after dispersal, category 4 = 10 to 14 months after dispersal. All outliers were present in this analysis (** indicates significance at α = 0.01)

Fixed Effects	Estimate	SE	t-value	Pr(>|z|)
Intercept	0.73423	0.23273	3.15488	0.00160
Condition – Compared to Category 2				
Category 1	0.12233	0.30837	-0.39671	0.69158
Category 3	**0.61337**	**0.23113**	**-2.65374**	**0.00796****
Category 4	0.32565	0.28422	-1.14578	0.25188
Random effects:	Variance	Standard deviation		
Individual	0.2286	0.4781		

Table 7: Table showing results from Tukey posthoc Test, comparing testosterone concentrations for all combinations of dispersal category. All outliers present in this analysis (* indicates significance at α = 0.05). Category 1 = 14 to 10 months before dispersal, Category 2 = 3 to 0 months before dispersal, category 3 = 0 to 3 months after dispersal, category 4 = 10 to 14 months after dispersal.

Categories	Estimate	SE	z value	Pr(>|z|)
1 – 2	-0.1223	0.3084	-0.397	0.9785
3 – 2	**-0.6134**	**0.2311**	**-2.654**	**0.0388***
4 – 2	-0.3257	0.2842	-1.146	0.6573
3 – 1	-0.4910	0.3042	-1.614	0.3663
4 – 1	-0.2033	0.3388	-0.600	0.9310
4 – 3	0.2877	0.2799	1.028	0.7299

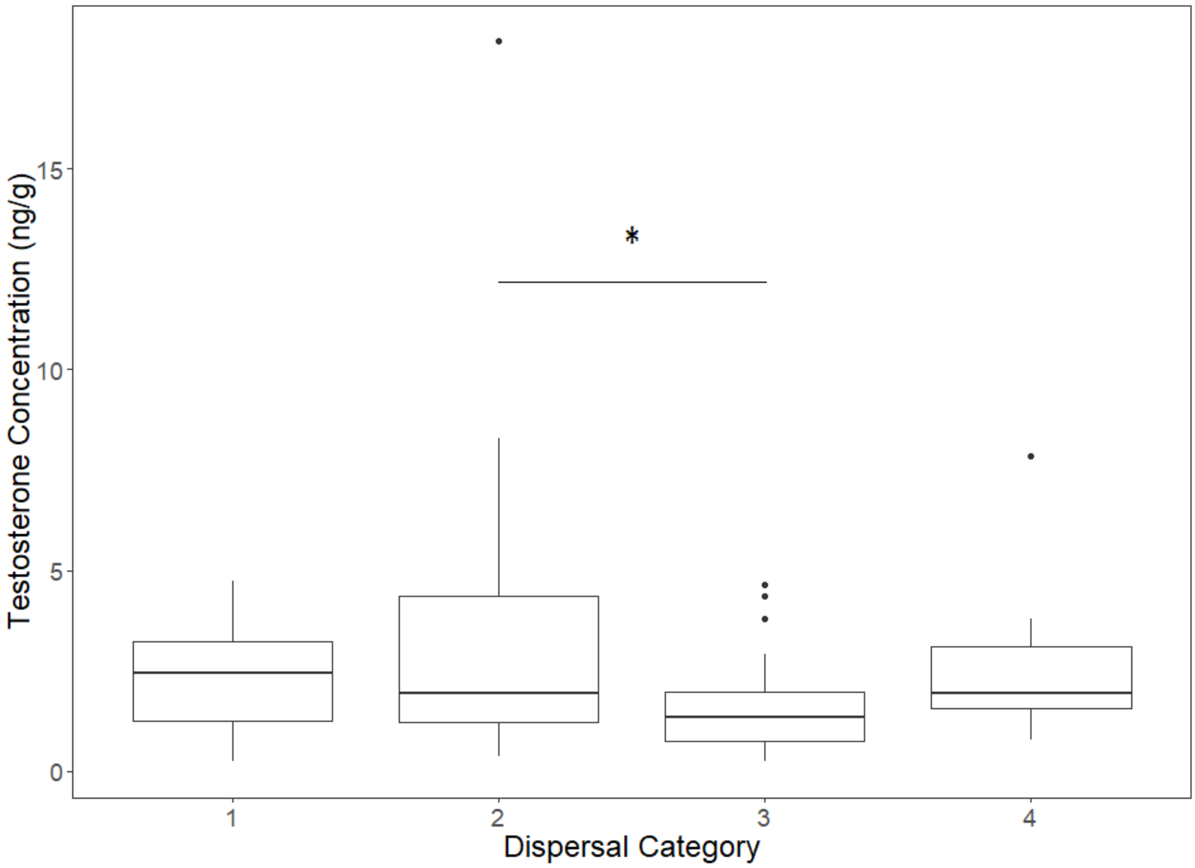


Figure 6: Box and Whisker Plot showing the median (1.601), interquartile range (1.991) and 95% confidence interval of testosterone concentrations within each of the four categories of time relevant to a dispersal event. All outliers are included. Category 1 = 14-10 months pre-dispersal; category 2 = 3-0 months pre-dispersal; category 3 = 0-3 months post-dispersal and category 4 = 10-14 months post-dispersal.

Test 2 – Largest outlier removed

After removing the largest outlier (693, Mvula), a GLMM showed that Category continued to have a significant effect on testosterone levels in male vervets with Category 3 (0-3 months post-dispersal) still being the only significant covariate (Table 8).

However, a posthoc Tukey test (Table 9) revealed that after removing the largest outlier, there was no longer a significant difference between testosterone levels in Category 2 and Category 3 (see Table 9)

Table 8: Results of GLMM comparing the testosterone concentrations between the four categories of 1 to 4. Category 1 = 14 to 10 months before dispersal, Category 2 = 3 to 0 months before dispersal, category 3 = 0 to 3 months after dispersal, category 4 = 10 to 14 months after dispersal. The largest outlier was removed from the analysis (* indicates significance at α = 0.05)

Fixed Effects	Estimate	SE	t -value	Pr(>|z|)
Intercept	0.65168	0.22410	2.90789	0.00363
Condition – Compared to Category 2				
Category 1	-0.06032	0.30220	-0.19963	0.84176
Category 3	**-0.53529**	**0.22847**	**-2.34291**	**0.01913****
Category 4	-0.20694	0.28150	-0.73512	0.46226
Random effects:	Variance	Standard deviation		
Individual	0.1892	0.4349		

Table 9: Table showing results from Tukey posthoc Test, comparing testosterone concentrations for all combinations of dispersal category. Only the largest outlier was removed for this analysis. Category 1 = 14 to 10 months before dispersal, Category 2 = 3 to 0 months before dispersal, category 3 = 0 to 3 months after dispersal, category 4 = 10 to 14 months after dispersal.

Categories	Estimate	SE	z value	Pr(>|z|)
1 – 2	-0.06033	0.30220	-0.200	0.9971
3 – 2	-0.53530	0.22847	-2.343	0.0867
4 – 2	-0.20694	0.28151	-0.735	0.8813
3 – 1	-0.47497	0.29607	-1.604	0.3721
4 – 1	-0.14661	0.33067	-0.443	0.9704
4 – 3	0.32385	0.27298	1.203	0.6212

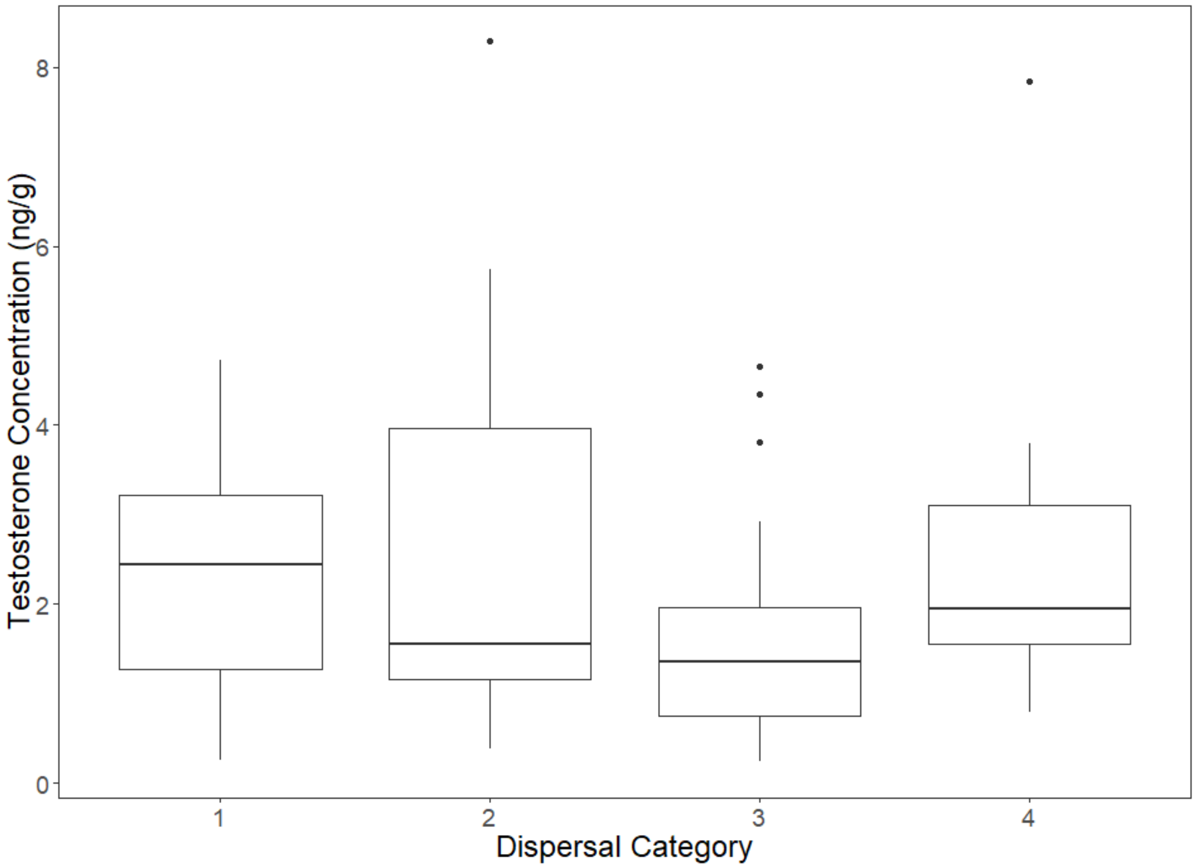


Figure 7: Box and Whisker Plot showing the median (1.577) and interquartile range (1.979) of testosterone concentrations within each of the four categories of time relevant to a dispersal event. The largest outlier was removed. Category 1 = 14 to 10 months before dispersal, Category 2 = 3 to 0 months before dispersal, category 3 = 0 to 3 months after dispersal, category 4 = 10 to 14 months after dispersal.

3.4. Testosterone concentration and standardised rank

The GLMM showed that there was no significant relationship between standardised rank and testosterone concentration in our samples (see Table 10 and Figure 8).

Table 10: Results of GLMM comparing standardised rank to testosterone concentration in male vervet monkeys.

Fixed Effects	Estimate	SE	t value	Pr(>|z|)
Intercept	0.1323651	0.3466546	0.3818356	0.7025833
Condition – Compared to Standardised Rank				
Standardised Rank	0.4103923	0.5474836	0.7495975	0.4534972

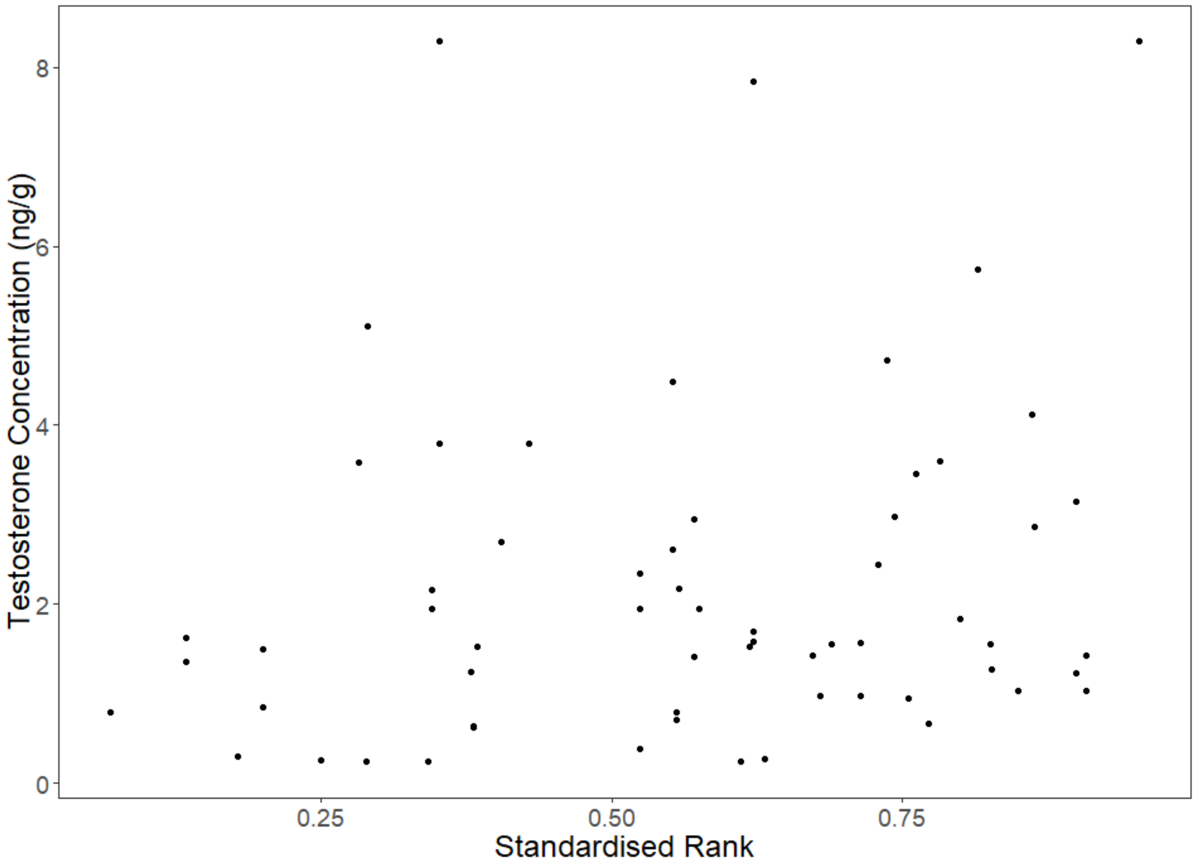


Figure 8: Scatterplot showing the non-significant relationship between Standardised Rank and Testosterone concentration.

3.5. Standardised rank and dispersal category

Table 11 shows the results obtained from the GLMM examining the relationship between standardised rank and dispersal category. The GLMM shows a significant relationship between Category 2 and Category 3 ($p < 0.0001$). To further examine this relationship, a Tukey's posthoc test was performed. The results from the Tukey's test (Table 12) show a significant difference between Categories 2 and 3 ($p < 0.01$), with standardised ranks being lower in Category 3 than in Category 2, (see Figure 9).

Table 11: Table showing the results of GLMM comparing rank and category. Category 1 = 14 to 10 months before dispersal, Category 2 = 3 to 0 months before dispersal, category 3 = 0 to 3 months after dispersal, category 4 = 10 to 14 months after dispersal.

Fixed Effects	Estimate	SE	t value	Pr(>|z|)
Intercept	0.64887090	0.06589527	9.847003	0.000000000
Condition - Compared to Category 2				
Category 1	-0.08157649	0.06132363	-1.330262	0.1834320068
Category 3	**-0.18217258**	**0.05131816**	**-3.549866**	**0.0003854274****
Category 4	-0.09247147	0.05945132	-1.555415	0.1198472891
Random Effects	Variance	Standard Deviation		
Individual	0.03049	0.1746		

Table 12: Table showing results from Tukey posthoc Test, comparing standardised rank for all combinations of dispersal category. (**indicates significance at α 0.01), Category 1 = 14 to 10 months before dispersal, Category 2 = 3 to 0 months before dispersal, category 3 = 0 to 3 months after dispersal, category 4 = 10 to 14 months after dispersal.

Categories	Estimate	SE	z value	Pr(>|z|)
1 – 2	-0.08158	0.06132	-1.330	0.5394
3 – 2	**-0.18217**	**0.05132**	**-3.550**	**0.0020****
4 – 2	-0.09247	0.05945	-1.555	0.4002
3 – 1	-0.10060	0.06492	-1.549	0.4038
4 – 1	-0.01089	0.06966	-0.156	0.9986
4 – 3	0.08970	0.06703	1.338	0.5343

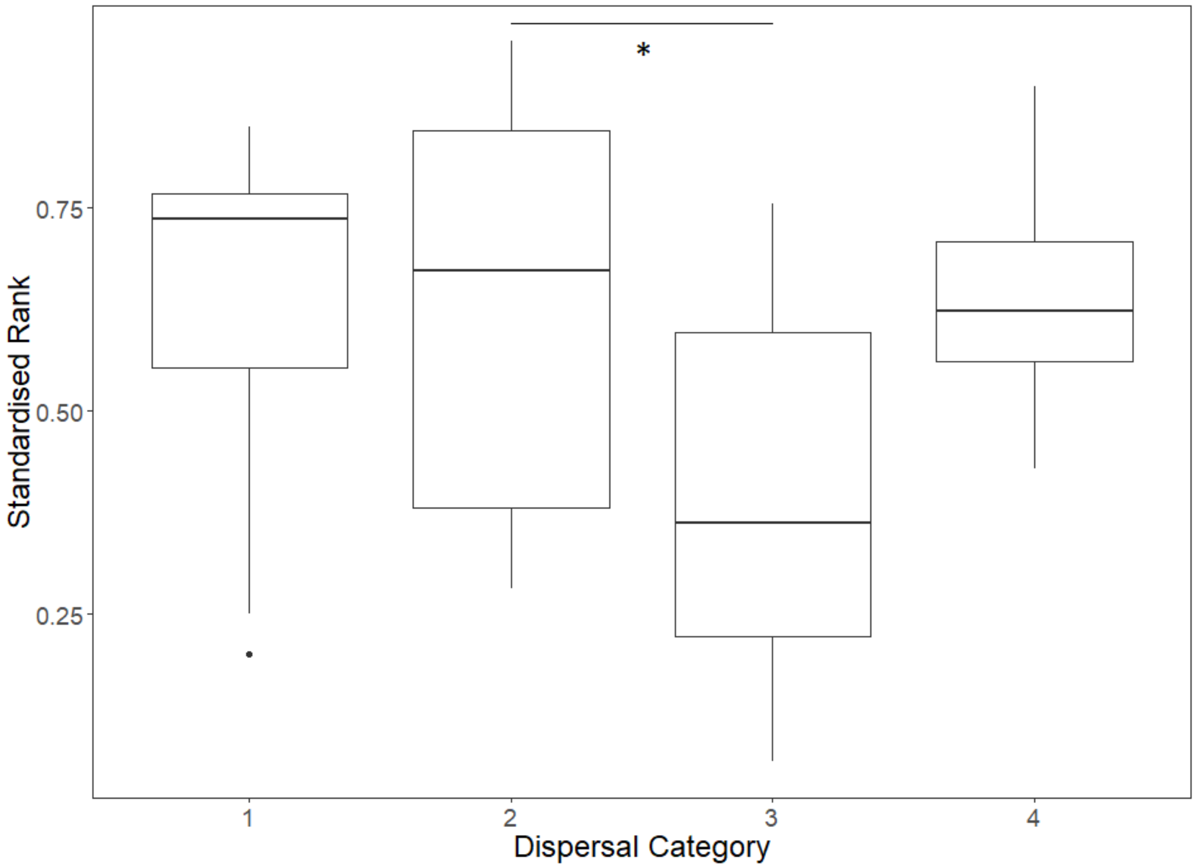
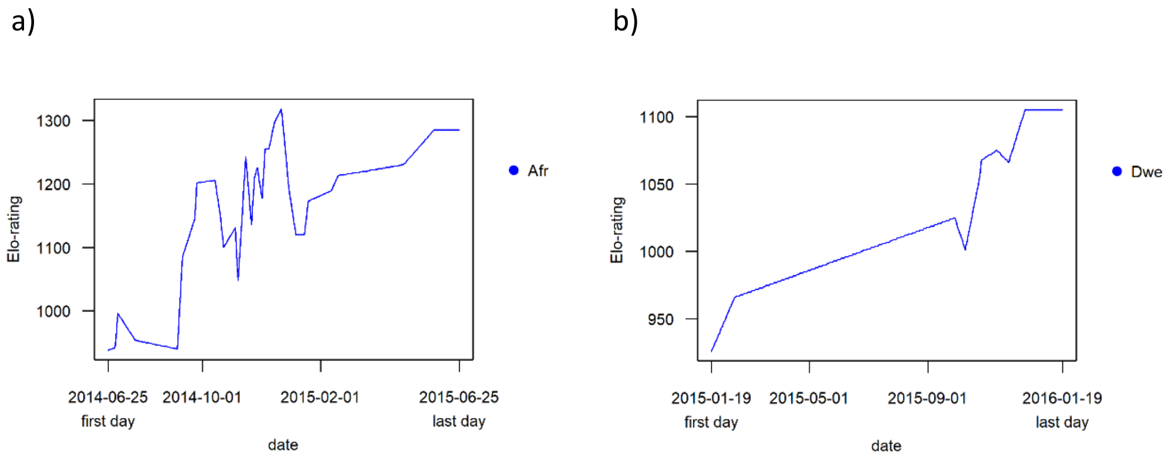


Figure 9: Box and Whisker Plot showing the relationship between Standardised Rank and Dispersal Category (Median = 0.573; Interquartile range = 0.373). Standardised rank in dispersal category 3 was significantly lower than in dispersal category 2 (p-value < 0.01). .Category 1 = 14 to 10 months before dispersal, Category 2 = 3 to 0 months before dispersal, category 3 = 0 to 3 months after dispersal, category 4 = 10 to 14 months after dispersal.

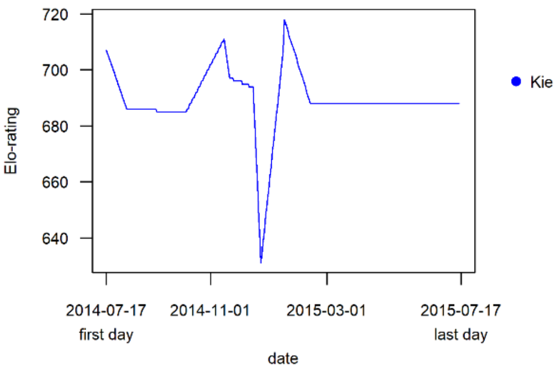
Table 13: Table showing Elo Rating in the periods 12 and 3 months before dispersal and on the day of dispersal. A higher Elo rating responds to a higher rank in the group. Y = Yes; N = No.

Individual	Elo Rating 12 Months Before Dispersal	Elo Rating 3 Months Before Dispersal	Elo Rating the day of Dispersal	Increase (12-3)	Increase (12-0)	Increase (3-0)
Afrikaans	906	1213	1285	Y	Y	Y
Dwergie	926	1001	1105	Y	Y	Y
Hibe	725	1248	1233	Y	Y	N
Hlokolozo	741	917	923	Y	Y	Y
Hwahwaza	1026	1186	1118	Y	Y	N
Kies	707	688	688	N	N	N
Mvula	579	616	682	Y	Y	Y
Nyoni	745	854	873	Y	Y	Y
Ububhibhi	922	1150	1166	Y	Y	Y
Unwabo	1070	929	1032	N	N	Y
Wolfie	422	496	496	Y	Y	N

The following graphs (Figure 10, a to k) show the Elo Rating (and subsequently rank change) of 11 natal dispersers over a 12-month period, from 12 months before dispersal to the day of dispersal. A higher Elo ranking responds to a higher rank in the group.

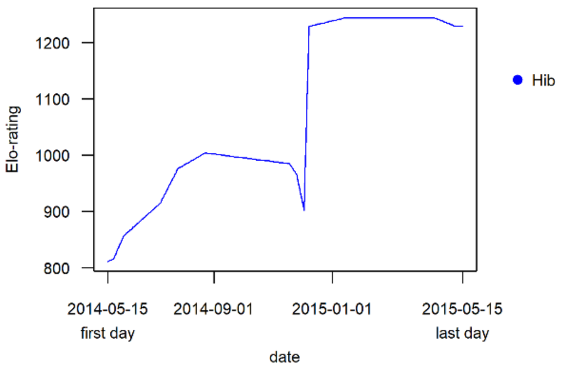


c)



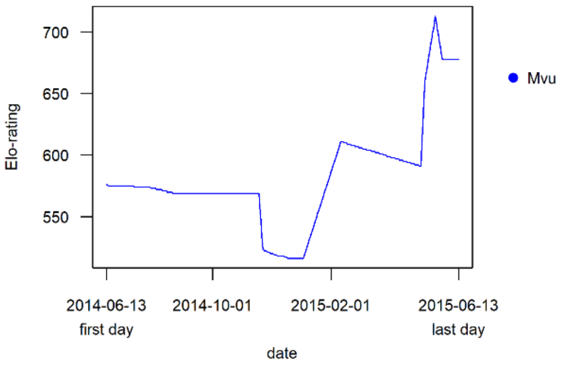
Elo-rating
720
700
680
660
640
2014-07-17
first day
2014-11-01
2015-03-01
2015-07-17
last day
date
Kie

d)



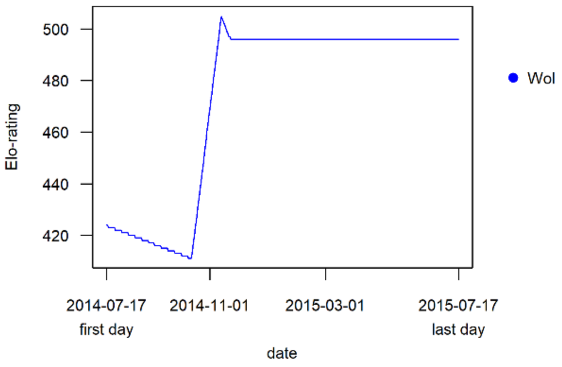
Elo-rating
1200
1100
1000
900
800
2014-05-15
first day
2014-09-01
2015-01-01
2015-05-15
last day
date
Hib

e)



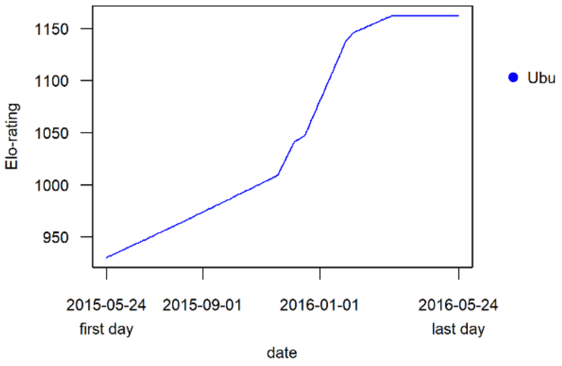
Elo-rating
700
650
600
550
2014-06-13
first day
2014-10-01
2015-02-01
2015-06-13
last day
date
Mvu

f)



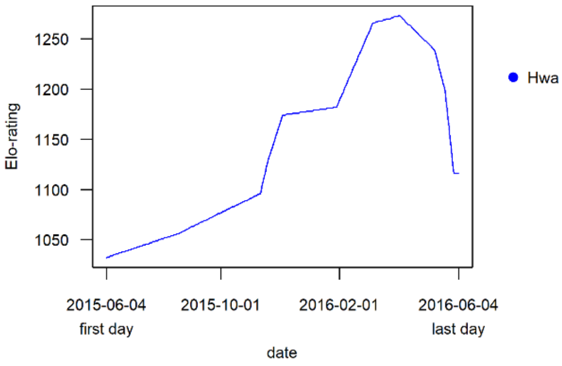
Elo-rating
500
480
460
440
420
2014-07-17
first day
2014-11-01
2015-03-01
2015-07-17
last day
date
Wol

g)



Elo-rating
1150
1100
1050
1000
950
2015-05-24
first day
2015-09-01
2016-01-01
2016-05-24
last day
date
Ubu

h)



Elo-rating
1250
1200
1150
1100
1050
2015-06-04
first day
2015-10-01
2016-02-01
2016-06-04
last day
date
Hwa

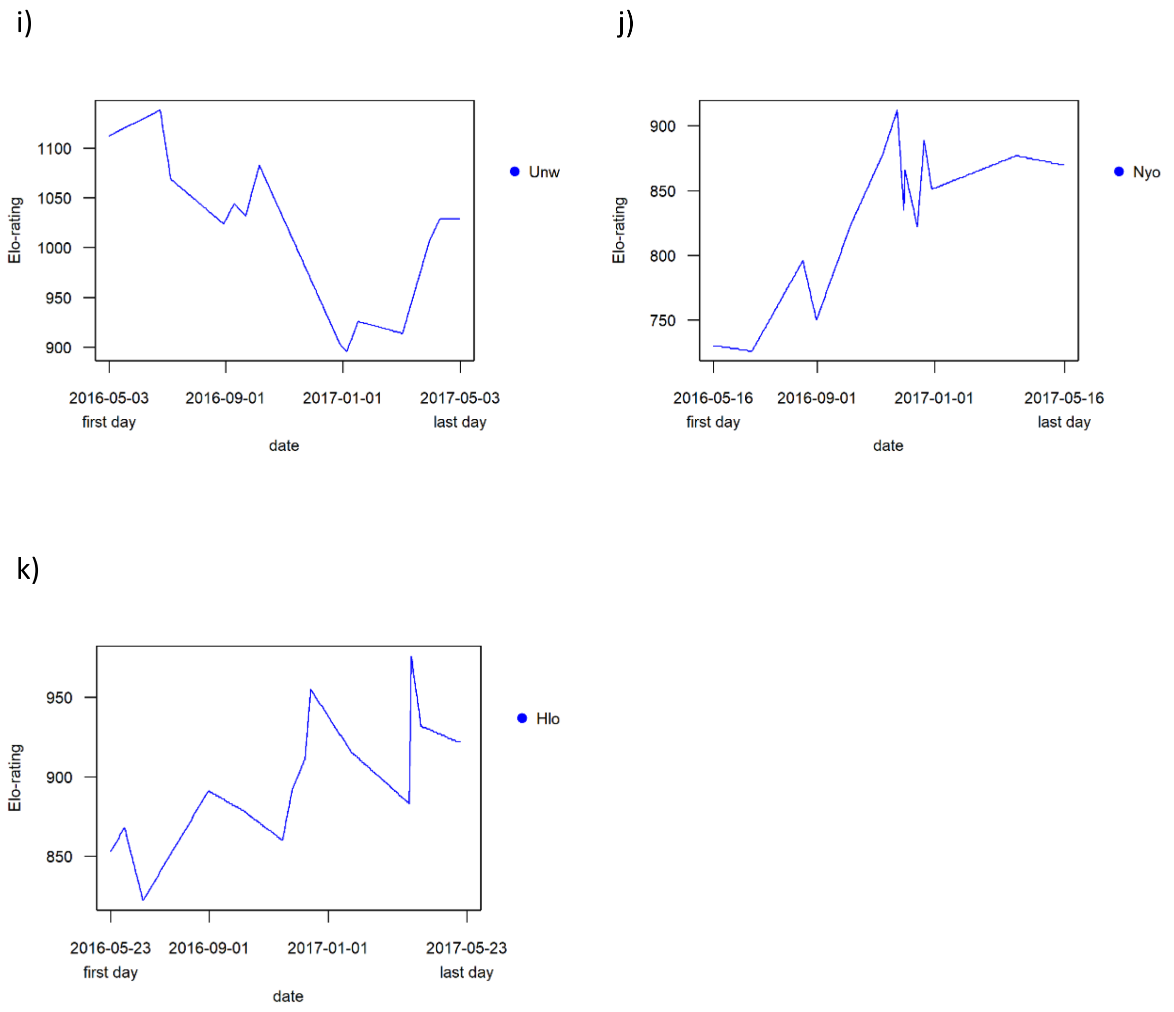


Figure 10: Elo ratings of 11 natal males over a 12-month period, from 12 months before dispersal, to the day of dispersal from their natal groups. A higher Elo ranking responds to a higher rank in the group. Nine out of 11 natal males showed increasing rank over the 12-month period. Note that the scales of the y-axis values are not standardised between the graphs.

3.6. Natal group size and pre-dispersal testosterone concentration

Figure 11 shows the relationship between natal group size and testosterone concentration. A GLMM (see Table 14) revealed that the number of individuals in the natal group significantly and positively predicted the testosterone concentrations of males before natal dispersal (estimate = 0.05, standard error = 0.016, t-value = 3.01, p-value = 0.003).

Table 14: Results of GLMM comparing natal group size to testosterone concentration.

Fixed Effects	Estimate	SE	t value	Pr(>|z|)
Intercept	-0.92302470	0.56407057	-1.636364	0.101763454
Condition – Compared to Natal Group Size				
Natal group size	0.04966641	0.01646127	3.017168	0.002551483

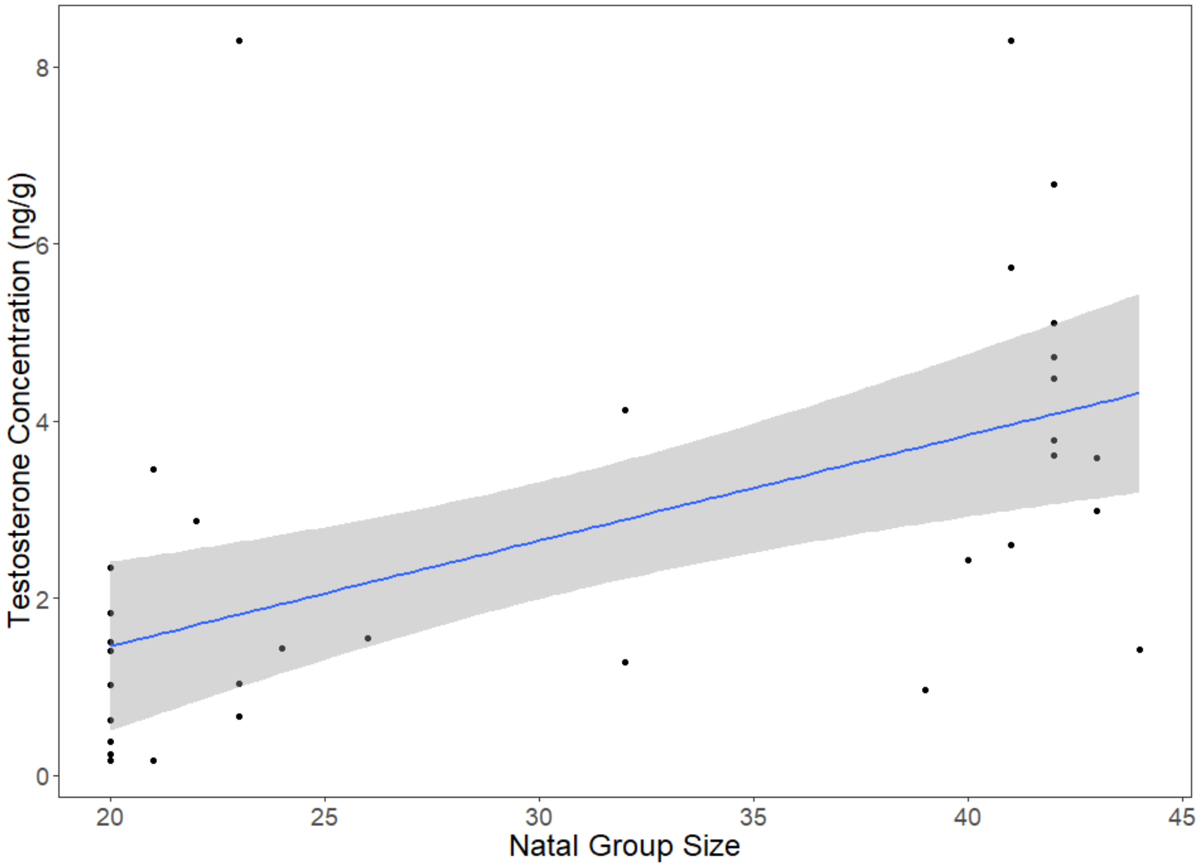


Figure 11: Relationship between natal group size (x-axis) and faecal testosterone concentration (y-axis) in dispersing males. Natal group size significantly and positively predicted testosterone concentration (p-value = 0.002).

4. DISCUSSION

In this study, I attempted to examine both the intrinsic and extrinsic correlates of dispersal in male vervet monkeys by measuring faecal testosterone (fT) and faecal cortisol (fC) levels before and after dispersal, while including the effects of group size and demography of the natal troops. The difficulties of sampling dispersing individuals, in particular males that disperse to unhabituated groups or unhabituated males that disperse into one of the study groups, restricted the study to a subset of natal dispersers that dispersed from one of our study groups to another one of our study groups.

4.1. Age at natal dispersal

The average age at natal dispersal of males in our population of vervets was 4.71 years and ranged from 4.40 to 5.40 years. Henzi and Lucas (1980) reported a similar age range for natal dispersal in their population of vervets, but Cheney and Seyfarth (1983) reported much more variation in their population, with only a small percentage of males dispersing before attaining 5 years of age. Most of the natal males in the latter study population dispersed between the age of 5 and 6 years, while some only dispersed after 6 years of age. This delay in natal dispersal could possibly be due to the high levels of predation that were observed in their study population. Cheney et al. (1981) conservatively attribute 30% of deaths in their study population to predation but estimate that it could be as high as 58%. Jack et al., (2012) suggested that high levels of predation may force natal males to delay their dispersal until they have matured and developed more physically, giving them a better opportunity to survive a dispersal event.

Although predation rates have not been described in my study population, mortality due to predation appears to be low (personal observation). To the best of my knowledge, only three deaths have been attributed to predators in over 6 years of data collection. However, unexplained disappearances of monkeys, especially adult females and juveniles, may also be due to predation and hence predation levels are certainly underestimated. Two vervets (an adult female and a juvenile) were killed by domestic dogs used by poachers for bushmeat hunting, while a third vervet was eaten by a python. The level of predation in our population was likely affected by the consistent presence of observers with our troops as the monkeys were followed six days a week. Only a few studies have reported predation rates and those reported by Henzi and Lucas (1980) are likely an underestimate given their study site was a small, 46ha nature reserve in South Africa, situated slightly north of the city of Durban's central business district and is surrounded by light industry and residential areas.

Compared to other *Cercopithecidae* primates, the age range of dispersal in vervets is narrow. Age at natal dispersal in rhesus macaques has been shown to range from 2.50 – 8.00 years (Weiβ et al., 2016), in ursine colobus monkeys from 2.50 to 7.50 years (Teichroeb et al., 2011) and in yellow baboons from 6.81 to 13.42 years (Alberts and Altmann, 1995). In other, more distantly related primates, age at natal dispersal has been shown to vary even more; natal dispersal in two populations of white-faced capuchins in Costa Rica varied between 1.20 and 11.30 years (Perry et al., 2017) and 1.58 to 11.17 years (Jack et al., 2012).

Jack et al. (2012) suggests that in species where little variation in age at natal dispersal is observed, a physiological trigger (such as hormones) is likely to be the proximate cue for natal dispersal. Accordingly, vervets would be predicted to have a physiological trigger. Although this does not necessarily exclude the possibility of environmental changes also affecting dispersal decisions, it does seem to suggest that a physiological change has to occur before or alongside environmental changes which then further encourages (or discourages) natal dispersal.

4.2. Natal group size and age at natal dispersal

Of all the variables I investigated, the only one that significantly predicted the dispersal age of natal males was natal group size; males from larger natal groups dispersed significantly later than males from smaller natal groups (Figure 3). Resource competition is a known cost of group living as individuals compete for the same resources (see Clutton-Brock, 2016, pp 61-63, for a review of the costs of group living). It has however been shown that larger groups can displace smaller groups and consequently monopolise the best foraging territory (Robinson, 1988). Despite the increased competition among group members over the same resources, the ability of larger groups to monopolise territories might be beneficial enough for natal males from larger groups to delay dispersal as to continue to benefit from their improved competitive ability (and consequently access to resources) of the larger group over that of smaller groups.

It may also be that larger groups may afford natal males more pre-dispersal mating opportunities and, by dispersing later, natal males will increase their possibility of mating before participating in natal dispersal (Minkner et al., 2018). This could, however, be dependent on sex ratio in the natal group, which was not found to have an effect on dispersal age in our population of vervets (see section 6.3.). Additionally, the number of mating opportunities natal males have in their natal groups may influence dispersal age. However, natal male vervets have been shown to father only a small percentage of the total offspring in their natal group (Minkner et al., 2018) and therefore it may be unlikely that natal male vervets will delay dispersal for the opportunity to mate in the natal group. The delay in dispersal could however be related to mating success, rather than reproductive success. In a population of yellow baboons, Alberts and Altmann (1995) found that natal males that successfully mated in their natal group, remained in their natal groups much longer than natal males that did not. In contrast to my results, studies on other primate species (white-faced capuchins: Jack et al., 2012; Rhesus Macaques: Weiβ et al., 2016) did not find a significant relationship between dispersal age of natal males and natal group size. Although this cannot be confirmed, it is likely that the small sample size, as well as the unequal distribution of the samples, may have affected my results. Of the 13 individuals I was able to use for the analysis, five individuals from BD dispersed to CR during the same year (2016) and three individuals from AK dispersed to BD during the same year (2017). During those specific years, BD fell into the large group category, having 40 or more individuals, while AK fell into the small group category, having 22 or less individuals. My data is consequently highly skewed to those categories and the possibility exists that other factors could have affected the dispersal decision of the individuals. Further studies with larger samples would be needed to confirm this effect in vervets.

Drickamer and Vessey (1973) found that in rhesus macaques, males tended to disperse from smaller to larger groups (although this effect was not statistically significant). Similarly, Jack et al. (2012) found that despite being a non-significant predictor, group size did affect natal dispersal and natal males were more likely to disperse from smaller groups than from larger ones. They also found that when the variable groups size was removed from the model, that occurrence of a takeover (the only significant predictor variable) no longer accurately predicted which males would not disperse. This indicates that group size is an important variable in capuchin natal dispersal, but the different social systems of capuchins and vervets should be borne in mind, with capuchins dispersing over a much larger age range than vervets in my study population.

4.3. Adult sex ratio, number of same sexed peers and age at natal dispersal

Unlike natal group size, neither adult sex ratio in the natal group, nor number of same sexed peers had a significant effect on the dispersal age of natal males. Studies in other primates, such as white-faced capuchins (Jack et al., 2012) and rhesus macaques (Weiβ et al., 2016) also failed to find a relationship between these variables. As with group size, both variables can be related to competition for access to females in gregarious species. Vervet males have been shown to successfully mate and father offspring in their natal group (Minkner et al., 2018) and therefore factors that determine natal group mating competition may influence their dispersal behaviour. One can argue that natal males living in groups with a low number of males to females, might stay in these groups longer as they will have more mating opportunities. Similarly, natal males in groups with a large number of males to females, might disperse earlier as they would have fewer mating opportunities. A similar argument can be made for natal males that have many same sexed peers in their natal group. However, while Minkner et al. (2018) did find that natal males do father offspring in their natal groups, the percentage was low (4.3% of the offspring) making it unlikely that a natal male will postpone dispersal. It is possible that rank may also affect these decisions; high ranking natal males might have a better opportunity to father offspring in their natal troop compared to lower ranking males. In the same study however, Minkner et al. (2018) found that male mating success was not related to male dominance rank and that males of different ranks mated equally often. This limited mating opportunity, apparently unrelated to rank, might help explain why no relationship was found between either number of same sexed peers or the natal group adult sex ratio and age at dispersal in my study. Consistent with these findings, Jack et al. (2012) found that the number of maternal brothers was not a significant predictor variable for dispersal in white-faced capuchins. While my analyses differed from Jack et al.

(2012), which included a wider range of peers, my results nevertheless showed that the number of same sexed peers was not significantly related to age at natal dispersal.

It would be interesting to know whether males dispersed to groups with a more favourable adult female to male adult sex ratio as reported for rhesus macaque males (Drickamer and Vessey 1973). This could indicate that males are attracted to unrelated females but it could also suggest that a key trigger of dispersal could be the perceived ease of access to females in a group with a larger female to male ratio. A superficial comparison of the adult sex ratio in the natal group versus the immigration group did not indicate any clear trends; of the 7 individuals, three dispersed to groups with smaller adult male to female ratios than their natal groups and four dispersed to groups with larger ratios (a ratio of 1 means one male to one female and a ratio of 0.50 means one male to two females, see Appendix E for the data). Henzi and Lucas (1980) described similar results in their population of vervets and found that the number of sexually mature females did not influence an individual's (n=13 individuals) likelihood of joining a particular group. It is important to note, however, that this study did not distinguish between natal and secondary dispersers, and only compared the number of sexually mature females between the two groups. Therefore, while adult sex ratio did not appear to affect dispersal age in my study, it is still unclear whether the sex ratio of the immigration group might affect immigration decisions in this species.

4.4. Cortisol

I had predicted that there would be an increase in fC levels after dispersal as dispersing individuals are predicted to experience increased levels of stress linked to dispersal (Marty et al., 2017). I also predicted that these cortisol levels will not remain elevated for long and that they will return to baseline levels within a few days of the dispersal event (Akinyi et al., 2017). Unfortunately, I was unable to detect cortisol in the majority of samples across the dispersal categories, with only 14 out of 86 samples (16%) having detectable levels. There are a few possibilities as to why so few samples had detectable levels of cortisol, beginning with the timing of the sample collection.

4.4.1 Potential limited timing of stress response in vervets

The stress response in primates has been shown to be short-lived and hence the timing of the collection of faecal samples is important. In captive vervet monkeys increased levels of fGCM (faecal glucocorticoid metabolites) have been shown to return to baseline levels within three days (43 to 74 hours) after the stressful event is experienced (Young et al., 2017). There is also a time delay of 25 to 33 hours between an individual experiencing a stressful event and the production of the glucocorticoids (GCs) to the excretion of the GCs in the faeces. Thus the GCs will only be observed in the faeces between a day and a day and a half after the associated event (Young et al., 2017). Extrapolating from these results to a wild population of vervets presents some difficulties. Faecal hormone metabolite concentrations have been shown to vary with changes in diet and wild animals experience large variation in the amount and quality of food they consume while captive animals have controlled diets. Although the mechanism is unclear, an increase in dietary fibre has been shown to increase the concentration of faecal hormone metabolites (Dantzer et al., 2011).

Young et al. (2017) examined fGCMs (faecal glucocorticoid metabolites) after the rank reversal of the alpha and beta female (a stressful event) in a wild population of vervet monkeys and found increased levels of cortisol from faecal samples that were collected 4 and 5 days after the event and that fGCM levels returned to baseline levels within 7 days of the event. When comparing the captive and wild studies, it is easy to see the differences in fGCM excretion between the two. For example, the captive study found cortisol returned to baseline levels within 3 days, while in the wild study it took approximately 7. This difference could however be attributed to the fact that in the captive study, the stressful event was an acute once-off occurrence (in this example an injection), while rank change in the wild study is better described as chronic stressor that could cause the secretion of cortisol for multiple days due to increased frequency of aggressive interactions. Importantly, Marty et al. (2017) found that in wild crested macaques, the greatest stress response is seen in the first few days after immigration into a new group after which the FGCM levels steadily declined. At day 7 after immigration, FGCM levels were back to baseline levels.

Both studies (Young et al., 2017 and Marty et al., 2017) therefore show the importance of the time delay between a male's date of immigration into a new group and the time the first sample was collected. If this time delay is too extended (in the case of vervets and macaques, more than 7 days), the initial stress response may be missed. In my study the average number of days between an immigration event of a study male and sample collection was 44.4 days, while the average number of days the first sample was collected after migration was 17.6 days. Only one sample was collected within 7 days before migration (Unwabo, 1516) and two samples were collected 14 days before migration (Hwahwaza, 1508 and Unwabo 1516). Seven samples were however collected within 7 days (Afrikaans 818, 826; Dwergie 1310, 1322; Kies 858; Nyoni 2173; Ububhibhi 1535) and 9 samples within 14 days (Afrikaans 818, 826; Dwergie 1310, 1322; Kies 858, 867; Mvula 813; Nyoni 2173; Ububhibhi 1535) of immigration into a new group. Due to the small number of samples, no meaningful analysis could be performed on this subset of samples. Of the afore mentioned samples, only two of the samples had detectable cortisol levels. These were Dwergie (1322) and Ububhibhi (1516). Ububhibhi's sample was collected one day before he departed from his natal group, while Dwergie's sample was collected 6 days after he departed from his natal group. A sample was collected from Hibe on the day that he slept with Baie Dankie group. Baie Dankie group was not his natal group and Hibe was seen with his natal group, Ankhase, the following day. Despite the fact that he slept with a non-natal troop, he still did not show detectable cortisol levels. This could possibly be explained by the delay in the appearance of cortisol in faecal samples. As the sample was collected on the day that Hibe slept with another troop, we would nevertheless expect that the cortisol levels of that day are indicative of the previous few days' events. So if the build up to dispersal was stressful, we would've expected cortisol levels to be detectable as it was for Ububhibhi's whose sample was collected one day before his dispersal. If dispersal is a stressful event as is suggested by the literature, then I would have expected more than one of the seven samples that were collected within 7 days after dispersal to have had quantifiable cortisol levels. It might be the case that natal dispersal does not induce a quantifiable stress response in our study group of vervet monkeys, but other explanations cannot be ruled out.

4.4.2. Stressors associated with dispersal

In vervet monkeys, dispersal from the natal troop is not due to aggression (Cheney and Seyfarth 1983). On the other hand, immigration into a new troop has been associated with increased levels of aggression as well as the intensity of aggression towards immigrant males

(Henzi and Lucas, 1980) and we would thus expect immigrant males to experience high levels of stress after having immigrated into a new group or during the immigration period. Of the nine samples that were collected within the first two weeks of immigration, seven were collected within the first week and none showed quantifiable levels of cortisol. Although anecdotal this suggests that the immigration period for these individuals was not associated with any quantifiable stress response.

Akinyi et al. (2017) studied faecal glucocorticoids in wild baboons and, similar to the current study, did not find markedly elevated levels of fGCs after dispersal. They proposed various possibilities for this; firstly, the stress associated with dispersal can be short-lived and individuals need to be sampled within days or hours of the dispersal event (as discussed above, Marty et al., 2017 and Young et al.,2017). Secondly, individuals are well-adapted to dispersal and the stress associated with it. The event is thus not as stressful as might be expected and does not elicit a heightened stress response. Thirdly, in their study, the majority of individuals dispersed to neighbouring troops that share home ranges with their natal troop. This would mean that the dispersing individual might already be familiar with the home range of the new troop or at least parts of it and thus avoid the stressor of moving to a completely new environment.

Similar to baboons vervet monkeys have overlapping home ranges allowing dispersing males to acquire important spatial information such as location of food sources or sleeping sites in non-natal troop home ranges. In addition to these factors, males are also often seen interacting non-aggressively with individuals from other troops before they disperse. During between group encounters, males are often seen playing with juveniles or grooming or copulating with females from another troop (Henzi and Lucas, 1980; Cheney and Seyfarth, 1990). Consequently, a dispersing male might already be familiar with individuals in the troop to which it has immigrated. Upon immigration, these relationships or acquaintances could play a crucial role in reducing the stress the immigrating individual experiences. Females might already support the new male which could decrease the amount of aggression received, while the formation of alliances with individuals in the new group could also be greatly accelerated.

Vervets have also been shown to migrate to troops which contain individuals from their previous troop, for example siblings, or to migrate alongside individuals of their current troop

(Cheney and Seyfarth, 1983; Young et al., 2019). Both of these dispersal patterns have been described in our vervet population (Eichenberger, 2017). These pre-existing relationships or rekindling of past ones can also be very important at reducing the stress associated with immigration. Lastly, by immigrating to neighbouring troops, the individual reduces the dispersal distance and hence not only time spent alone but time spent traveling that could otherwise be spent foraging. If the individual times his dispersal correctly, for example leaving his natal troop when a between group encounter finishes, he would spend little to no time alone and would also benefit from the advantages of group living such as predator detection (van Schaik et al., 1983). All these factors combined could significantly decrease the amount of stress an individual experience during migration and could explain why I did not detect increased levels of cortisol in males that had immigrated.

4.5. Testosterone:

When all samples were analysed, male vervets from my sample had significantly lower testosterone levels in the three months following dispersal, compared to the three months preceding dispersal. When the largest outlier was removed, a GLMM revealed dispersal category to have a significant relationship with testosterone concentration. However, a post-hoc analysis failed to find a significant difference in testosterone between the dispersal categories. Therefore, this study found no strong evidence that testosterone decreased following natal dispersal in male vervets. I did find a significant decrease in rank of males in the three months following dispersal compared to the three months preceding dispersal. The literature on the hormonal correlates of dispersal in vervet monkeys is limited and to the best of my knowledge, a single paper exists that briefly examined the relationship (Young et al., 2019). Consequently, the discussion below will largely be based on comparisons with other primate species, mindful of the phylogenetic limitations inherent in doing so.

4.5.1 Rank, testosterone and dispersal

Rank was found to differ significantly between categories 2 and 3 and rank was significantly lower in the three months after dispersal, compared to the three months before dispersal. A positive relationship between rank and androgen concentrations has been described in other primate species (Baboons: Beehner et al., 2006; White faced Capuchins: Jack et al., 2014), although the relationship does not hold across all primates (Tufted Capuchins: Lynch et al., 2002). In addition to rank position, a change in rank, and more specifically the direction of that rank change, has been shown to be significantly correlated to androgen concentrations in primates. Beehner et al. (2006) found a significant correlation between testosterone levels and the direction of rank change with males that were moving down the dominance hierarchy having significantly lower testosterone levels compared to males that were moving up the dominance hierarchy. Consequently, we would have expected to see decreased testosterone levels in Category 3, compared to Category 2, but our results showed no strong evidence of this effect and I found no significant relationship between standardised rank and testosterone concentration.

Nonetheless, dispersing males in our study dropped in rank in their new group relative to their natal group. Although ranks between the natal and immigration group are not directly comparable due to differences in group size and perhaps in the steepness of the hierarchy, the ranks were standardised to control for differences in groups size and the proportion of individuals in the group ranking above the dispersing males nonetheless increased after their migration. Males that have dispersed from their natal group often enter the immigration group at the bottom of the hierarchy (Strier, 2016). This has been shown in vervets (Cheney and Seyfarth, 1983) as well as in macaques (van Noordwijk, 1985; Sprague et al., 1996) and hyenas (Holekamp and Smale, 1998), and our findings of a decrease in rank upon immigration lend support to these previous findings in vervets.

It is important to note that the results did show variation in the magnitude of the rank change among the males, with some showing much greater change than others. This may be related to natal rank; a higher ranking male might experience a substantial fall in rank after dispersing, whereas a male lower ranked in his natal group might simply stay in a similar, lower-ranked position in the new group. Unfortunately, we could not use Elo rankings to calculate the rank of immigrating males immediately following dispersal as Elo requires a fairly large number of interactions between the relevant individual and other troop members. These observations are often not available in the first weeks/month after immigrating into a new group. When a male from a wild troop immigrates into one of the study groups, it often takes a considerable amount of time for that individual to be sufficiently habituated to allow observers to approach within a distance that allows the observer to collect reliable data. Behavioural data collection was also not focussed specifically on the collection of behavioural data from males and was rather focussed on collecting data ad libitum from the entire troop, which meant that often not enough data points were collected within the first month to accurately determine an immigrants rank.

Interestingly, I also found that many of the males seemed to experience changes in rank prior to dispersal; by comparing Elo ratings for each of the individuals 12 months before dispersal and on the day of dispersal, I was able to show that 9 of the 11 males increased in rank (Elo rating) in their natal groups prior to dispersal (see Table 13 and Figures 10, a-k). Vervet females have a stable linear hierarchy and offspring (whether male or female) inherit their mothers rank (Cheney and Seyfarth, 1990). It is thus assumed that natal males' rank is bound by their mothers' rank, but the observed increase in rank as a male approach's dispersal age challenges this and suggest that their increasing size may allow them to rise in the hierarchy. The current results show that most males, and particularly a male from a low-ranking mother, will exhibit a clear change in rank as he approaches dispersal age despite his mother's rank remaining constant.

4.5.2. The activational role of testosterone in dispersal

Phoenix et al. (1959) suggested that androgens (such as testosterone) play an activational role in mating behaviour during adulthood. If testosterone did play an activational role in dispersal in vervet monkeys, we would expect an increase in testosterone around the time of dispersal (category 2). This is however not the case and no significant difference in testosterone concentration was observed in category 2 when compared to category 1, a period which should reflect baseline testosterone levels.

Young et al.'s (2019) paper on vervet monkeys showed an increase in fAM (faecal androgen metabolites) was closely related to an increase in dispersal probability; as the number of migrations increased during the dispersal season, so did testosterone levels in males and the authors suggest a profound relationship between the two. The paper is however, based on adult male vervets that have already dispersed from their natal groups and it is not clear whether the samples were from males that participated in a dispersal event over the study period or not. So how these results translate to natal dispersers is uncertain

My results differ from the findings of Young et al. (2019) as they do not show an indication of having increased in the period leading up to dispersal (category 1 and 2). These results may then suggest that testosterone does not seem to have an activational effect for male sexual behaviour in male vervet monkeys in our population. It is however important to note that a large gap exists between categories 1 and 2 (a minimum of 7 months) and that fluctuations in fT levels might have occurred in that time. Additionally, as was mentioned earlier, there were fewer samples available for category 1 than for categories 2 and 3, and 3 of the 4 outliers that were identified in our study were from category 2, all of which displayed high levels of testosterone. This could suggest that an increase in testosterone does occur during that period, but that our sampling effort was insufficient to detect the effect. It may be the case that with a larger number of samples, an increase may be seen in testosterone before dispersal, but further study is needed to confirm or refute this. However, as the increase in fAM around dispersal is so pronounced in Young et al. (2019), an increase of over 200%, I expected fT levels would increase over the period.

4.6. Natal group size and pre-dispersal testosterone concentration

Lastly, my results show that natal males in larger groups had significantly higher testosterone concentrations than natal males in smaller groups (see Table 14 and Figure 11). A positive relationship between aggression and testosterone concentrations has been described in primates (Alberts et al., 1992; Anestis, 2006) and the increased testosterone levels observed in natal males from larger groups is likely associated with increased competition over resources. Intra-group competition over resources increases with increasing group size (Clutton-Brock, 2006) and it is thus likely that individuals from larger groups experience higher levels of aggression than individuals from smaller groups and consequently have higher levels of testosterone. Earlier I showed that a natal male’s rank increases as he approaches dispersal age. This could also have influenced the relationship between natal group size and pre-dispersal testosterone levels in natal males. As the rank of natal males increases as they approach dispersal age, these males might partake in aggressive interactions more frequently as they might become more likely to win an aggressive interaction. As competition has been shown to increase with increasing group size, this effect might become more evident in larger groups.

5. CONCLUSIONS, LIMITATIONS AND FUTURE RESEARCH

This aim of this thesis was to investigate both intrinsic and extrinsic correlates of dispersal in a population of wild vervet monkeys. My results indicate that peer dispersal does occur in our population of vervet monkeys, but at much lower rates than has been reported in other populations. Age at natal dispersal, however, correlates well with earlier reports in vervet monkeys (Henzi and Lucas, 1980) and shows a narrower age range for natal dispersal than has been reported in other primate species. I found no evidence that adult sex ratio nor number of same sexed peers in the natal group effects the age of dispersal, but I did find that males from larger groups dispersed later than males from smaller groups. This may be due to benefits of staying longer in a larger group, but the sample size was relatively small and biased towards particular groups, so caution should be exercised when interpreting these results. This study particularly aimed to examine the hormonal correlates of natal dispersal through the comparison of faecal testosterone and cortisol levels before and after dispersal. I found no effect of dispersal upon cortisol levels, but in most of the samples the concentration of cortisol was below the detection limit. The results did not indicate a significant change in testosterone levels after dispersal and immigration into a new troop. Rank position decreased after the males' natal dispersal, but no significant direct relationship was found between testosterone and rank. I did, however, find that pre-dispersal testosterone levels were higher in males from larger groups than smaller groups. While I suggest that the difference in testosterone levels observed between natal males from larger and smaller groups is likely a consequence of within-group competition over limited resources, further studies would be required to support this hypothesis.

The primary limitation of this study lay in the small number of available samples, as well as their uneven distribution across dispersal categories. Unfortunately, few samples were collected from males in the days directly preceding and following their dispersal, which would have been very beneficial to gaining a clear picture of hormone levels over the dispersal period. Additionally, a large proportion of the males dispersed to groups that are not followed by researchers, which constrained the analyses I was able to perform. For example, it would have been interesting to examine whether natal males showed a preference for dispersing to larger or smaller groups, but due to inconsistent data collection in some of the immigration groups (mainly CR), enough reliable data on the size and demography of the immigration groups was not available. Six of the 13 natal males in our study dispersed to CR, meaning only seven individuals were available to conduct comparisons. Of these seven, five individuals dispersed from AK to BD. Bearing this in mind, all seven of these individuals dispersed to groups with larger group sizes than their natal groups, possibly indicating that there is a tendency for natal males to disperse to groups with larger groups sizes than their natal groups. However, further studies would be required to confirm this.

Variation in testosterone levels before and after dispersal would clearly benefit from further study, as would the impact of dispersal upon cortisol levels, and the role of natal and immigration group demographics in dispersal. Future studies will benefit from more focused sample collection, specifically targeting natal males of approximate dispersal age, along with a larger population size (more study groups), which will allow for a larger sample size as well as minimising the risk of losing dispersing individuals to non-study groups. Future studies should focus on collecting samples immediately before and after dispersal to minimise the time elapsed between sample collection and the dispersal event. This will allow researchers to more accurately assess the effect of dispersal on faecal hormone levels and will help shed further light on the triggers of dispersal in wild vervet monkeys. Finally, focusing behavioural data collection on recently immigrated males will allow researchers to more quickly determine their rank positions in the new group and further inform our understanding of the relationship between testosterone and rank in the context of natal dispersal.

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8. APPENDICES:

Appendix A: Purification of faecal samples:

Day 1:

Eppendorf tubes containing 1ml of faeces and methanol solution were removed from the -80°C freezer and allowed to thaw. Samples were then vortexed for 30s after which they were centrifuged for 4 minutes at 4°C at 14 000 rpm. 0.4ml of the supernatant was then transferred to a new 2ml Eppendorf tube and evaporated in a speedvac at 45°C and 14 bar pressure.

Samples were then reconstituted by adding 1ml of a 2% MeOH solution and vortexing the sample twice for 30s each time. The sample was then spiked with 10ul of Internal Standard and vortexed for 10s.

The entire sample was moved to a 15ml Falcon tube and 1 ml of pre mixed stock solution of phosphate buffer and Glucocodinase (990ul Phosphate Buffer and 10ul Glucocordinase) was added to the sample in the 15ml falcon tube. The 15ml falcon tubes were then placed in a shaker and allowed to shake overnight.

Day 2:

4.5ml of pure distilled water was added to the 15ml Falcon tube. The tube was then vortexed (2x20s) and centrifuged for 4 minutes at 4400 rpm.

The SPE Columns (Evolute 600 -0002-B 25mg/3ml) were activated by running 2ml of HPLC grade 100% Methanol and then 2ml of HPLC grade 5% Methanol through them. The samples were loaded in the columns, and passed through the columns. A small amount of liquid was left in the bottom of the falcon tube to avoid adding impurities to the columns. The columns were then washed with 1 ml 100% Water and then 1ml of HPLC grade 100% Hexane. The columns were then eluted with 1ml of HPLC grade 100% Ethylacetate and collected in 2ml Eppendorf tubes.

0.8ml of 0.1% NH4 was then added to the new Eppendorf tubes, after which it was vortexed for 30s and then centrifuged for 4min at 4°C at 14 000 rpm. The liquid separated and formed two layers, with the ethylacetate on top. The ethylacetate was removed and placed in a new

Eppendorf tube. 0.8ml of ethylacetate was then added in the tube containing the NH4 and the procedure of vortexing, centrifuging and transfer of the ethylacetate repeated.

The ethylacetate was then evaporated in the speedvac. The samples were then reconstituted by adding 150ul of 50% MeOH, vortexed for 30s, placed in an ultrasound for 2 minutes and then centrifuged for 4 minutes at 4°C at 14 000 rpm.

100ul of the supernatant was then collected and transferred to HPLC vials with conical inserts and capped. These samples were stored in a freezer at -80°C until they were read by the HPLC.

Appendix B: Table showing data used in our testosterone analysis as well as category and rank analysis. NA means that sufficient data points were not available to determine an individual's standardised rank at the time of sample collection.

Sample Number	Individual	Category	Concentration in ng/g	Standardised Rank
620	Mvula	2	3.58125	0.282051282
639	Mvula	2	5.1	0.289473684
646	Hwahwaza	1	4.725	0.736842105
663	Kies	2	3.7875	0.351851852
672	Ububibi	1	4.48125	0.552631579
693 (Outlier)	Mvula	2	18.16875	NA
702	Ububibi	1	2.60625	0.552631579
714	Kies	2	8.2875	0.351851852
719	Afrikaans	2	5.7375	0.814814815
769	Hwahwaza	1	2.4375	0.72972973
813	Mvula	3	2.925	NA
818	Afrikaans	3	4.65	NA
826	Afrikaans	3	3.80625	NA
858	Kies	3	2.19375	NA
867	Kies	3	0.590625	NA
878	Mvula	3	1.96875	NA
912	Hwahwaza	1	2.98125	0.743589744
933	Wolfie	3	0.8175	NA
937	Afrikaans	3	1.53	0.384615385
954	Kies	3	0.27	0.631578947
965	Afrikaans	3	0.234375	0.342105263
1008	Wolfie	3	1.059375	NA
1030	Wolfie	3	0.3	NA
1046	Kies	3	0.24	0.611111111
1072	Dwergie	2	0.97125	0.68
1098	Kies	3	0.70875	0.555555556
1116	Wolfie	3	1.78875	NA
1141	Wolfie	3	0.920625	NA
1195	Dwergie	2	1.426875	0.673076923

1310	Dwergie	3	1.95	0.344827586
1322	Dwergie	3	2.15625	0.344827586
1357	Ububibi	2	1.275	0.827586207
1358	Hwahwaza	2	4.125	0.862068966
1363	Dwergie	3	1.24125	0.379310345
1391	Ububibi	2	1.54875	0.826086957
1412	Hwahwaza	2	1.430625	0.909090909
1455	Unwabo	1	0.6675	0.772727273
1461	Mvula	4	3.6	0.782608696
1474	Hwahwaza	2	8.2875	0.954545455
1508	Hwahwaza	2	1.03125	0.909090909
1516	Ububibi	2	2.86875	0.863636364
1532	Unwabo	1	3.45	0.761904762
1535	Ububibi	3	4.35	NA
1558	Unwabo	1	1.8375	0.8
1584	Nyoni	1	1.5	0.2
1597	Unwabo	1	1.029375	0.85
1599	Mvula	4	2.94375	0.571428571
1619	Hlokolozo	1	0.2475	0.25
1632	Hwahwaza	3	2.7	0.404761905
1634	Ububibi	3	1.56375	0.714285714
1641	Hwahwaza	3	1.5225	0.619047619
1646	Wolfie	4	3.15	0.9
1657	Mvula	4	0.969375	0.714285714
1701	Wolfie	4	1.228125	0.9
2004	Nyoni	2	0.62625	0.380952381
2012	Nyoni	2	0.628125	0.380952381
2027	Unwabo	2	1.408125	0.571428571
2047	Hlokolozo	2	0.38625	0.523809524
2051	Hlokolozo	2	2.34375	0.523809524
2065	Hwahwaza	4	1.95	0.523809524
2117	Hwahwaza	4	3.7875	0.428571429
2126	Ububibi	4	1.95	0.575
2156	Hwahwaza	4	2.175	0.558139535
2173	Nyoni	3	1.9125	NA
2238	Hlokolozo	3	0.234375	0.288888889
2241	Unwabo	3	0.94125	0.755555556
2245	Nyoni	3	1.625625	0.133333333
2256	Hwahwaza	4	7.8375	0.622222222
2278	Hwahwaza	4	1.693125	0.622222222
2283	Hlokolozo	3	0.29625	0.177777778
2284	Hwahwaza	4	1.576875	0.622222222
2298	Ububibi	4	0.796875	0.555555556
2349	Nyoni	3	0.785625	0.068181818
2370	Nyoni	3	0.8475	0.2
2387	Nyoni	3	1.355625	0.133333333
2403	Hwahwaza	4	1.54875	0.688888889

Appendix C: Table showing data used in calculating the effect of adult sex ratio in natal group on dispersal age.

Individual	Date of Dispersal	# Males	# Females	Adult sex ratio (M/F)	Adult sex ratio (F/M)	Dispersal age (days)	Dispersal age (years)
Hwahwaza	2016/06/04	3	4	0.7500	1.3333	1723	4.72
Ububhibhi	2016/05/24	3	4	0.7500	1.3333	1646	4.51
Unwabo	2017/05/03	2	4	0.5000	2.0000	1654	4.53
Nyoni	2017/05/16	2	4	0.5000	2.0000	1667	4.57
Rheban	2017/12/05	2	7	0.2857	3.5000	1865	5.11
Hlokoloza	2017/05/23	2	4	0.5000	2.0000	1613	4.41
Avon	2018/04/06	1	6	0.1667	6.0000	1607	4.40
Spook	2016/06/16	6	12	0.5000	2.0000	1703	4.67
Poeding	2016/06/11	6	12	0.5000	2.0000	1674	4.59
Ogies	2016/06/03	5	12	0.4167	2.4000	1675	4.59
Noktober	2016/06/11	6	12	0.5000	2.0000	1690	4.63
Rooikat	2017/04/27	6	14	0.4286	2.3333	1970	5.40
Akkedis	2016/05/28	4	12	0.3333	3.0000	1664	4.56

Appendix D: Table showing data used in calculating the effect of the number of same sexed peers in natal group on dispersal age.

Individual	Number of same sexed peers on departure date	Dispersal Age (days)	Dispersal Age (years)
Hwahwaza	1	1723	4.72
Ububhibhi	1	1646	4.51
Spook	6	1703	4.67
Poeding	6	1674	4.59
Ogies	6	1675	4.59
Noktober	6	1690	4.63
Rooikat	6	1970	5.4
Akkedis	6	1664	4.56
Unwabo	4	1654	4.53
Nyoni	4	1667	4.57
Rheban	1	1865	5.11
Hlokoloza	4	1613	4.41
Avon	2	1607	4.4

Appendix E: Table showing the data used in calculating the effect of the adult sex ratio (ASR) in the natal and immigration group on age at natal dispersal.

Individual	Natal Group		ASR Natal Group (M/F)	Immigration Group		ASR Immigration Group (M/F)
	#Males	#Females		# Males	# Females	
Hwahwaza	3	4	0.750	5	12	0.417
Ububhibhi	3	4	0.750	4	12	0.333
Unwabo	2	4	0.500	9	14	0.643
Nyoni	2	4	0.500	8	14	0.571
Rheban	2	7	0.286	10	15	0.668
Hlokoloza	2	4	0.500	8	14	0.571
Avon	1	6	0.167	2	7	0.286
Spook	6	12	0.500	N/A	N/A	N/A
Poeding	6	12	0.500	N/A	N/A	N/A
Ogies	5	12	0.417	N/A	N/A	N/A
Noktober	6	12	0.500	N/A	N/A	N/A
Rooikat	6	14	0.429	N/A	N/A	N/A
Akkedis	4	12	0.333	N/A	N/A	N/A

Appendix F: List of animals found on Mawana Game Reserve (birds not included):

African Elephants (*Loxodonta africana*)
Giraffe (*Giraffa cameloparddalis*)
Blue Wildebeest (*Connochaetes taurinus*)
Waterbuck (*Kobus ellipsiprymnus*)
Greater Kudu (*Tragelaphus strepsiceros*)
Nyala (*Tragelaphus angasii*)
Impala (*Aepyceros melampus*)
Blesbok (*Damaliscus pygargus dorcas*)
Common Duiker (*Sylvicapra grimmia*)
Plains Zebra (*Equus quagga*)
Mountain Reedbuck (*Redunca Fulvorufula*)
Common Warthog (*Phacochoerus africanus*)
Aardvark (*Orycteropus afer*)
Cape Porcupine (*Hystrix africaeaustralis*)
Honey Badger (*Mellivora capensis*)
Black-backed Jackal (*Canis mesomelas*)
Spotted Hyena (*Crocuta crocuta*)
Brown Hyaena (*Hyaena brunnea*)
Aardwolf (*Proteles cristatus*)
Leopard (*Panthera pardus*)
Common Large Spotted Genet (*Genetta maculata*)
Slender Mongoose (*Galerella [Herpestes] sanguinea*)
White-tailed Mongoose (*Ichneumia albicauda*)
Serval (*Leptailurus serval*)
Caracal (*Caracal caracal*)
Vervet Monkey (*Chlorocebus pygerythrus*)
Chacma Baboons (*Papio ursinus*)
Thick-tailed Galago (*Otolemur [Galago] crassicaudatus)*
Southern African Rock Python (*Python natalensis*)
Mozambique Spitting Cobra (*Naja mossambica*)
Boomslang (*Dispholidus typus*)
Black Mamba (*Dendroaspis polylepis*)
House Snake (Boaedon capensis)
Spotted Bush Snake (*Philothamnus semivariegatus*)
Eastern Tiger Snake (*Telescopus semiannulatus semiannulatis*)