

Western Gorilla Social Structure and Inter-Group Dynamics

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Statement of Length

The word count of this dissertation is 44,718 words excluding appendices and references.

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Western Gorilla Social Structure and Inter-Group Dynamics

Robin Morrison

The study of western gorilla social behaviour has primarily focused on family groups, with research on inter-group interactions usually limited to the interactions of a small number of habituated groups or those taking place in a single location. Key reasons for this are the high investment of time and money required to habituate and monitor many groups simultaneously, and the difficulties of making observations on inter-group social interaction in dense tropical rainforest. However, gorilla groups are known to have extensively overlapping home ranges, show affiliative inter-group interactions and often aggregate at resource hotspots. There is also genetic evidence of kin-biased behaviour between dispersed kin. This is all suggestive of a complex society in which inter-group interactions may follow an underlying multi-level social structure where affiliations are influenced by kinship, social exposure, ranging patterns, territoriality or foraging decisions. This thesis investigates the large scale society of western lowland gorillas, using novel technologies and analytical methods to overcome the considerable difficulties in studying large numbers of gorillas simultaneously. I use biases in movement patterns to investigate the cognitive rules used, and decisions made by this intelligent, social species, to navigate the limited space and resources they share with their neighbours.

Using observational data from two forest clearings in the Republic of Congo, I quantify community structure by network modularity analysis and hierarchical clustering, demonstrating the presence of kin-based multi-level social structure in western lowland gorilla. The sizes of these gorilla social units follow a hierarchical scaling pattern similar to that observed in other mammalian multi-level societies including humans. The social structure detected at these forest clearings is consistent with a super-spreader structure, suggesting that clearings may act as important transmission hubs for disease, novel ideas, behaviour or culture. This demonstrates that intervention strategies targeting gorillas with home ranges near to forest clearings, particularly solitary males, may be highly effective for limiting the transmission of certain diseases. Modelling the movement patterns of a gorilla population across their ranges using camera trap data demonstrates that gorilla groups appear to actively avoid one another, both through avoidance of other groups at resource hotspots, and avoidance of areas regularly used by other groups. Gorilla groups visit sites less often the closer they are to another group's home range centre, with groups avoiding larger, more dominant group's home range centres to a greater extent. This, along with the increased

avoidance of visiting a location on the same day as another group when close to their home range centre, is highly suggestive of the presence of territorial defence in western gorillas.

The findings in this thesis demonstrate the presence of a kin-based multi-level social structure in western gorillas, with considerable similarities to that present in humans, suggesting that a key component of human social complexity may have evolved far earlier than previously asserted. They suggest that the social brain enhancements observed within the hominin lineage were not necessary to enable human multi-level social structure. I show that western gorillas demonstrate biases in their movement patterns consistent with the presence of some broader elements of territoriality, with regions of priority or even exclusive use, close to their home range centres. My findings strongly emphasise the importance of gorillas as a model system for human social evolution. This is due to both the common underlying multi-level social structure and the considerable similarities in inter-group territorial dynamics. In contrast to previous assumptions that interactions between gorilla groups are primarily random or due to aggressive mate competition, I find that these interactions appear to be based around a complex social structure influenced by kinship, territoriality and dominance.

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Acronyms

AIC	Akaike information criterion
BLR	Binomial logistic regression
BP	Binomial probability
DRC	Democratic Republic of Congo
GLM	General linear model
HSM	Hierarchical social modularity
LCA	Last common ancestor
MCMC	Markov chain Monte Carlo
MCP	Minimum convex polygon
MM MF	Multi-male multi-female
NRG	Non-reproductive group
OMU	One male unit
RG	Reproductive Group
SR	Simple ratio
UPGMA	Unweighted pair group method with arithmetic mean
WLG	Western lowland gorilla

Chapter 1: Introduction

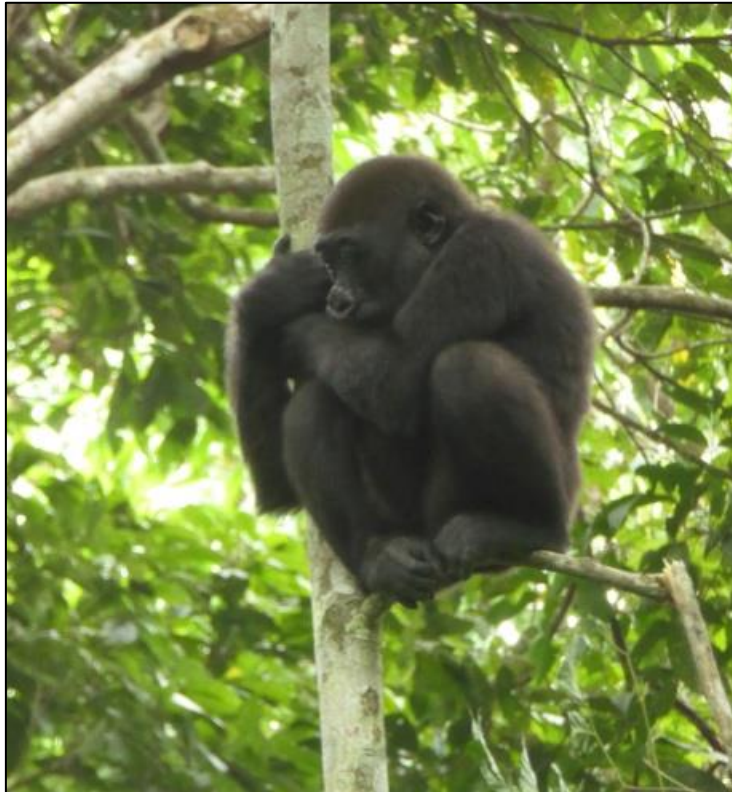


Photo by Robin Morrison at Ngaga Research Station, SPAC Foundation Congo

1.1 Background

Social structure (a term often used synonymously with social organisation) is the overall pattern that emerges from the social behaviours of each individual in a population, and it is these individual behaviours that are acted upon by natural selection (Hinde, 1976). The social structure of a species is determined by the pattern of ecological relationships between nearby conspecifics, both those within and between social groups (Whitehead, 1997). It has important consequences for feeding, reproduction, conflict, cooperation, and much more, and is in turn shaped by such factors, influencing the daily environment to which individuals are exposed. Understanding the social structure of a species is essential for predicting the way in

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which individuals will come into contact with one another, enabling the transmission of culture and ideas (Richerson and Boyd, 1998; Henrich, Boyd and Richerson, 2008), disease (Fincher et al., 2008) and genes (Storz, 1999). It is also essential for understanding how contacts between individuals have occurred in the past, which has dramatic consequences for understanding the evolution of a species. For example, through the effect social structure has on gene flow, and therefore the rate at which genetic drift has occurred, relative to other evolutionary processes (Storz, 1999).

In this introductory chapter three important factors influencing social structure will be briefly outlined: territoriality, kinship and disease. Primate social structure will then be discussed more broadly before moving onto what we know about gorilla social structure and the factors influencing it in detail. Human social structure and how studies of social behaviour in other apes can inform our understanding of human social evolution will then be focused on, which will be followed by outlining how social structure has been found to influence the transmission of disease. Finally, the methods by which gorillas have been studied in the past and how they may be used to build a better understanding of gorilla social structure will be discussed, specifically the relationships occurring between groups, before describing the hypotheses investigated on this topic within this thesis.

1.1.1 Territoriality

The presence of territoriality fundamentally affects the social structure of a species by influencing the rate and type of inter-group encounters. This is because in a territorial species, encounters are unlikely to occur at random, as each group will be aware of their territorial boundaries, with ranging outside the territory being an active decision. One common definition of territoriality is the presence of regions of an animal's home range that are actively defended against intruders to enable exclusive use by the individual or social unit (Bartlett and Light, 2017). However broader definitions have also been proposed which include areas where overlap occurs but priority use by resident groups is observed (Boitani and Fuller, 2000; Maher and Lott, 1995). The evolution of territoriality is hypothesised to be dependent on the economic defendability of the territory or resources used by a species, so that for territoriality to occur, the benefits of exclusive use of the resources must be greater than the costs of defending them (Brown, 1964). Conventionally, territoriality has been

thought of as a relatively rigid, innate state in a species (Boitani & Fuller 2000; Asensio et al. 2018). However, studies altering the distribution of resources in habitats and therefore the economic defendability of these resources have indicated that territoriality can be highly variable both within species, and within the same individuals under differing circumstances, across a broad range of species (Carpenter, Paton and Hixon, 1983; Wyman and Hotaling, 1988; Adams, 2001; Savini et al., 2015).

1.1.2 Kin-biased behaviours

Another trait that strongly influences the overall social structure of a population is kin-biased behaviour. Kin selection theory predicts that behaviours that benefit another individual will be biased towards related individuals. This is in order to gain indirect fitness benefits (Hamilton, 1964), through favouring individuals with a high proportion of the same genes, and is one of the key factors used to explain the evolution of altruism. Behaviours that benefit unrelated or related individuals may also be evolutionarily stable through reciprocal altruism or mutualism, with no basis in kinship. Mutualism occurs where both parties immediately benefit from cooperation, with these benefits exceeding the costs (Clutton-Brock, 2009). Reciprocal altruism occurs where cooperation leads to a short-term cost to one party, however this cost is out-weighed in the long term by benefits received when assisted in the future by parties they have previously helped (Trivers, 1971; Clutton-Brock, 2009).

Where kin-biased behaviours occur, social interactions between related individuals can differ from those between unrelated individuals greatly. However, this increased support of kin is dependent on the frequency with which kin come into contact. Dispersal of individuals from their natal groups is observed across the animal kingdom, usually with dispersal of one or both sexes, at or before the onset of sexual maturity (Lawson Handley and Perrin, 2007). This is thought to enable the avoidance of inbreeding and competition between relatives, however it can also limit the potential for kin-biased behaviours. In mammals, male biased dispersal is seen most commonly, with affiliative behaviours observed between females, whilst in birds, female biased dispersal is more common (Greenwood, 1980).

1.1.3 Disease

The social structure of a population can have important consequences on the rate at which different individuals come into contact and therefore the way in which disease is spread. To understand how a disease spreads through a population, rates of transmission are calculated. These rates are thought to be a product of the contact rate occurring between individuals and the probability of transmission between individuals when they meet. This probability of transmission is due to traits of the disease itself, such as its mode of transmission and infectivity. Contact rates however, relate to the social structure of the population in which the disease is spreading, meaning that information on the social structure of a population can be highly informative for understanding the transmission of the different diseases present in that population (Heesterbeek et al., 2015; Grassly and Fraser, 2008).

1.2 Primate social structure

Primates are a highly social clade showing a great diversity of social structure (Müller and Soligo, 2005) from solitary individuals to complex multi-level societies. Phylogenetic analyses of primate sociality suggest that social aggregations first arose in primates around 52 mya, and that this switch to social living was driven by increased predation pressure, due to the transition from nocturnal to diurnal activity (Shultz, Opie and Atkinson, 2011). The model produced from these analyses suggests a stepwise transition from solitary living, to unstable multi-male multi-female (MM MF) social groupings, to stable family groups. It also indicates that once these family groups arise, they are unlikely to transition back to MM MF groups, although this reversion is seen to some extent from polygynous (uni-male) family groups back to MM MF (Figure 1.1).

Apes in particular show an incredible level of diversity in their social structure, with pair-bonded family units observed in gibbon species, solitary individuals or mother-offspring units in orangutans, largely polygynous groups in gorillas, and large multi-male multi-female groups in chimpanzees (Smuts et al., 1987).

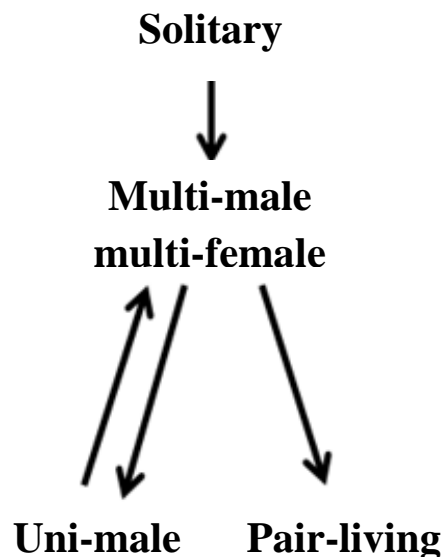


Figure 1.1. Reversible Jump Model of transitions in primate sociality (Shultz, Opie and Atkinson, 2011)

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Chimpanzee and bonobo social structure differs greatly to those observed in both of their closest relatives, gorillas and humans. Their societies are described as fission-fusion systems (Anderson et al. 2002; Symington 1990), with small transient subgroups forming out of the larger closed group. This is also observed to some extent in orangutans (Delgado Jr., Van Schaik and Delgado, 2000; van Schaik, 1999). However, orangutans are far more solitary than other apes, with subgroup interactions occurring far less frequently. In humans, family groups have developed greater complexity to form multi-level (also known as hierarchical) societies, where multiple stable family groups are affiliatively bonded with each other to form higher grouping levels. Those multi-family groups then form associations and these tiers of social structure continue upwards, with the level of social interaction within each tier decreasing as the level of grouping increases (Grueter, Chapais and Zinner, 2012). Multi-level social structure is observed in other primate species including papionins (Schreier and Swedell, 2012) and colobines (Grueter and Van Schaik, 2010). However, comparisons of human and non-human primate social structure generally assume that multi-level social structure is unique to hominins within hominidae, and absent in chimpanzee, gorilla and orangutan populations (Grueter, Chapais and Zinner, 2012).

Incidences of severe aggression between adult males have been observed in both gorillas and orangutans, usually associated with sexual competition. However avoidance appears to be a more common strategy in these species (Galdikas, 1985; Bermejo, 2004). Overlapping ranges have been observed in both the largely solitary social structure of orangutans, and the polygynous groups of gorillas, and therefore both species are widely assumed to be non-territorial (Singleton and Van Schaik, 2002; Watts, 1998; Bermejo, 2004). In contrast, social systems in the *Pan* and human lineage are thought to be highly territorial (Ghiglieri, 1987). There is clear evidence for territoriality in chimpanzees (*Pan troglodytes*), which show both exclusive use of a geographical area and violent defence against neighbouring individuals (Watts and Mitani, 2001; Mitani, Watts and Amsler, 2010). Aggression between neighbouring chimpanzee communities has even been found to alter territorial boundaries, allowing dominant groups to extend their territories, improving access to resources (Crofoot and Wrangham, 2010). This territoriality is thought to be greatly reduced in bonobos (*Pan paniscus*), where peaceful between-group encounters are observed (Idani, 1990; Furuichi, 2011), raising the question of whether bonobos are truly territorial.

1.3 Gorilla social structure

The genus gorilla is formed of 2 species, the eastern gorilla (*Gorilla beringei*) and western gorilla (*Gorilla gorilla*), both of which inhabit equatorial Africa (Scally et al., 2012; Groves, 2001). The eastern gorilla species is made up of two subspecies: the mountain gorilla (*Gorilla beringei beringei*) and the eastern lowland gorilla (*Gorilla beringei graueri*). Mountain gorillas exist in two isolated populations located across Rwanda, Uganda and the Democratic Republic of Congo (DRC), which are estimated to be made up of roughly 1000 individuals in total. They are the only subspecies of gorilla not to be considered ‘critically endangered’ by the IUCN, after a recent reassessment to ‘endangered’ status, due to their increasing population size (Hickey et al., 2018). The eastern lowland gorilla (*Gorilla beringei graueri*), also known as Grauer’s gorilla, has an estimated population size of 3,800 and is found only in DRC (Plumptre et al., 2016). The western gorilla species includes two subspecies: the cross river gorilla (*Gorilla gorilla diehli*) and the western lowland gorilla (*Gorilla gorilla gorilla*). Cross river gorillas are found on the Nigeria-Cameroon border and their population size is estimated as roughly 250-300 individuals (Bergl et al., 2016). In comparison to the other gorilla sub-species, western lowland gorillas (WLGs) are far more numerous (with population estimates of 362,000) and far more widespread, with populations found in the Republic of Congo, DRC, Gabon, Cameroon, Angola, Central African Republic and Equatorial Guinea (Maisels et al., 2018).

1.3.1 Gorilla groups

Gorillas live in stable family groups consisting of a single adult male, multiple adult females, and their offspring (Robbins et al., 2004), with the exception of mountain gorillas, in which groups often include multiple males which are not always related (Bradley et al., 2005). Upon reaching maturity, females of both species usually disperse from their natal groups (Harcourt, 1978; Stokes, Parnell and Olejniczak, 2003), transferring directly into another group or to a solitary male. Males tend to disperse from their natal groups shortly after reaching maturity, at which point they become solitary males until they can acquire females and form a group of their own. In mountain gorillas, mature males are also known to transfer to all male groups or

remain within their natal groups where they may eventually take over as the dominant male (Watts, 1996). Female gorillas may transfer between groups on multiple occasions, and these dispersal patterns have been shown to relate to a number of social and demographic factors including group size and infanticide avoidance (Stokes, Parnell and Olejniczak, 2003). In WLGs, groups have been observed to divide into subgroups for short periods of time before reuniting as a larger group (Remis, 1997). This subgrouping behaviour is thought to enable a reduction in within group feeding competition during periods of high fruigivory (Watts, 2002).

1.3.2 Between-group interactions in gorillas

Between-group interactions in mountain gorillas were investigated by Robbins and Sawyer (2007) who observed some form of aggression in 75% of encounters but physical aggression in only 2.5% of encounters. The second most common behaviour shown by the groups was tolerance in 55% of encounters. Between-group interactions in western lowland gorillas showed even higher tolerance (64% of encounters) and lower aggression (21% of encounters). Furthermore, cases of co-nesting, with separate groups nesting overnight within 30-50 m were observed on five occasions (Bermejo, 2004). This is vastly different to the interactions observed when highly territorial chimpanzee communities come into contact with one another, where the response is either avoidance, flight, or extreme aggression (Watts and Mitani, 2001; Crofoot and Wrangham, 2010). The high level of tolerance observed between some gorilla groups leads to the question of whether these differing responses to gorilla group encounters could be due to a multi-level social structure in which certain gorilla groups have strong affiliations.

1.3.3 Kin-biased behaviours in gorillas

It had been thought that the dispersal observed in both sexes of gorilla prevented the possibility of kin-biased behaviours in gorillas. However, there is evidence to suggest that female WLGs are more likely to disperse to groups in which another female relative is already present, indicating the potential for kin recognition and kin-biased behaviour in related individuals resident in different groups (Arandjelovic et al., 2014; Bradley, Doran-Sheehy and Vigilant, 2007). Further potential for extra-group kin-biased behaviour has been observed in silverback male WLGs, which were found to form neighbourhoods in which

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related males lived in close proximity to each other (Bradley et al., 2004). It is therefore feasible that the close proximity of related groups may enable affiliative between-group interactions based on relatedness, providing potential benefits for territory and female defence.

Alternative evidence suggests that related silverbacks may not live in close proximity as no kin dyads were found in a sample of 8 silverbacks from a 40 km² area in Gabon (Inoue et al., 2013) and male gorillas have been found to disperse greater distances than females (Douadi et al., 2007). It is therefore possible that this tolerance between rival silverbacks does not occur where related individuals are not in close proximity, or that it has a basis in geographic proximity rather than kinship, with more tolerant interactions observed between silverbacks that interact more regularly and may have an already established dominance hierarchy. It could also have a basis in resource abundance, with inter-group tolerance allowing groups to maximise their time spent feeding and avoid wasting time and energy on aggressive between-group encounters in resource abundant areas. When the presence of other groups does not diminish their access to resources, this strategy could provide immediate benefits to both groups. Alternatively, reciprocal altruism could occur in situations where one group aids another in defence of females, if this help is likely to be reciprocated at a later stage.

1.4 Human social evolution

Considerable research has focused on describing modern human social structure. However, understanding the way in which this evolved is an area of anthropology that has been relatively neglected (Chapais, 2013). This is due to the intrinsic difficulties of reconstructing behavioural trends in extinct hominins, where direct observation is impossible and fossil and archaeological evidence is limited (Tooby and DeVore, 1987). Therefore, to better understand the evolution of the human social system it is necessary to develop a greater understanding of the social structure present in our closest extant relatives.

1.4.1 The comparative method

The comparison of human social behaviour with that of other animal species is a well utilised method for investigating which social traits are derived in the human lineage and which were likely present in common ancestors (Grueter, Chapais and Zinner, 2012; Swedell and Plummer, 2012; Chapais, 2010; Foley and Gamble, 2009; Shultz, Opie and Atkinson, 2011). Extensive comparison between the social systems of humans and the chimpanzee/bonobo sister clade has been carried out (Ghiglieri, 1987; Sayers and Lovejoy, 2008; Chapais, 2013). This has been used to justify both the evolution of family units, and complex between group social interactions after the chimpanzee-human split (Foley and Gamble, 2009). However, the comparative method is highly dependent on having a good understanding of the traits present in a variety of species. Whilst there is extensive research on the small scale social interactions of many ape species (usually those taking place within social groups), there is very limited research on the larger-scale social interactions such as those between groups, which make up a crucial component of social structure in many species. Some research on the large-scale social network structure of chimpanzee groups has been conducted (Rushmore et al. 2013; Anderson et al. 2002), and very recently the inter-group interactions of mountain gorillas (Mirville et al., 2018a; b). Even less is known about the social structure of western gorillas, particularly that occurring above the group level, despite growing evidence for larger community-level social structure beyond the group (Forcina et al., 2019). This lack of knowledge about the higher-level social structure in other ape species has led to difficulties understanding the process by which the complex, multi-level social structure present in modern humans has evolved.

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It is often assumed that the basal social traits at the human-chimpanzee split were very similar to those observed in extant chimpanzee and bonobo societies (Sayers and Lovejoy, 2008). A major problem with this assumption is a lack of comparison with an outgroup. When comparing between only two related species, inference of ancestral traits can only be attempted when both traits are present, as this would suggest that the trait evolved prior to the divergence of these species. Any differences in traits could be due to the evolution or loss of a trait in either phylogeny after divergence. An outgroup is therefore fundamental to infer what may have been present in the last common ancestor. In anthropology there is a tendency to assume any trait present in humans and absent in chimpanzees has evolved in humans subsequent to their divergence, whilst traits present in chimpanzees but absent in humans are often assumed to have been present in the common ancestor and subsequently lost in the human lineage (Duda and Zrzavý, 2013). This human-centric view assumes that the vast majority of evolutionary change has occurred in the human lineage. However, it is equally probable that this evolutionary change could have occurred in the chimpanzee lineage or prior to the human-chimpanzee split.

To understand when traits evolved and which traits were present in the earliest hominins, it is necessary to use an outgroup. As the next closest human relative, gorillas provide an ideal outgroup giving the necessary context to human-chimpanzee comparisons. Given the information in Figure 1.2a, it cannot be known whether a trait evolved within the human lineage or was already present in the last common ancestor (LCA) of humans and chimpanzees. However, when the gorilla outgroup is also compared, we can see that if the trait is also present in gorillas, it most likely evolved prior to the gorilla-human-chimp split but was lost in the chimpanzee lineage (Figure 1.2b). If the trait is not present in gorillas, it suggests the trait evolved in humans, and therefore was not present in the earliest hominins (Figure 1.2c). Historically there has been far less research on gorillas than chimpanzees, and the vast majority of the research that has occurred has focussed on mountain gorillas, a high-altitude sub-species of very low population size, that may not well reflect the genus as a whole (Doran and Mcneilage, 1998).

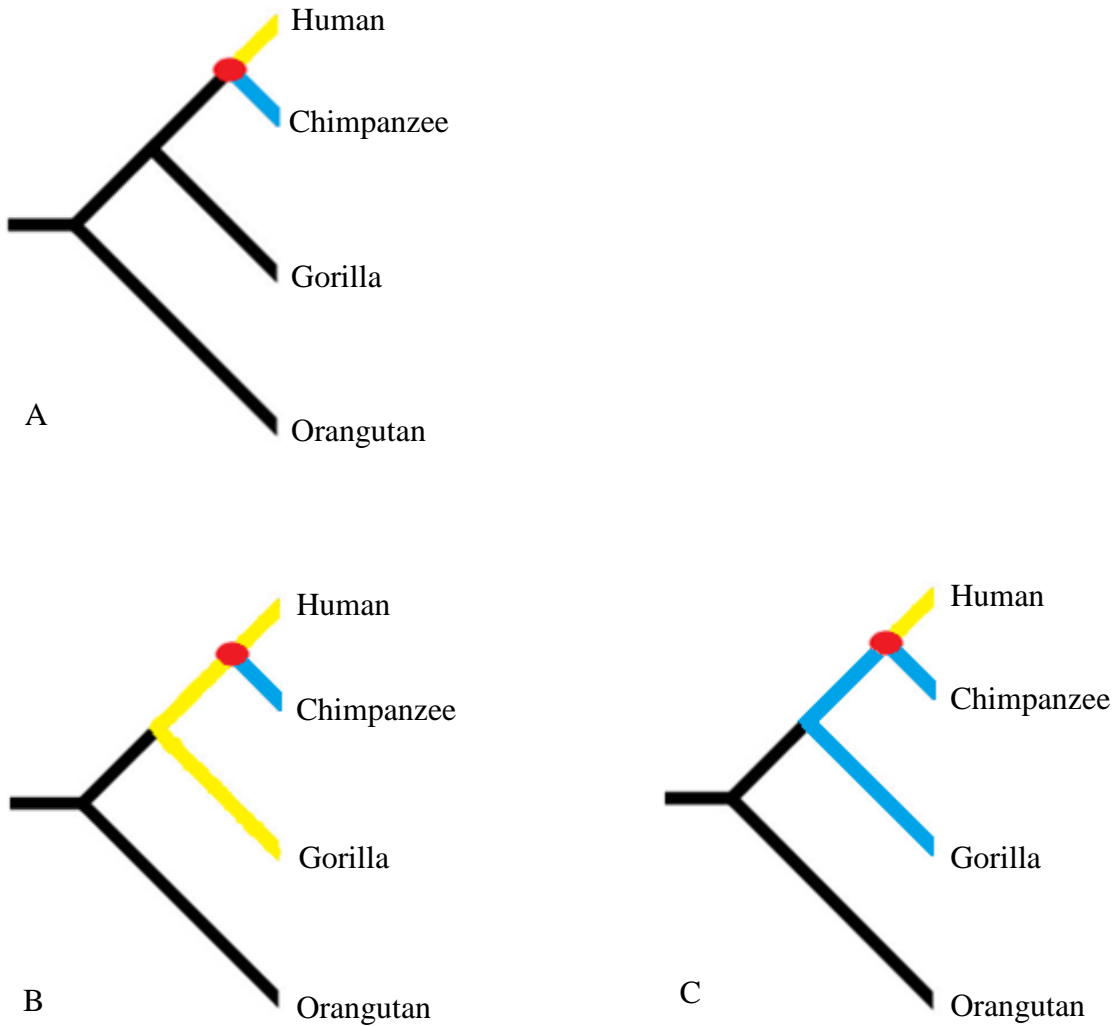


Figure 1.2. Comparison of traits (yellow and blue) between species to predict whether a hypothetical trait was present in the Last Common Ancestor (LCA), indicated in red. A) When only comparing two species you cannot predict when the yellow trait arose. B) When comparing with an outgroup that also shows the trait, it is most parsimonious to assume that the trait evolved prior to divergence from the outgroup. C) When comparing with an outgroup that does not show the trait (blue), it is most parsimonious to assume that the trait arose within the human lineage.

1.4.2 Multi-level social structure

Much of the debate around human social evolution focuses on the structure of the basic social unit at the divergence of humans and chimpanzees. The ancestral male kin-group hypothesis (Chapais, 2008) suggests that the ancestral hominin species, the last common ancestor (LCA) of chimpanzees and humans, formed multi-male, multi-female groups with a promiscuous

mating system, most similar to what is seen in chimpanzee groups today. Alternatively, stable breeding bonds could have appeared first in polygynous groups, with the ancestral hominin social structure being most similar to modern gorillas (Chapais, 2008). Evidence from the fossil record has been used in support of both sides of this debate (Larsen, 2003). However, throughout, the assumption has been that whichever the basic social unit, this was likely to represent the entirety of social structure present, with affiliations between these units, fundamental to human multi-level social structure, evolving well after the human-chimpanzee split (Foley and Gamble, 2009; Grueter, Chapais and Zinner, 2012). Whilst strong territoriality in chimpanzees suggests an absence of multi-level social structure (Manson and Wrangham, 1991), the structure of between-group affiliations in gorillas has never been fully investigated. If a multi-level social structure were observed in extant gorilla populations, this could suggest that this component of complex human social structure was already present at the gorilla-human-chimpanzee split, and would shed light on the social structure present in the ancestral hominin species.

1.4.3 Human territoriality and warfare

Extant human hunter-gatherer societies show a range of territorial behaviour from maintaining strict and exclusive use of an area by defence, to a more flexible use of resources and space (Dyson-Hudson et al., 1978), to friendly or peaceful intermingling with other groups (Duda and Zrzavý, 2013). Whilst warfare is rare in many human societies, the capacity for warfare appears to be a human universal, with territorial acquisition a central factor (Crofoot and Wrangham, 2010). Evidence of warfare has been found in the human lineage as far back as pre-historic hunter gatherers (Lahr et al., 2016), however little is known about the extent of warfare before this time and it remains a topic of great debate. Intergroup aggression in primates has been proposed to show evolutionary continuities with human warfare (Crofoot and Wrangham, 2010), with particular similarities between chimpanzees and humans (Wrangham and Glowacki, 2012). Chimpanzees show levels of between group aggression that are far greater than other troop-living primates, including coalitionary killing of individuals in neighbouring groups (Manson and Wrangham, 1991; Wilson et al., 2014). This has been proposed as evidence of warfare being a shared evolutionary trait between chimpanzees and humans (Wilson and Wrangham, 2003), and territorial defence providing an evolutionary basis for present day warfare. An understanding of the extent of territoriality

occurring in gorillas would provide further perspective for the evolutionary context of warfare and allow a greater understanding of the basal traits from which it evolved.

1.4.4 Kin-biased behaviour in humans

Strong male kin bonding is one social trait seen in chimpanzee societies (Mitani, 2009), thought to have been important in early hominin societies, enabling advantages such as cooperative predator defence (Foley and Gamble, 2009). Due to the dispersal of both sexes in gorillas, the extent of kin-biased behaviour in this species has been assumed to be fairly limited, with increased male kin bonding occurring after the split of gorillas from the chimpanzee-human common ancestor (Foley and Gamble, 2009). However, some evidence has been found to support the presence of kin-biased behaviour in gorillas (Arandjelovic et al., 2014; Bradley, Doran-Sheehy and Vigilant, 2007), including male kin bonding (Bradley et al., 2004). Alternative evidence suggests this bonding may be unlikely to occur due to the dispersal distances of male gorillas (Douadi et al., 2007), with neighbouring males showing little kinship (Inoue et al., 2013).

1.4.5 Disease as a constraint on social evolution

Due to the high mortality rates observed from infectious disease, it has long been hypothesised that the evolution of social interactions may have been constrained by selection to minimise exposure to disease (Freeland, 1976). There is much evidence to indicate the high costs of disease, in mortality rates of extant humans and apes (Bermejo et al., 2006; Murray and Lopez, 1997; Ryan and Walsh, 2011), as well as evidence that social structure and population densities influence disease prevalence (Davies et al., 1991; Wallinga, Edmunds and Kretzschmar, 1999; Nunn, Gittleman and Antonovics, 2000; Morris and Walsh, 2015; Kappeler, Cremer and Nunn, 2015). In humans, pathogen prevalence has been shown to correlate with cultural differences and collectivism, with stronger divisions observed between groups in tropical regions with higher pathogen prevalence (Fincher et al., 2008). This suggests that this high pathogen prevalence may be selecting for limited social interactions between groups. Generating a model of disease transmission through the gorilla social network may enable a better understanding of the epidemiological consequences of the social structure present in gorillas. This will improve understanding on the constraint disease places on sociality, with implications for understanding early human evolution and the

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evolution of disease in the human and primate lineage. In particular, it may aid our understanding of how the movement of human ancestors out of the forest, decreasing disease spill over and disease burden, may have allowed larger human groups and a super-spreading structure to develop, enabling the rapid transmission of culture.

1.5 The influence of social structure on disease transmission

Traditional epidemiological models have assumed that populations are evenly mixed, with the probability of contact between any pair of individuals being equal. In reality, populations are rarely this homogeneous, with social structure dramatically influencing the frequency with which different individuals come into contact (Heesterbeek et al., 2015; Grassly and Fraser, 2008). For example, pathogens are thought to transmit more rapidly and more widely in populations with more dispersal between groups, more interactions between groups and greater variability of group sizes (Craft, 2015).

One extreme example of the effect of sociality on disease transmission and mortality has been identified in the offspring of habituated chimpanzee groups. Kuehl et al. (2008) showed clear cycling patterns in infant mortality rates, with peaks of mortality associating with time points at which infants reached their age of greatest social play and therefore greatest social contacts with other infants. This then appeared to cause the reproductive cycles of mothers who lost infants to sync up, whose subsequent offspring would then reach their peak social play ages together. At this point mortality from respiratory pathogens in infants would again peak, with many mothers losing offspring, restarting their reproductive cycles and causing a continuing self-organised cycle of mortality. Variation in contact rates for particular demographics of a population due to social structure can therefore have important consequences for disease transmission and mortality.

1.5.1 Disease transmission through social networks

Using social networks to inform disease transmission models first became popular modelling sexually transmitted diseases in humans (Klovdahl, 1985), gaining further notoreity through its use identifying super-spreaders of Severe Acute Respiratory Syndrome (SARS) (Centers for Disease Control and Prevention, 2003; Meyers et al., 2005). Super-spreading structure occurs where certain individuals or groups come into contact with a far greater number of individuals or groups than the average for the population, as shown in Figure 1.3. The potential for this in gorilla groups has been indicated by increased contact at areas of high value resources such as forest clearings (known locally as *bais*), particularly for groups located close to such resources (Parnell, 2002a; Benavides et al., 2012). Super-spreading can dramatically speed up the rate at which a disease is transmitted (Lloyd-Smith et al., 2005) and

is also thought to have important consequences for the transmission of ideas, culture and genes, and therefore the process of evolution.

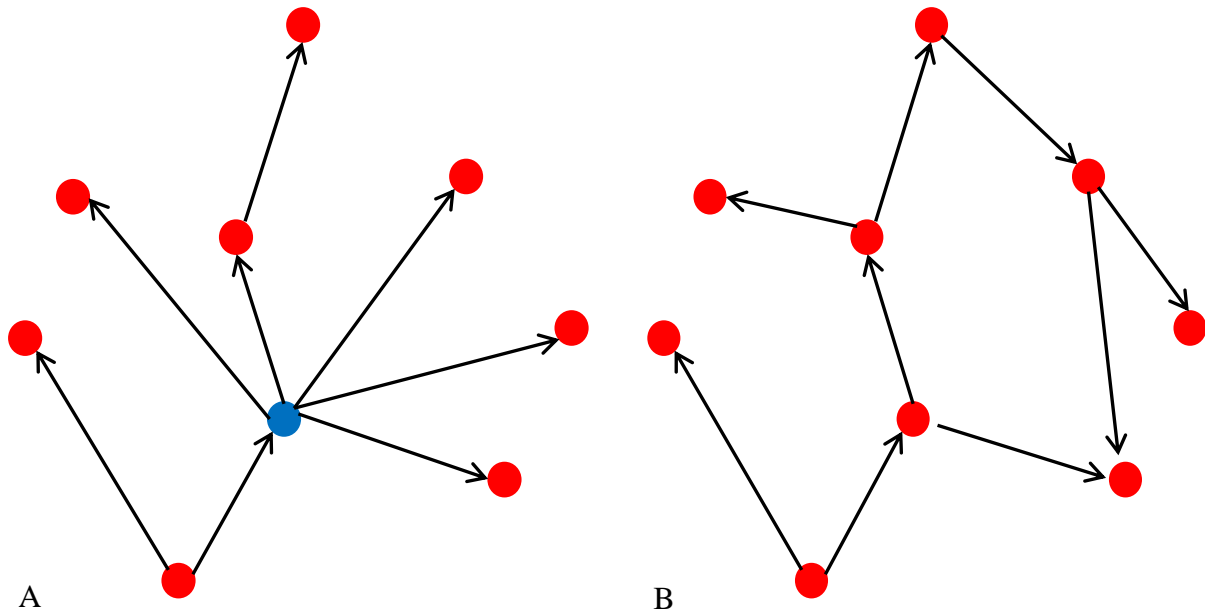


Figure 1.3. Transmission Networks A) with a super-spreading individual (shown in blue) and B) without super-spreading. With super-spreading present something can spread more rapidly through the population if it reaches a super-spreader early on.

Using social networks as a means to model the spread of diseases has been relatively underused in wild animal populations (Craft and Caillaud, 2011). However, it has recently begun to be used more widely with between 5 and 10 published studies using the technique annually (Craft, 2015). Use of the technique to investigate a chimpanzee community showed low amounts of super-spreader structure, although adult females and juveniles with large families were found to have significantly higher association rates than other individuals (Rushmore et al., 2013). This study did not, however, investigate transmission between neighbouring chimpanzee communities so its results can only inform on the prevention of disease spread within a community and not between neighbouring ones. In general, contact

between chimpanzee communities is thought to be minimal due to high territoriality (Watts and Mitani, 2001) and it is possible that this lack of a multi-level social structure could provide a selective advantage, minimising the spread of disease. This theory is supported by the finding that chimpanzees from two different communities were distinguishable by their differing gut microbiomes (Park et al., 2012).

The effect of territoriality on disease transmission was investigated in lion populations by Craft et al. (2011). These populations showed a surprising level of connectivity despite direct contacts between neighbouring prides being rare, indicating that territoriality does not always prevent disease transmission. This appeared to be due to a strong effect of occasional contacts between non-neighbouring prides, and not due to nomad individuals travelling between groups acting as superspreaders. However, contact between non-neighbouring groups was thought to occur due to prides following migratory prey and therefore this may not be more broadly applicable to other species or populations.

1.5.2 Testing the association between disease transmission and sociality

The majority of studies on disease transmission through social networks have investigated the social structure of a population and used this to estimate the disease transmission network. However, Bull et al. (2012) directly tested the association between disease transmission and social connectivity by demonstrating that pairs of Australian sleepy lizards that shared bacterial genotypes of *Salmonella enterica* were more highly connected in the social network of the population. This finding was further supported and developed by Vanderwaal et al. (2013) who investigated the transmission network in a wild giraffe population by sampling *Escheria coli* bacteria strains present in individuals, in addition to behavioural contact data, allowing a comparison of social network structure and the disease transmission network. They found that giraffes with a greater number of social connections usually had a greater number of connections in the transmission network, and a strong correlation between the social network developed from behavioural data and the transmission network developed from genetic analyses of *E. coli* strains. More recently, the association between social networks and gut microbe transmission patterns was identified in a primate society. Tung et al. (2015) showed interaction rates in the social network of wild baboons explained considerable variation in the gut microbiome, identified from shotgun metagenomic data. In chimpanzees, much of the gut microbiome was found to be transmitted through social

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interactions rather than from parent to offspring, with social contact promoting similar host microbial communities (Moeller et al., 2016). Together these findings provide a clear argument for the strong link between the social networks of animal hosts and the transmission networks of their microbiota, whether pathogenic or beneficial.

1.6 Studying wild gorilla populations

The first studies of gorilla behaviour were conducted in the 1960s by George Schaller and Dian Fossey, and focused on the mountain gorilla (MG) populations of the Virunga Mountains. From 1967 onwards, long-term study of MGs at the Karisoke Research Centre was conducted, and until recently contributed the vast majority of scientific knowledge on the genus (Taylor & Goldsmith 2002). In comparison to MGs, relatively little is known about the far more numerous and widespread WLG. Due to the dense and often inaccessible forest habitats of WLGs, the difficulties of tracking the species, and the considerable time periods necessary for their habituation, rigorous behavioural research on this species was not successful until the 1990s.

Major breakthroughs in the study of WLGs came first from the monitoring of forest clearings; particularly the research programmes initiated at Mbeli Bai (in 1995) and Maya Nord (in 1996), enabling the first direct, long-term observations of WLGs. This was followed by the first successful habituation programmes for WLGs which began at Lossi and Mondika in 1995 led by Magdalena Bermejo and Diane Doran, respectively, and Dzangha-Sangha in 2001 led by Chloe Cipoletta. After several decades, there are now multiple successful research sites working with habituated WLG groups in Central African Republic, Gabon, Cameroon and Republic of Congo; however, Mbeli Bai is the only forest clearing site at which gorillas remain consistently studied. In recent years, technological advances in areas such as camera trapping, telemetry, and drones have provided potential novel strategies for studying gorilla populations, but these remain relatively unexplored thus far (Head et al., 2012).

1.6.1 Monitoring at forest clearings (bais)

Herbaceous swamp clearings (bais) are prevalent across much of the WLG range, including Central African Republic, Gabon and Republic of Congo. Gorillas visit these forest clearings due to the presence of high mineral content vegetation (Magliocca and Gautier-Hion, 2002), on which WLGs usually feed for many hours at a time. This allows individual gorillas to be identified and studied from research platforms located on the edge of these forest clearings (Figure 1.4).



Figure 1.4. Researcher (Robin Morrison) at Mbeli Bai, WCS Congo

Such research sites provide an impressive source of long-term data on large gorilla populations, with data collection involving little to no disturbance of the population. However, gorilla groups are estimated to spend only about 1% of their time in bays, visiting less than twice a month on average (Stokes, 2004), such that monitoring of gorillas in forest clearings can only provide an incomplete account of the behaviours taking place in the populations studied. This method is also highly reliant on the identification of individual gorillas from considerable distances. For the most part this difficulty is overcome by extensive periods of training for researchers at these study sites. However, human error will inevitably lead to some misidentifications, particularly at greater distances from the observation platform or in difficult weather conditions. This is further complicated by the possibility that individuals may not visit a clearing for years at a time and may not be recognisable upon their return leading to their identification as an entirely new individual. Despite these difficulties, forest clearing observations provide important long term demographic data and enable unbiased observation of gorilla populations with minimal disturbance from researchers (Breuer et al., 2009; Parnell, 2002b; Levréro et al., 2007; Magliocca and Gautier-Hion, 2003; Stokes, 2004).

1.6.2 Habituation

Habituation of gorilla groups has been the primary method by which the day-to-day life of gorillas has been studied. In contrast to the infrequent monitoring of groups when they choose to visit a clearing, habituation allows data to be collected on the same group daily,

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enabling a far more in-depth understanding of the behaviour of these groups (Masi, Cipolletta and Robbins, 2009). This method is considerably more invasive than monitoring from clearings, with researchers regularly approaching to within 10m of gorillas, which may itself alter the behaviour of the individuals being observed (Crofoot et al., 2010). However it also enables close behavioural observation across a range of habitats, which is not possible from forest clearing monitoring.

Research on habituated groups varies between sites, from sites where researchers visit groups only for a few hours a day, to sites where researchers attempt full day follows from nest site to nest site, recording behaviour throughout the day. The process of habituation in WLGs takes roughly 2-6 years depending on the group and the habitat (Setchell and Curtis, 2011; Doran-Sheehy et al., 2007). This means that larger, stable groups with younger dominant males are usually targeted for habituation, to reduce the likelihood of group disintegration after the considerable investment of time and money necessary for habituation. Therefore, whilst a large proportion of gorilla behavioural research is dependent on habituated groups, those individuals do not represent a random sample of the gorilla population. Solitary males and bachelor groups are yet to be studied by habituation, and the biases involved in choosing a group for habituation mean that certain group types are far less likely to be studied than others.

A further disadvantage of habituation is the potential for gorilla behaviour to be altered in response to the close proximity of researchers. Whilst it is believed that over the years of habituation, gorillas should gradually become so used to human observers that they have little influence on their behaviour, we cannot truly know how groups may have behaved if no one was there to observe them. Furthermore, the presence of human observers may have considerable influence on the pattern of female transfer, especially into habituated groups. Again, the extent of this influence is unknown: however, female transfer into habituated groups appears to be fairly rare, with most cases involving transfer from another habituated group. It would seem likely that the strong human presence may reduce the likelihood of an unhabituated female transferring into a group, and also reduce the likelihood of her remaining with that group. Despite these limitations, habituation provides the only currently feasible method to provide a thorough picture of the daily behaviour of WLGs and is therefore fundamental for providing detailed data on feeding behaviour, movement patterns and within-group social dynamics.

1.6.3 Camera trapping

Camera trapping is a technique that has been used for scientific purposes since the early twentieth century (Chapman, 1927). However technological advances in the last few decades have enabled a transition from relatively crude, trip-line activated cameras, to high-tech motion and heat activated digital cameras (Swanson et al., 2015). Camera traps all follow the same basic concept of a camera, protected by a weather proof case, activated automatically by a mechanism that triggers when an animal moves in front of it (Rowcliffe and Carbone, 2008). The technique of camera trapping has proven highly successful for the detection of rare and elusive species and has therefore been used widely to investigate abundance, range and habitat use of species for which monitoring has previously proven difficult (Silver et al., 2004; Karanth et al., 2006; Ancrenaz et al., 2012). With recent technological advances, the amount and quality of data that can be collected using camera trapping has rapidly increased, whilst the costs associated with these studies has decreased. Many studies have used identification of individuals from camera trap photos and videos in their analyses, for example to enable capture-recapture based estimates of abundance (Silver et al., 2004; Karanth et al., 2006; Soisalo and Cavalcanti, 2006; Wang and Macdonald, 2009).

Camera trapping has only recently begun to be used as a method to study wild gorilla populations, with the first published studies focusing on habitat use and distribution (Head et al., 2012; Vanthomme et al., 2013; Nakashima et al., 2013). Head et al. then used individual identification of gorillas from camera trap footage to enable density and home range estimation (Head et al., 2013). However, their use of between 8 and 45 camera traps over a 20 month period resulted in only 103 images that could be positively identified, demonstrating the high sampling effort necessary to generate gorilla data using camera trapping. Camera trapping represents one of the least invasive methods of studying gorillas, with the potential to provide insight into natural behaviour in the absence of human observers. However, the low likelihood of gorillas passing and activating any given camera, and the even lower likelihood that they remain in the vicinity long enough for much behavioural data to be collected, sets a considerable limit on the types of question that can be investigated using camera trap footage. Furthermore, consideration of both the site in question and the behaviours of gorillas in that region are crucial to enable the positioning of cameras for sufficient data collection.

1.7 Research Questions

The aim of this thesis is to investigate the large-scale social structure of western lowland gorillas, using novel technologies and analytical methods to overcome the considerable difficulties in monitoring large numbers of gorillas simultaneously. After an overview of the study sites and methods used in this thesis (Chapter 2), the following questions are investigated:

Chapter 3

Question 1: Do western gorillas have a multi-level social structure?

Question 2: What is the basis for this multi-level social structure?

Hypothesis H₁: Kinship: group leaders and solitary males in the same higher-level social units (above the group level) are made up of related males.

Hypothesis H₂: Range overlap: groups and solitary males in the same higher-level social units have greater range overlap.

Chapter 4

Question 3: Do social tiers in a multi-level gorilla social structure scale consistently by size (hierarchical scaling pattern), and if so, is that pattern consistent with that observed in other multi-level mammalian societies?

Question 4: Could the reproductive capacity of females explain a hierarchical scaling pattern of social unit sizes via kinship associations?

Question 5: How do our findings on gorilla social structure influence our understanding of the evolution of ape social systems?

Chapter 5

Question 6: Do we observe super-spreader structure at forest clearings?

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Question 7: Is this super-spreader structure likely to be present across gorilla ranges?

Question 8: Can we predict which individuals or groups are likely to act as super-spreaders?

Question 9: Can we predict transmission of a yaws outbreak through the social network?

Chapter 6

Question 10: How does the location of conspecifics influence western gorilla foraging patterns?

Hypothesis H₁: Gorilla groups avoid each other to reduce competition.

Hypothesis H₂: Gorilla groups actively associate with each other, enabling social benefits such as cooperative foraging.

Question 11: Do gorillas interact preferentially with their neighbours relative to non-neighbouring groups?

Question 12: Do western gorillas exhibit elements of territoriality in their space use?

Hypothesis H₁: gorilla groups avoid areas in the centre of another group's home range.

Hypothesis H₂: gorilla groups avoid each other more when close to the centre of one of their home ranges.

Hypothesis H₃: gorilla groups avoid regions close to another group's home range depending on the relative size of that other group in relation to themselves due to dominance effects.

Hypothesis H₄: gorilla groups avoid regions close to another group's home range depending on the combined size of both groups due to the reduced likelihood of finding adequate resources.

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Chapter 2: Study Sites, Data Sets and Methods



Photo by Robin Morrison at Mbeli Bai Study, WCS Congo

2.1 Study sites and data sets

The data used in this PhD were collected from four Western Lowland Gorilla (WLG) study sites: Ngaga Research Site, Lokoué Bai, Maya-Nord Bai and Mbeli Bai. All four sites are located in northern Republic of Congo, within the Congo-basin rainforest, the world's second largest tropical forest (Figure 2.1). I spent 3-4 months at both Ngaga Research Site and Mbeli Bai (the two sites from which the majority of the data for this research are gathered) undertaking and managing data collection. Many people contributed to the large datasets used from both locations, as specified below. Data from both Lokoué Bai and Maya-Nord Bai are published datasets from research programmes that are now completed and I therefore was not able to visit these sites to learn about, or contribute to, their data collection.

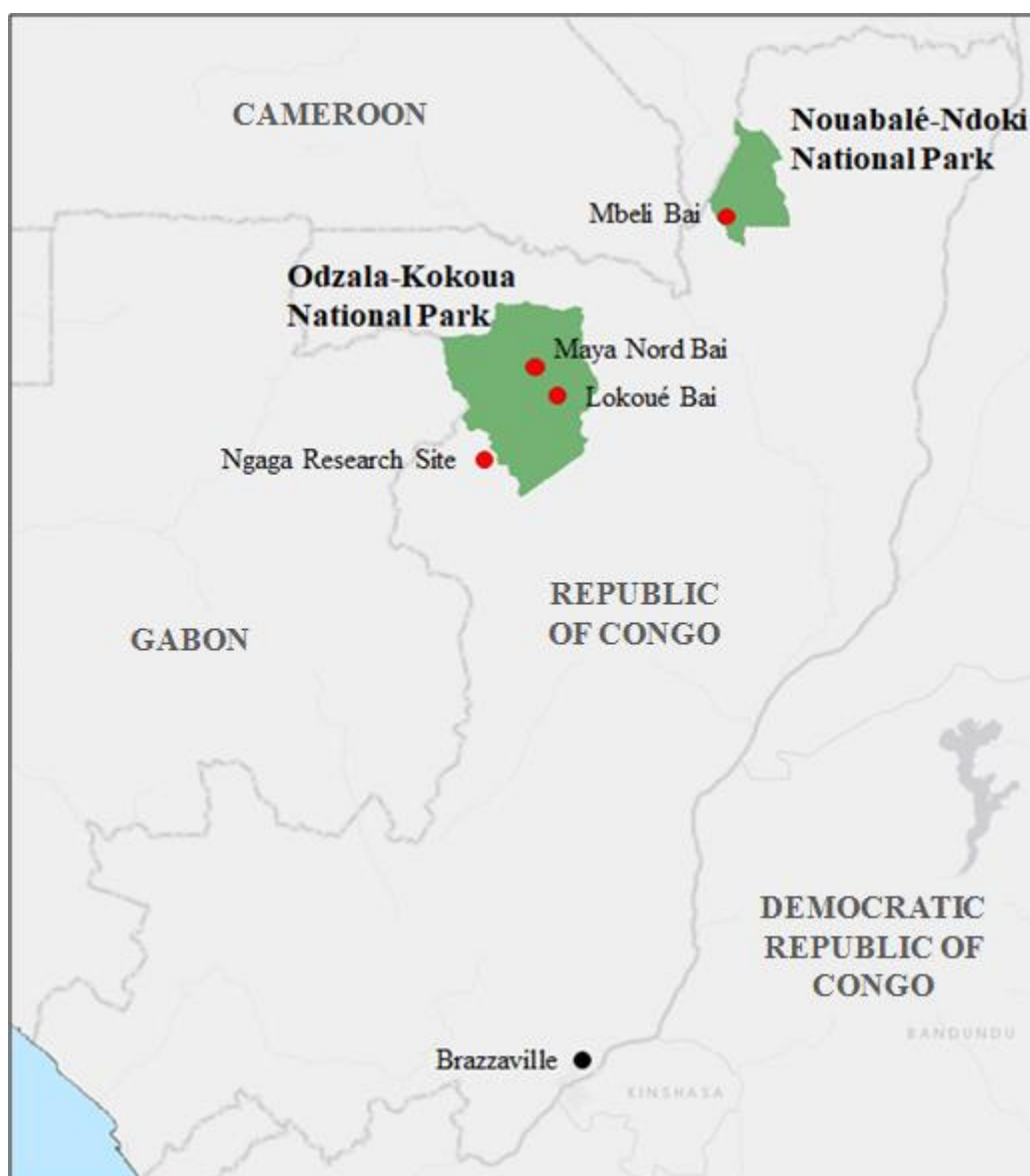


Figure 2.1. Locations of study sites (red) and national parks (green) within Republic of Congo from which data have been collected.

2.1.1 Odzala-Kokoua National Park

Ngaga Research Site, Lokoué Bai and Maya Nord Bai are all located either within or in the peripheral regions of the Odzala-Kokoua National park, and within the Dja-Odzala-Minkebe Tridom Landscape. The Odzala- Kokoua National Park is the largest protected area in the Republic of Congo, covering 13,000 km². This area contains an estimated 24,000 great apes, 22,000 of which are WLGs (Lamprecht et al., 2012). However, this estimate represents a

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decline in gorilla numbers, of nearly 50% between 2005 and 2012. This is thought to be primarily due to an increase in hunting within the park and the after effects of the Ebola epidemic which spread to the area in 2002, particularly affecting the west of the park, where it was present until at least 2005 (Lamprecht et al., 2012; Caillaud et al., 2006). The density of gorillas varies across the park with an estimated 0.88 gorillas per km² in the North and 2.34 gorillas per km² in the South, however prior to the Ebola outbreak, during the period in which the Lokoué data was collected, gorilla densities of up to 10.2 individuals per km² were recorded in regions of the park (Bermejo, 1999). Due to the close proximity of this area to the equator, there is a bimodal climate consisting of two rainy seasons and two dry seasons, with annual rainfall between 1600mm and 2000mm (CBFP, 2006).

2.1.1.1 Ngaga Research Site

The Ngaga Research Site (0°24 N, 14°36 E) is located on the periphery of the Odzala-Kokoua National park, 12 km south-west of the park boundary. The Ebola outbreak of 2002 passed close by to this region but did not spread to the gorilla population here which continues to maintain a high density of WLG groups, as well as 11 other primate species including chimpanzees. Habituation and research of gorillas in this area began in 2010, with tourism commencing in 2012. There are currently four gorilla groups at this site undergoing habituation.

The Ngaga dataset used in this thesis constitutes data collected by camera trapping between January 2015 and July 2016, amounting to 5403 camera trap days. During this period, 568 distinct gorilla visits were recorded, including those from a total of 24 identified groups. Camera traps were monitored and deployed by the author, together with Magdalena Bermejo, Germán Illera, Dylan Morris, Emily Greathead and the Ngaga Research Site tracker and research team. Individual gorillas were identified and group sizes estimated by Magdalena Bermejo.

2.1.1.2 Lokoué Bai, Odzala National Park

Lokoué Bai is a 4ha forest swamp clearing (0°54 N, 15°10 E) located close to the Lokoué river in the east of Odzala-Kokoua National Park. Monitoring of this gorilla population began in April 2001 by Sylvain Gatti and Florence Levrero, continuing until September 2002. Monitoring then began again in November 2003 continuing until September 2005 (290 monitoring days total). During this time an Ebola epidemic rapidly reduced the number of gorillas visiting the bai, with 95% mortality of the bai population observed by the end of the study period (Caillaud et al., 2006). Due to the low number of gorillas visiting the clearing after the Ebola outbreak, regular monitoring was not continued after 2005; however, sporadic monitoring has taken place.

The Lokoué data set used in this PhD is taken from Florence Levréro's PhD thesis. The data cover a period of 409 days, providing visit data on 21 solitary males and 27 groups, made up of a total of roughly 205 individual gorillas. Between April 2001 and September 2002 the bai was monitored daily from 7:00 to 16:30 from a 4m platform on the forest edge, with individual gorillas identified using 10 x 42 binoculars and 60 x 80 spotting scopes. During this period the prevalence of lesions due to an outbreak of Yaws disease was also recorded. For a more detailed account of collection methods for this dataset see Levréro (2005).

2.1.1.3 Maya-Nord Bai, Odzala National Park

Maya-Nord Bai (1° 08 N, 15° 00 E) is located in the north of the Odzala-Kokoua National Park. It is an 18 ha saline swamp clearing, discovered by researchers in 1996 via radar imaging. After preliminary observations in October 1996, full day monitoring (approximately 6:00 to 17:00) ran from November 1996 to June 1996 (104 observation days). Observations were made from a 4-m high platform on the forest edge and individual gorillas were recognised using 10 ×40 mm Leitz binoculars and a 60 × 80 Kowa scope. The published data used from this research project includes the number of solitaries and groups identified and the age/sex class composition of these groups and the overall population (Magliocca, Querouil and Gautier-Hion, 1999).

2.1.2 Nouabalé-Ndoki National Park

The Nouabalé-Ndoki National Park (NNNP), established in 1993, covers 4,240 km² of forest bordering the Central African Republic (CAR) to the west, and connecting with the Dzanga and Ndoki protected areas. These three areas, along with Lobéké in Cameroon form the Sangha Trinational; the world's first trinational, trans-boundary world heritage site. The NNNP represents one of the most pristine regions of rainforest in the world, having never been logged and with a low human population density of 1-2 inhabitants per km² in regions surrounding the park. It receives an average of 1,250 mm of rainfall annually. The NNNP is home to three long-term ape research sites: Mondika Research Site, the Goualougo Triangle Ape Project and the Mbeli Bai Study. At Mondika, the behaviour, ranging and feeding ecology of gorillas has been studied since 1996 through the habituation of wild gorilla groups, with 3 groups currently habituated at this site (Doran-Sheehy et al., 2007; Luef, Breuer and Pika, 2016). The Goualougo Triangle Ape Project, which began in 2003 when this region was annexed onto the NNNP, primarily monitors a habituated chimpanzee community but also non-invasively monitors the gorillas present in the region, with a goal to undertake research with direct applications for ape conservation (Morgan et al., 2006). The Mbeli Bai Study is the NNNPs longest running research site, located in the south-east tip of the park and focuses on monitoring the visits of a variety of species to the Mbeli Bai forest clearing, enabling long-term non-invasive monitoring of social behaviour and demography.

2.1.2.1 Mbeli Bai, Nouabalé-Ndoki National Park

Mbeli Bai (02°15 N, 16°24 E) is a 13 ha forest swamp clearing containing mineral rich soils and aquatic vegetation, that attracts animals from the surrounding forest, including a large population of WLGs. The study site was officially established in 1995 to monitor the gorilla, elephant, sitatunga and buffalo populations visiting the forest clearing. These populations have been monitored almost continuously for over 2 decades, enabling a total of 479 individual gorillas and 536 forest elephants to have been studied at the site by the end of 2016 (Parnell, 2002; Breuer et al., 2010; Stokes, 2004; Robbins et al., 2016; Breuer et al., 2009; Breuer, Ndoundou-Hockemba and Fishlock, 2005).

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Data used in this PhD were collected between 2010 and 2016 from a 9-m observation platform. Data during this period were collected daily (approximately 6:45-16:45), using spotting scopes, binoculars and photography, with data collection overseen by Thomas Breuer, Marie Manguette, Jana Robeyst and Milou Groenenberg. A more detailed account of data collection methods can be found in Breuer et al. (2009). Data collection continues to date, having subsequently been overseen by the author and Claudia Stephan. Data collection was not possible for a considerable proportion of 2016 and therefore data collected prior to this period is used in this PhD.

2.2 Analytical methods

2.2.1 Individual identification

The identification of individual gorillas has historically used qualitative features, and this method has been used to identify individuals and groups at all three forest clearing sites, from which data has been used in this thesis. Gatti et al. (2004) used the following features for identification of 377 different gorilla individuals:

- “1) scars, wounds, or skin diseases that left highly visible, irregular marks*
- 2) physical handicaps*
- 3) for dependent infants, the presence of their identified mother*
- 4) face shape and ‘nose prints’*
- 5) pelage patterns, stature, and head-top shape (for adult males), and group composition”.*

This method is highly labour intensive and also prone to human error, although it has proven highly effective in the past. Head et al. (2013) used this method to positively identify 22% of gorilla camera trap images, with the reliability of these identifications investigated using an inter-observer reliability test. Experienced observers showed the highest reliability scores (0.84 for male gorillas and 0.74 for females) which were significantly higher than those for inexperienced observers and ecoguards. This remains the only widely used method of identification in gorillas, with high levels of training and experience thought to considerably reduce the problem of human error. However, as Head et al. (2013) demonstrated, there is still considerable discrepancy in identifications even between experienced observers.

The field of animal biometrics has recently emerged with an aim to reduce the problems of human error and labour costs of traditional identification methods using automated software (Kühl and Burghardt, 2013). These methods have been applied to gorilla and chimpanzee camera trap footage to distinguish between the genera with 89-97% accuracy in ideal conditions, using face-detection algorithms developed from those used for humans (Ernst and Kublbeck, 2011). This was further developed to identify chimpanzee individuals, with

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detection and identification of wild individuals possible roughly 70% of the time (Loos and Ernst, 2013). Both global features such as distance ratios between facial landmarks, and local features such as differences under the eyes and around the nose, were used to distinguish between individuals. It has subsequently been developed further to enable individual identification of chimpanzees from video footage (Loos and Kalyanasundaram, 2015). This will potentially provide a less time-consuming alternative method of data processing. However the development of software enabling reliable automated individual identification of gorillas from photo or video footage appears to still be some way off.

A further option is the use of citizen science or crowd sourcing. This has been used most notably in the case of the Snapshot Serengeti Project in which 28,000 online volunteers provided 10.8 million classifications (Swanson et al., 2015). The volunteers recorded the species, number of individuals, certain behaviours and the presence of offspring in footage from a camera trap project in the Serengeti National Park, Tanzania. A similar project is currently underway classifying chimpanzee camera-trap footage as part of the ‘Chimp and See’ project of the Max Planck Institute for Evolutionary Anthropology (Max Planck Gesellschaft, 2015). Project volunteers are given the option to try and identify individual chimpanzees; however, it is unknown how good the general public would be at individual identification and any project relying on this strategy would need to verify crowd sourced identifications by comparing against those of an experienced researcher.

Individual identification is a crucial requirement for collecting long term behaviour on individual animals and their social groupings. Whilst qualitative features of the individuals have been historically used, a variety of technological advances are beginning to provide alternative methods that may provide higher accuracy and reduce human error. The potential for these three main methods were assessed in the process of developing data collection methods for the Ngaga data set, as discussed above. Whilst novel technologies are likely to provide useful solutions to issues of human error in identification in the future, they are not yet at a progressed enough stage for identification of individual gorillas to provide a better alternative to traditional methods via human recognition of qualitative features.

2.2.2 Camera trapping

Head et al. (2013) conducted the first attempt to estimate gorilla group home ranges from camera trap data. They monitored eight groups in a 60 km² study area using between 8 and 45 camera traps over a 20-month period, totalling roughly 17,400 camera-trap days (if no days were lost due to camera malfunction). They estimated gorilla density in the region at roughly 1.2 gorillas per km², recording 471 gorilla images (roughly one image for every 36.9 days of camera trap deployment). Gorilla groups could be positively identified in 103 (22%) of the total gorilla images. The home ranges they estimated from camera trapping were 84.7% the size of those estimated from direct observations, suggesting that camera trapping may provide a valuable non-invasive and less resource-intensive method for monitoring wild gorilla populations.

To investigate the potential for camera traps to provide information on the ranging patterns of the Mbeli Bai gorilla population, I conducted a two month pilot study. During this time 33 cameras were placed at 18 locations between 0.5 and 2 km from the bai. These cameras functioned for a total of 972 camera traps days, recording 27 separate gorilla visits (>1 hr between each visit at a site). I assessed 9 (33%) of these visits to provide adequate footage for a potential identification, as they showed clear footage of the face of an individual. Gorillas were recorded at 11 of the 18 total locations, with a gorilla visit recorded on average every 16.5 days, 38 days and 43 days for cameras located at fruiting trees, termite mounds and forest trails, respectively. These results demonstrated the feasibility of detecting gorilla groups via camera trapping in the Mbeli region, especially through the use of fruiting trees, with a considerable increased rate of detection when compared with the results of Head et al. (2013). However, the low number of potentially identifiable footage over the 2-month period indicated that a considerable investment of research time would be necessary to enable robust home range estimates via this method.

At the Ngaga Research Site, we have observed a novel root feeding behaviour, whereby gorillas will dig to feed on the roots of primarily *Maranthes glabra* trees. This unusual behaviour, as yet unobserved in any other gorilla populations despite the widespread prevalence of this tree species, provides an excellent opportunity to record gorilla groups via camera trapping. The digging behaviour of gorillas clears the area surrounding the tree of low level vegetation, enabling a clearer view of gorillas in the tree's vicinity. Adult gorillas will

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usually sit for many minutes, and in some cases, hours, feeding on the roots, enabling the thorough identification of the group from multiple video recordings. Unlike short term food sources such as ripe fruits, many root sites appear to remain “in-season” for months or years at a time, allowing camera traps to provide useful gorilla footage over a longer time frame. This feeding behaviour provides a unique opportunity at the Ngaga Research Site for intense non-invasive monitoring of the gorilla population via camera trapping at root sites.

Comparison between the success of camera trapping at Mbeli Bai and Ngaga Research Site was performed by comparing capture rate and individual identifications across all 972 camera trap days at Mbeli Bai and the first 972 camera trap days of the Ngaga camera trap project. During these periods 146 gorilla visits, of which the gorilla group could be identified in 128, were recorded at Ngaga, compared with 27 gorilla visits of which 9 had the potential to be identified at Mbeli. Visits were recorded on average every 6.7 days at Ngaga root sites, considerably more frequently than the 16.5 days, 38 days and 43 days for cameras located at fruiting trees, termite mounds and forest trails surrounding Mbeli bai. Whilst direct comparison is hindered by a lack of precise population density estimates at each of these locations, these results suggest that where possible, monitoring of root feeding sites may provide a considerably more efficient method of monitoring gorilla populations. They also demonstrate that camera trapping at Ngaga, utilising the root feeding behaviour will provide considerably more information on the ranging patterns of gorilla groups, with much more research effort required at Mbeli Bai to collect similar amounts of data.

2.2.3 Bai monitoring

Bai monitoring represents the best-established method for monitoring large populations of gorillas. As discussed in Chapter 1, research sites such as Mbeli Bai provide invaluable long-term data on past and present relationships within and between gorilla groups. Whilst camera trapping at root sites clearly has exciting potential for monitoring inter-group interactions across their ranges, this novel method will take considerable time to develop. With data collection only beginning in 2015, we are a long way off from developing the 20+ year dataset available at Mbeli Bai. Therefore, this PhD will first use historic forest clearing data from bai monitoring to investigate the underlying social structure present in gorilla bai

populations, before investigating how camera trapping at root sites can expand on these findings.

2.2.4 Modelling inter-group dynamics

Traditionally, aspects of primate society have been studied as linear variables e.g. through regression and correlation, studied in isolation and combined to explain the society as a whole. These traditional studies do not necessarily account well for real world properties such as the nonlinear dynamics of processes, simultaneous interactions of individuals and local spatial configuration (Kohler and Gummerman, 2000). To reduce these problems, systems approaches such as social network analysis and model comparisons have been increasingly applied to investigations of social systems, particularly in social epidemiology (El-Sayed et al., 2012).

2.2.4.1 Social network analysis

The network approach to studying social systems builds complex social structures from individual interactions (Farine and Whitehead, 2015; Silk et al., 2017; Whitehead, 2008). Each network consists of nodes and edges with nodes representing individual animals or groups, and the edges representing the interactions between them. This allows traditionally studied individual encounters to be placed in their wider social context, enabling an understanding of the population level dynamics (Krause, Croft and James, 2007). Simply understanding the frequency of certain behaviours within a population will not always tell the full story, as it is the way in which an individual is interconnected with other individuals demonstrating a certain behaviour that can influence evolutionary processes. Network theory uses a variety of descriptors to describe an individual's connections such as degree, path length, clustering coefficient, betweenness and centrality (Table 2.1). These descriptors can also be applied to the network as a whole to describe the more global properties of the system. The use of network analysis allows the investigation of how disease and other factors flow through this system between network nodes. In this way it is possible to build an understanding of the role played by individuals, groups and overall network structures in influencing transmission within the network (El-Sayed et al., 2012). I used social network

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analysis to quantify the social structure present in both the Lokoué and Mbeli Bai populations (Chapters 3 and 4), and investigate the potential to predict disease transmission through the Lokoué Bai population (Chapter 5), exact methods of which are given in the individual chapters.

Table 2.1. Definitions of social network descriptors from Krause et al. (2007) and Croft et al. (2008).

Path Length	<i>number of connections on the shortest path between two individuals</i>
Clustering Coefficient	<i>the degree to which an individual's immediate neighbours are connected</i>
Centrality	<i>The extent to which an individual's position in the network is important to the structure of the network (degree and betweenness are both measures of centrality).</i>
Degree	<i>number of immediate neighbours</i>
Betweenness	<i>the number of shortest paths between pairs of individuals that pass through a particular individual</i>

2.2.4.2 Bayesian inference

The use of model selection using Bayesian statistics is rapidly increasing in the field of ecology, as it allows the robust comparison of the explanatory power of multiple potential models (Hooten, Hobbs and Ellison, 2015; Ellison, 2004). In contrast to frequentist statistics where the probability of the data occurring given a specific hypothesis is calculated, Bayesian inference measures the probability of a hypothesis being true given the available data, allowing clear comparison of, and discrimination between, a variety of alternative hypotheses. This has been a key motivation behind its growing use in population and community ecology where there is a particular need to discriminate between many competing hypotheses, and assess the level of uncertainty in different model parameters (Ellison, 2004).

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Another key difference between frequentist and Bayesian statistics is the ability to explicitly incorporate prior knowledge into Bayesian approaches enabling models to take account of previous findings, which can be particularly useful when modelling the movement patterns or behaviours of species on which a considerable amount of information is already known. I used Bayesian model comparison to model the movement patterns of gorilla groups at the Ngaga Research Site, investigating how movement patterns were influenced by conspecific gorillas (Chapter 6). This approach allows estimation of the groups' home-range centres within the model, taking account of the relative quality of different resource sites and of how the movement patterns of neighbouring gorillas might influence their own movement.

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Chapter 3: The Multi-level Social Structure of Western Lowland Gorillas



Gorilla gorilla gorilla

Photo by Robin Morrison at Mbeli Bai Study, WCS Congo

3.1 Abstract

The primary focus of research on western gorilla social structure has historically been family groups, due to their potential for habituation. However, these groups have extensively overlapping home ranges and often aggregate at resource hotspots. There are also reports of affiliative interactions between groups and genetic evidence that silverback males may choose to live in close proximity to neighbouring groups led by related silverbacks. This evidence is all suggestive of the potential for social affiliations between groups to represent a higher level of social structure. Despite this, there remains no quantifiable model of gorilla inter-group interactions and little understanding of the structure of western gorilla society above the family group level. One major reason for this is that western gorilla home ranges

span large swaths of thick tropical forest, making observations on inter-group social interaction difficult. To circumvent this problem, I analysed western lowland gorilla (WLG) observational data from two mineral rich forest clearings in the Republic of Congo, using network modularity analysis and hierarchical clustering to quantify social structure within these populations. In both gorilla populations, two hierarchically nested tiers of social structure were detected. These occurred through associations between gorilla groups and solitary males and were demonstrated to have a basis in kinship at one of these forest clearing sites. These findings demonstrate the presence of a previously unquantified multi-level social structure in WLGs, with similarities to human social bands or clans. This strongly supports a multi-level approach to understanding gorilla society over traditional group-based approaches and suggests that such an approach may enable the detection of further social tiers and increased social complexity in some of our closest evolutionary relatives.

3.2 Introduction

Humans have a highly complex, multi-level social system, in which bonds between multiple stable family groups form higher-level social units, and bonds between these social units in turn create higher level social groupings. This is demonstrated in hunter-gatherer societies, where multiple families may form bands for subsistence activities, and multiple bands may form communities using a shared dialect (Grueter, Chapais and Zinner, 2012). Small-scale bands made up of multiple family units clustered by kinship and affiliation, showing reciprocal sharing, altruism and cooperative production, form a model of social structure thought to be shared by the majority of human societies over the last several tens of thousands of years (Kaplan, Hooper and Gurven, 2009). In traditional human societies, higher level social tiers are formed from extended family, so that as the tier level increases, the level of relatedness of individuals within those tiers decreases (Wittemyer, Douglas-Hamilton and Getz, 2005; Grueter et al., 2012). Strong kin bonding within these social tiers is thought to have provided important benefits such as cooperative predator defence (Foley and Gamble, 2009). Whilst some elements of human society appear unique, such as cumulative culture and extensive cooperation between non-relatives (Hill et al., 2011), the underlying multi-level social structure has been observed in a diverse array of animals including elephant and dolphin species (Wittemyer, Douglas-Hamilton and Getz, 2005; Cantor et al., 2012; Sah et al., 2017). It has widely been assumed to be absent in all non-human ape species (Foley and Gamble, 2009; Grueter, Chapais and Zinner, 2012; Grueter et al., 2012), but has been observed in papionins (Schreier and Swedell, 2009, 2012) and colobines (Grueter and Van Schaik, 2010), although these are thought to represent separate evolutionary events.

Western gorillas predominantly live in stable single-male family groups (Robbins et al., 2004; Bradley et al., 2005) which occupy overlapping home ranges (Bermejo et al., 2006; Bermejo, 2004) and often aggregate at resource hotspots (Walsh et al., 2007). There are numerous reports of affiliative interactions between these groups (Bermejo, 2004; Magliocca and Gautier-Hion, 2003) and even the regular movement of individuals between groups (Forcina et al., 2019). This suggests the potential for a multi-level social structure in WLGs in which gorilla groups cluster into larger communities made up of multiple groups that interact more frequently and more tolerantly. Due to the dispersal of both sexes in gorillas (Parnell,

2002b; Stokes, Parnell and Olejniczak, 2003), the extent of kin-biased behaviour in this species has been assumed to be fairly limited (Moore, 1992), with increased male kin bonding occurring after the split of gorillas from the chimpanzee-human common ancestor (Foley and Gamble, 2009). However accumulating evidence suggests the importance of kin-biased behaviour in gorillas (Arandjelovic et al., 2014; Bradley, Doran-Sheehy and Vigilant, 2007), with particular emphasis on inter-group male kinship due to the detection of groups led by highly related males living in close proximity (Bradley et al., 2004). However further genetic studies have suggested that male kin-biased behaviour may not be possible in other regions as neighbouring dominant males showed little kinship (Douadi et al., 2007; Inoue et al., 2013), potentially due to the greater dispersal distances of male gorillas.

Social network analysis provides an approach to studying social systems yet to be utilised in gorilla research, where complex social structures are built from individual interactions. This allows traditionally studied individual encounters to be placed in their wider social context, enabling an understanding of the population level dynamics (Krause, Croft and James, 2007). Whilst there is considerable research on group level social dynamics in gorillas, social structure above this level has not been thoroughly investigated or quantified. Here I use a social network approach to analyse long term data sets of gorilla group visits to two forest clearings in The Republic of Congo. I investigate whether visit patterns at these clearings are suggestive of the presence of a multi-level social structure in gorilla populations and investigate its underlying causes. This analysis follows the underlying assumption that gorilla groups and solitaries are aware of the location of neighbouring gorillas, particularly when in close proximity, and that the location of other gorillas therefore has the potential to influence their movement patterns. This assumption seems acceptable due to the long distances (up to 2km) over which chest-beating and other forms of gorilla auditory communication can be heard (Mirville et al., 2018).

As the study of social networks and societies more generally spans a vast range of subject areas, some confusion has arisen over the terminology used. Multi-level social structure in particular has been referred to, often synonymously with modular (Grueter and Van Schaik, 2010), hierarchical (Hill, Bentley and Dunbar, 2008), nested (Foley and Gamble, 2009) or meta-group (Walker et al., 2011) social structure. Here I use the term multi-level social system to refer to a social system in which core stable units are associated to form at least two hierarchically inclusive social tiers (Grueter et al., 2012), whilst the term modularity will be

used to describe the specific network metric relating to the proportion of links within and between groups (Newman, 2006).

3.3 Methods

3.3.1 Data sets

Two long term data sets of gorilla visits to forest clearings (known locally as bais) in the Republic of Congo were used in the analysis. The Lokoué data set, published by Levréro (2005), covers a period of 409 days from April 2001 to September 2002 and includes visit data on 205 individuals forming 48 gorilla units (27 groups and 21 solitary males). The Mbeli dataset is formed of data collected during 2010-2015 when the clearing was monitored year round (2191 days) and includes visit data on 271 individuals, forming 44 gorilla units (19 groups, 18 solitary males and 7 solitary males that formed groups during the study period). The Mbeli dataset was split into 3 separate 2-year datasets (Mbeli dataset A: 2010-2011, Mbeli dataset B: 2012-2013, and Mbeli dataset C: 2014-2015) of 730, 731, and 730 days respectively, to reduce problems from births, deaths, migrations and group disintegrations.

As WLGs move either in long-term stable groups or as solitary males, these formed the basic social unit investigated in the analysis. Groups or solitary males that visited fewer than 8 times during individual datasets were removed from the analysis. Maturing males were considered independent from their natal groups from the last point at which they were observed with said groups. Only solitary males that were independent prior to the start of the dataset study period were included in the analyses. Mbeli datasets A-C did not represent independent samples as they included many of the same individuals, at the same location, but at different time points, therefore representing pseudo-replicates of the same population. Analysis of these three time points was done to investigate whether modularity within this same population could be detected consistently across these different time points and whether social affiliations remained constant. In contrast, the Lokoué dataset was entirely independent of the Mbeli datasets, consisting of different individuals that did not overlap in space or time.

3.3.2 Generating networks

Networks were built to investigate association patterns occurring between groups and solitary males, with each node in the network representing a distinct group or solitary. Rates of

association (association metrics) between these nodes were calculated using the occurrences of visits to the forest clearings by groups or solitaries on the same day. Presence in the clearing within the same day was deemed an appropriate indicator of association due to the long periods gorilla groups spent in the bais (up to 2-3 hrs), and that auditory communication is possible across distances (>2km) greater than the average daily path lengths of gorillas (1.7-2.0 km). This suggests that gorilla units present in the bai within the same day are within distance of auditory communication (Mirville et al., 2018; Bermejo, 2004; Cipolletta, 2004; Doran-Sheehy et al., 2004). This broad approach to classifying associations was chosen to enable a considerably larger sample size and remain sensitive to potential long range social interactions. Metrics of association were calculated using two methods.

Method 1: The simple ratio association index (SR)

An association value was calculated for all pairs of groups or solitaries following the index specified in equation 3.1 (Ginsberg and Young, 1992; Whitehead, 2008). Values were calculated using the Asnipe R package (Farine, 2013), which was also used to generate 1000 null models for the dataset through data stream permutations.

$$(3.1) \text{ The simple ratio index} = \frac{x}{x + y_{AB} + y_A + y_B}$$

Where:

x = the number of sampling periods in which A and B were observed associated (in this case, the number of days on which both A and B were observed in the clearing, referred to as co-visits)

y_{AB} = number of sampling periods with A and B identified but not associated (in this case, this category was not possible given the definition of an association used here)

y_A = number of sampling periods with just A observed (in this case, the number of days on which A but not B were observed in the clearing)

y_B = number of sampling periods with just B observed (in this case, the number of days on which B but not A were observed in the clearing)

Method 2: The binomial probability association index (BP)

To account for environmental effects on visit rate and reduce the influence of extreme association values calculated from units (groups or solitaries) with low numbers of visits to the clearing, I developed an additional association index. This was based on the binomial probability of observing a pair of groups or solitaries in the clearing on the same day, more than the number of times demonstrated in the data (observed co-visits), as specified in equation 3.2, given how often both units visited over the entire study period.

(3.2) Cumulative probability distribution for a discrete random variable X , where $F(x)$ represents the cumulative probability distribution and $f(x)$ represents the probability mass function:

$$F(x) = P(X \leq x)$$

$$F(x) = \sum_{m=0}^x f(m) = f(0) + f(1) + \dots + f(x)$$

The binomial probability index (BP) was calculated as the square root of the cumulative binomial probability of seeing greater than the observed number of co-visits by a pair of units, across all days in the dataset as specified in equation 3.3.

(3.3) The binomial probability index:

$$BP = \sqrt{1 - F(x)}$$

$f(x)$ within the binomial probability formula was calculated using the total number of visits for each unit, whilst controlling for variation in the relative popularity of the clearing to gorillas due to potential seasonal or environmental factors, such as ripe fruits on the clearing edge (Walsh et al., 2007). This was controlled for to account for the potential for such factors to lead to units encountering one another more often, driving inflated association values. Relative popularity (RP) was calculated as shown in equation 3.4, by summing the number of units that visited the clearing on the day in question, the five days previous, and the five days after, to produce the expected proportion of total units to visit on that day.

$$(3.4) \text{ Relative popularity (RP)} = \frac{\text{Visit frequency in 11 day window}}{11 \times \text{Total visit frequency}}$$

The probability of a co-visit for each pair of units was calculated for each day by multiplying the number of times each unit visited the clearing over the entire period, and the relative popularity of that day. This was summed across all days to produce the expected number of co-visits across the study period for that pair. The first 5 days and last 5 days were not included in these analyses.

$$(3.5) \text{ Expected co-visits} = \sum \text{RP}^2 \times V_a \times V_b$$

Where V_a = Total visits by group A

and V_b = Total visits by group B

This expected co-visits value, divided by the total number of days was used as the mean probability of a co-visit within the binomial formula. $F(x)$ was calculated using the ‘pbinom’ function in R, with observed number of co-visits, mean probability of a co-visit, and the total days within the dataset, as input values.

Adjustments to the raw co-visit values to create association indices by factoring in both environmental variation and the overall number of times each group visited, enabled variation in visit rate from these factors to be controlled for, and generated a prediction of the active association or avoidance of units. These values are therefore likely to predict contact rates outside the clearing and estimate social preference by removing the effect of chance encounters. However, the novel BP index was unable to account for variation in individual home ranges, as ranging patterns of gorillas outside the forest clearings were largely unknown. Therefore, environmental conditions in home ranges could have influenced the gorilla association patterns detected. This problem should however have been minimised by the large sample sizes of individual gorillas in the datasets, and the considerable time periods covered. Furthermore, such an environmental driver to association patterns would not make the associations themselves any less valid. Human social networks are well predicted by spatial overlap, with close spatial proximity both increasing the likelihood of new social ties

forming, and decreasing the likelihood of those social ties breaking down (Rivera, Soderstrom and Uzzi, 2010). If high range overlap increased the likelihood of contact between gorillas, this could in itself lead to closer social affiliations developing.

Null models were created by generating data sets where the presence of a unit on a specific day was determined by a random probability (random number generation between 0 and 1 under a uniform distribution) in combination with their visit rate over all days and the visit rate of all gorillas on that day. BP association index matrices were then calculated for all 1000 random datasets using the same method as the observed data, as discussed above. Networks were generated for all association matrices, from observed and randomised datasets using the *igraph* R package (Csardi and Nepusz, 2006). Agreement in pairwise SR association values across consecutive time periods were investigated using a mantel test in the ‘ape’ R package with 1000 permutations.

3.3.3 Modularity and detection of multi-level structure

The Louvain multi-level modularity optimisation algorithm (Blondel et al., 2008) in the *igraph* R package (Csardi and Nepusz, 2006) was used to detect modules (sub-communities in which units showed greater association with one another than the overall population) within each dataset and generate modularity values using both association index types. Modularity values from the datasets were compared with the 1000 null models for each dataset and association index. P-values were calculated as the proportion of null models with modularity values equal to or greater than that of the data. Multi-level structure was then further investigated in the Lokoué and Mbeli C (2014-2015) datasets using two approaches.

A hierarchical clustering approach (c.f. Wittemyer, Douglas-Hamilton and Getz, 2005) utilizing the R-package ‘cluster’ was used to build clustered dendrograms using the ‘average’ (UPGMA) method (Maechler et al., 2018). The cumulative number of bifurcations by dendrogram height was then plotted. Analyses were run on BP association indices. Values were transformed ($x^{2/3}$) to enable the rate of cumulative bifurcations in null models to fit a linear relationship. The region of distances for which gradient changes were investigated was specified as encompassing distance values above which >50% of random models already had an initial bifurcation, and values below which <50% had already fully bifurcated to remove gradient changes due to transitioning from a plateau to a linear incline prior to the first

bifurcation and after the final bifurcation. R^2 values were calculated in R to identify how well the data were predicted by linear models. Changes in gradient in the observed datasets were then identified using Wilcoxon Two Sample Test, for each distance datapoint, and that with the lowest P-value was selected as the knot. Consistency between higher-level social units detected by modularity analysis and lower-level social units detected from hierarchical clustering was investigated using a binomial linear model to predict co-membership of the same higher tier from co-membership of the same lower tier.

As plotting the cumulative number of bifurcations with height did not show a clear linear relationship in the SR null models, despite various data transformations, only association matrices produced using the BP index were investigated using this method. An alternative tier detection method was developed to investigate the association matrices produced from the simple ratio. This method utilised the variable resolution parameter in the 'cluster_resolution' igraph algorithm (Lambiotte, Delvenne and Barahona, 2008). Modularity was calculated for all SR networks and null models, for resolution values between 0 and 2 by increments of 0.01, producing modules that ranged in size from one unit to including all units. P-values were then calculated as the proportion of null models at the same resolution value, with modularity values equal to or greater than that of the data. These were then plotted against mean module size of the real networks. As the Lokoué population had such strong modularity ($p < 0.001$) for the majority of resolution values, the sample size was reduced from 48 silverbacks to 34, by including only those that visited at least 10 times during the study period (previously 8). This enabled clear variation in modularity P-values with resolution (and therefore social unit size).

Further simple ratio association values were calculated using inter-unit interactions that took place in the clearing when individuals were $\leq 100\text{m}$ apart during 2015 and 2016. Agreement of these pairwise SR association values with those calculated same day visits of groups during the same time period was investigated using a mantel test in the 'ape' R package with 1000 permutations. Social modules from inter-unit interactions (at $\leq 100\text{m}$) were identified using the Louvain multi-level modularity optimisation algorithm (Blondel et al., 2008) and compared with those identified from same day visit data when using only groups and solitaires for which inter-unit interaction data was available. Agreement in presence/absence of silverbacks in the same module between both methods was tested using a chi squared test.

3.3.4 Kinship

Published genetic data (Levréro, 2005) of silverback male pairwise relatedness from the Lokoué population (n=20) and silverback male pairwise relatedness estimated from long term behavioural observations (presence in the same group prior to sexual maturity) from the Mbeli population (n=16) were used to predict co-membership of the same higher-level social unit using binomial logistic regression. Genetic data from Lokoué was generated from faecal samples, collected by tracking to nest sites and genotyped at 8 microsatellite loci (Douadi et al., 2007). Data published from this analysis was binary, with 1 indicating an estimated relatedness of ≥ 0.2 and 0 indicating an estimated relatedness of < 0.2 (Levréro, 2005). This cut-off should assign all pairs that are half-siblings (relatedness=0.25) or more closely related, a value of 1, with some room for error in estimate precision. Presence in the same group prior to sexual maturity from the behavioural data at Mbeli Bai should match with this estimate as individuals would be expected to share at least one parent and therefore be half siblings if they grew up in the same group, however extra-group matings and migration into new groups prior to sexual maturity could considerably reduce the accuracy of this estimate.

Higher-level social units (modules) detected by the initial modularity analysis from the Louvain multi-level modularity optimisation algorithm, using both association index measures, were investigated for kin-biased associations. Association type (group-group, solitary-group or solitary-solitary) was included in the regressions to control for differences in interactions between solitaires and groups. The kinship of silverbacks in the smaller higher-level social units detected by hierarchical clustering and variable resolution modularity analysis could not be investigated due to the low sample of pairs in the same module for which relatedness was known.

Kinship at Lokoué Bai was further investigated by predicting whether a silverback male would return to the clearing the day after an initial visit dependent on a) whether a related male had been present on that initial visit day and b) whether a related male was present on the day after (the day of possible return). Binomial logistic regression (BLR) was used to investigate these hypotheses.

3.3.5 Range proximity

Limited range estimates were available for 9 groups and 3 solitaries in the Lokoué population, based on following tracks from the clearing (Levréro, 2005). Range proximity was crudely estimated between these groups and solitaries by measuring the pixel distance between estimated range locations using GNU Image Manipulator Program (GIMP) version 2.8.22. Pairwise distances between the home ranges of units were used to predict membership of the same module from the Louvain multi-level modularity optimisation algorithm. BLR was used to assess whether joint module membership in both the SR and BP-based networks could be predicted from inter-home range distances. Inter-unit type (group-group, group-solitary and solitary-solitary) was included as a control. The relationship between association estimates (SR and BP) and inter-unit home range distance was investigated using a general linear model (GLM).

3.3.6 Assortativity

The tendency for groups of a similar size and groups with similar visit rates to be connected in the network was tested using Newman's (2002) measure of assortative mixing in the 'igraph' R package. Assortativity was calculated for the real network and the 1000 null models, with p-values calculated as the proportion of null models with assortativity values equal to or greater than that of the real data.

3.4 Results

3.4.1 Modularity

Modularity analysis was run on social networks built from both SR and BP association indices based on same day clearing visits. The initial modularity analysis used an algorithm that seeks the optimal linkage strength between individuals when defining modules. The strongest modularity signal detected by this algorithm using the SR index was for a previously unreported tier of association involving a weighted average of 8.1 gorilla groups or solitaires (8 at Lokoué, 8.25 at Mbeli (using the Mbeli C dataset)). Statistical support for modularity at this level was very strong for Lokoué and two of the Mbeli sampling intervals and weaker for the third Mbeli sampling interval (Table 3.1). After correcting for seasonal variation in visitation rates, the BP association index based on the binomial probability of same day visits still produced strong statistical support, similar to that from the classic SR index, suggesting that environmental variables within the clearing were unlikely to be driving the observed pattern. At Mbeli, pairwise associations between group and solitary gorillas using the SR index were highly consistent between consecutive time periods (Mantel test: 2010-11 with 2012-13: $Z=0.355$ $p = 0.002$, 2012-13 with 2014-15: $Z=0.663$ $p = 0.001$), and even non-consecutive time periods (Mantel test: 2010-11 with 2014-15: $Z=0.341$ $p = 0.004$), suggesting long term stability in affiliative relationships rather than short term competitive interactions, such as solitary male attraction of sexually maturing daughters or “theft” of adult females.

The modularity algorithm used initially detects a single optimal level of modularity and is biased upwards in the size of modules it detects. Therefore, to search for multiple peaks in modularity indicating the presence of multiple social levels, the algorithm’s resolution parameter was manually varied. This parameter defines how relatively strong links within a group of individuals must be to assign a discrete module and, therefore, the number of modules in a given population (Lambiotte, Delvenne and Barahona, 2008). Modularity in the networks at a given resolution was directly compared against modularity in the null models at the same resolution, to determine how the significance of modules varied with mean module size. For both study populations, using the SR index, this revealed a peak in modularity (trough in random probability) at a mean module size close to that detected in the initial

modularity analysis, and an additional peak in modularity (trough in random probability) containing an average of 2.03 gorilla groups or solitaries (Figure 3.1)), suggesting an additional level of social structure.

Table 3.1. Modularity values for all four networks by association index. P-values (in brackets) calculated by comparison with 1000 networks built from randomisations of the original data.

	Simple ratio	Binomial probability
Lokoué	0.191 (<0.001)	0.040 (0.001)
Mbeli A (Period 2010-11)	0.104 (0.069)	0.055 (0.003)
Mbeli B (Period 2012-13)	0.091 (0.03)	0.047 (0.077)
Mbeli C (Period 2014-15)	0.082 (0.009)	0.052 (0.025)

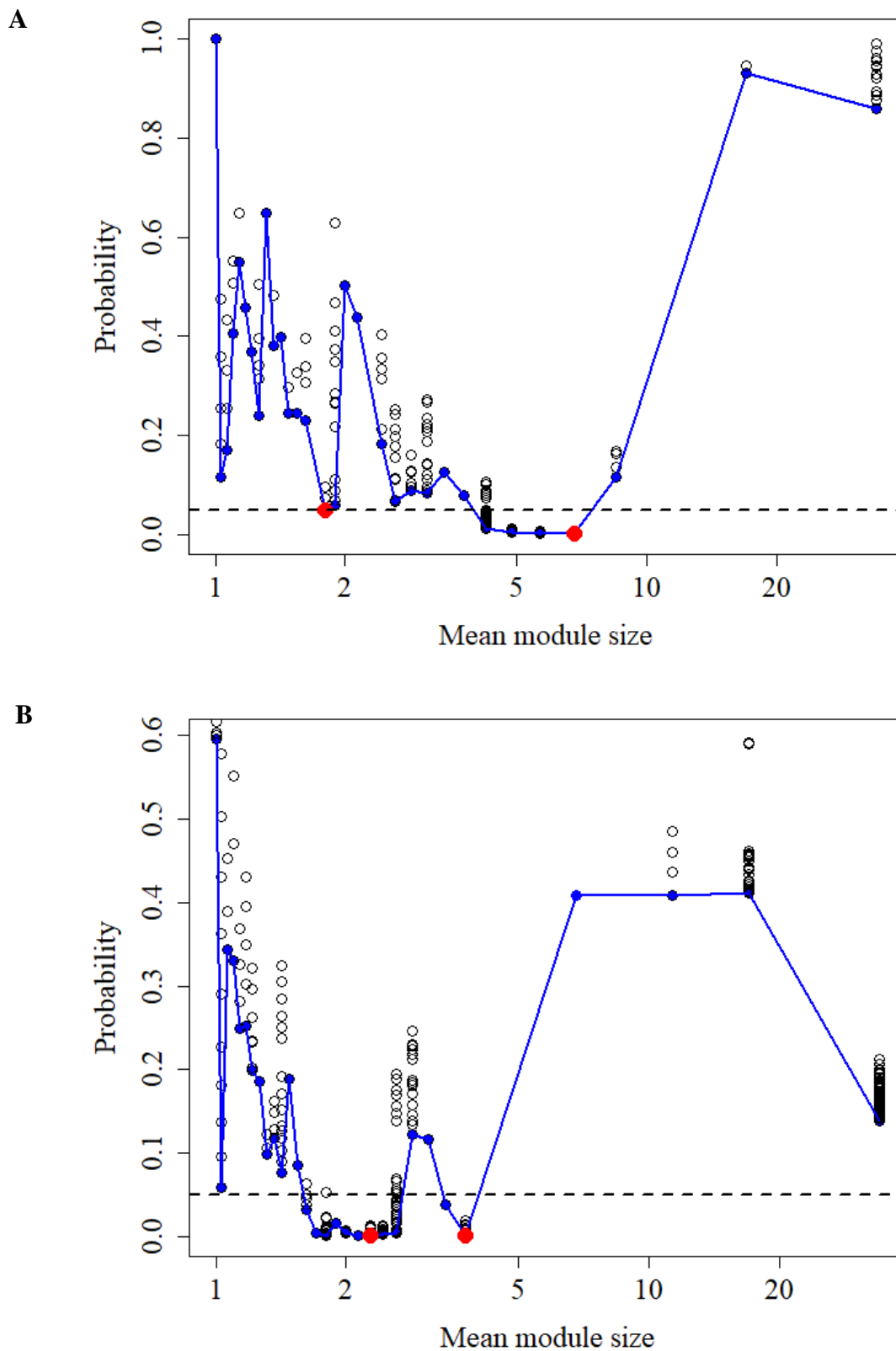


Figure 3.1. P-values of modularity scores for a given size of module for A) Lokoué and B) Mbeli (using dataset C), produced by varying the modularity resolution parameter. Most significant value in both troughs of probability indicated in red.

3.4.2 Hierarchical clustering

Clustering analyses were applied to the BP association values. Analysis of the rate at which bifurcations accumulated with association distance (d) when moving from tip to base of each dendrogram, placed significant knots at $d = 0.29$ ($w=722$, $p = 0.0147$) for Lokoué and $d = 0.26$ ($w=498.5$, $p=0.0285$) for Mbeli (Figure. 3.2). The number of units (groups and solitaires) involved in associations below this bifurcation distance averaged 2.29 for Lokoué and 1.94 for Mbeli, a first order association size very similar to that suggested by the modularity analysis. The resulting dendrograms (Figure 3.3) showed a pattern of preferential association between small clusters of units. For both populations, membership of pairs of units in the first tier associations detected by clustering strongly predicted their presence in the second tier associations detected by modularity analysis (BLR: Lokoué $z=7.144$ $\Pr(>|z|)<0.0001$, Mbeli $z=5.245$ $\Pr(>|z|)<0.0001$), demonstrating consistency between the two approaches, and that the structure detected was hierarchically inclusive.

3.4.3 Social interaction

Simple ratio association values were calculated for interactions that took place in the bai when individuals were $\leq 100\text{m}$ apart. Pairwise association values based on same day visits were highly consistent with association values based on interactions within 100m (Mantel test: $Z=0.242$ $p=0.001$), demonstrating that close proximity social interaction could be well predicted by visit pattern. Modularity analysis on the social network based on interactions at $\leq 100\text{m}$ produced social units for which presence or absence of a pair of silverbacks in the same social module agreed with those based on same day visits in 290/465 cases (62.24%, X^2 (3 , $N=465$) $=8.84$, $p=0.0029$), further demonstrating the utility of using associations based on movement patterns to predict social interaction at a close spatial scale, whilst still remaining sensitive to potential long range social interactions such as chest beating.

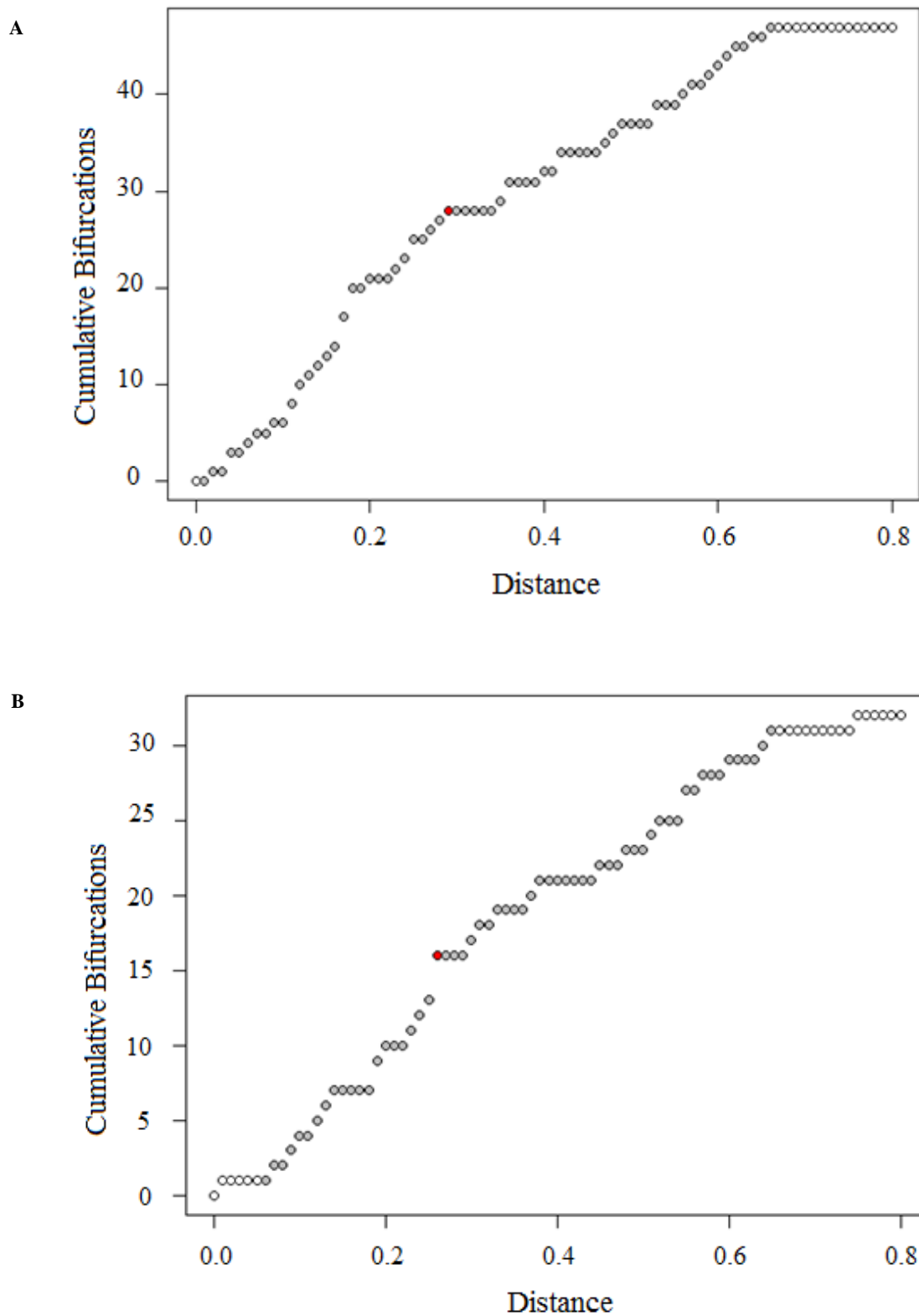


Figure 3.2. Plots of cumulative bifurcations by distance with significant knots indicated in red. Lokoué (A) with knot height = 0.29 and Mbeli dataset C (B) with knot height = 0.26. Grey filled circles indicate values used in knot detection.

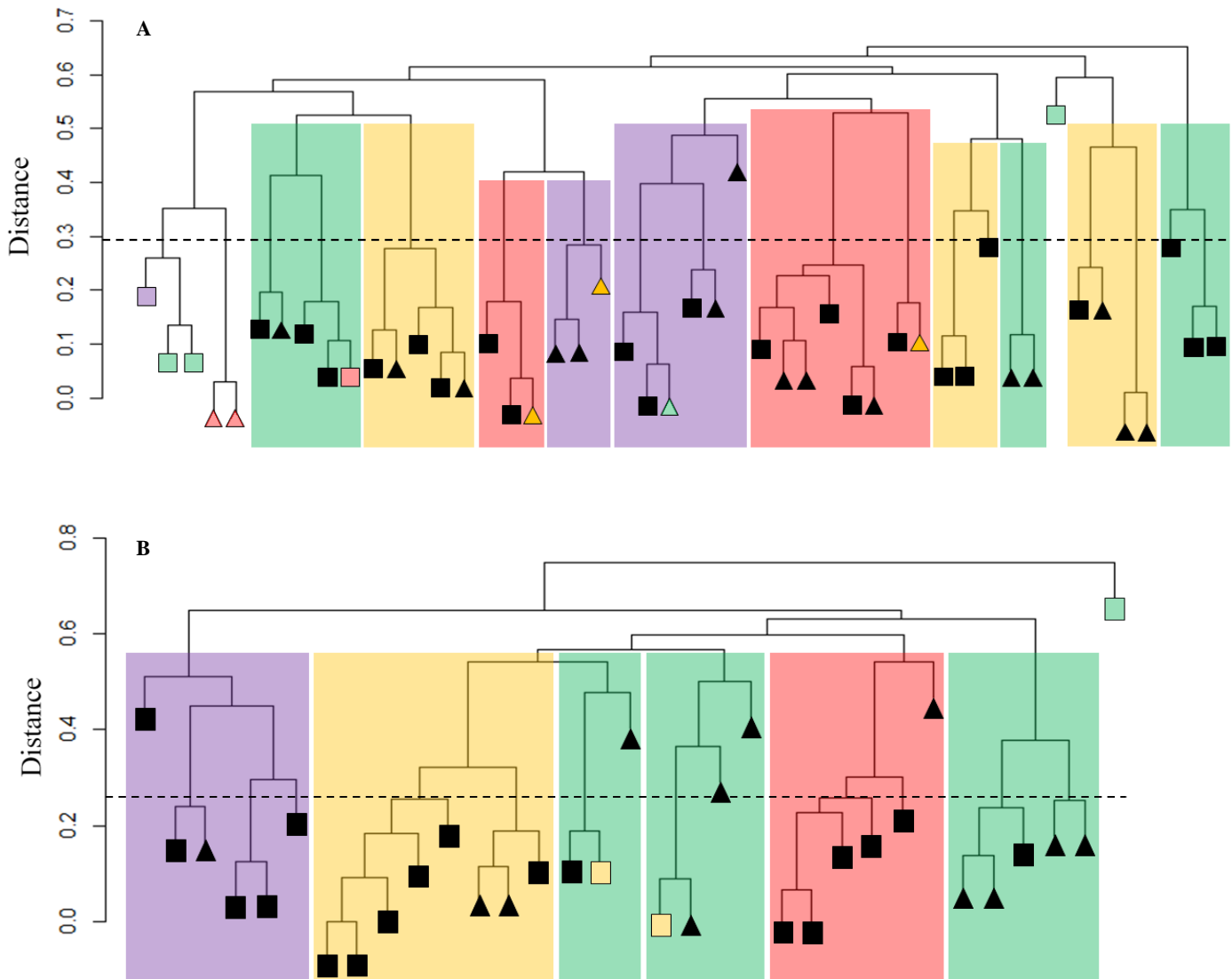


Figure 3.3. Multi-level structure of the Lokoué (A) and Mbeli (B) populations produced by hierarchical clustering using the binomial probability association index. Height of significant knot indicated by dashed line. Social units detected by modularity analysis, indicated by background shading. Squares indicate groups, triangles indicate solitary males. Disagreements between groupings by hierarchical clustering and modularity analysis indicated with colour of triangles or squares. For Mbeli Bai we used the C dataset.

3.4.4 Kinship

Binary genetic relatedness of pairs of Lokoué silverbacks predicted their joint membership in the same higher tier modules fairly well. Social units from the BP association index were better predicted by relatedness (BLR: $z=2.0$, $\Pr(>|z|)=0.045$) than those using the SR index (BLR: $z=1.8$, $\Pr(>|z|)=0.072$), consistent with some underlying kin basis to the pattern with additional variation introduced from environmental variables. However, related silverbacks represented only 14.6% and 12.8% of total pairs within the same module for which relatedness was known, for BP and SR modules respectively (Appendix 3.1), demonstrating that a considerable proportion of affiliations were occurring between units led by unrelated silverback males (or those less closely related than half-siblings). The kinship of silverbacks in lower tier modules could not be investigated due to the low sample of pairs in the same module for which relatedness was known. Silverback males were also more likely to return to the clearing the day after an initial visit, both when a related male had been in the bai the previous day (BLR: $z=2.9$, $\Pr(>|z|)=0.004$) and when a related male was in the bai on the day of possible return (BLR: $z=2.2$, $\Pr(>|z|)=0.030$). In contrast to the results from the Lokoué dataset, observational estimates of kinship in the Mbeli population from presence in the same group prior to sexual maturity did not predict membership of the same module using either the SR index (BLR: $z=0.4$, $\Pr(>|z|)=0.69$) or the BP index (BLR: $z=1.0$, $\Pr(>|z|)=0.343$).

3.4.5 Range Use

The ability of pairwise distances between group and solitary range estimates to predict the presence of pairs in the same module was investigated. Distance between ranges did not predict common membership of the same module in either the simple ratio (SR) network (BLR: $z=0.63$, $\Pr(>|z|)=0.527$) or the binomial probability (BP) network (BLR: $z=-0.28$, $\Pr(>|z|)=0.783$), and this remained the case when pair type (group-group, group-solitary and solitary-solitary) was included as a control (BLR: SR: $z=0.69$, $\Pr(>|z|)=0.488$, BP: $z=-0.29$, $\Pr(>|z|)=0.769$). Furthermore, no relationship between association index and distance between home range was identified (GLM: SR: $t=-0.78$, $\Pr(>|t|)=0.437$, BP: $t=-0.16$, $\Pr(>|t|)=0.876$).

3.4.6 Assortativity

Assortative mixing by group size was not observed (Table 3.2), indicating that groups of similar size (and therefore, of similar levels of dominance) were not more likely to be associated with each other in the Lokoué population. There was also no assortativity by visit rate observed in the network, indicating that groups that visited more often did not tend to be more associated with each other.

Table 3.2. Assortativity in the Lokoué network by group size and visit rate, analysing both the population as a whole and only between groups associations

Assortativity	by group size	by visit rate
Observed	-0.08255136	-0.1008898
Random	-0.02573	-0.10587
P	0.983	0.415

3.5 Discussion

The classification of a social system as multi-level requires the association of multiple stable core units to form larger social tiers (Grueter et al. 2012). The strong correlation between pair-wise association values across consecutive two-year periods indicates the presence of long-term associations between gorilla groups and solitary males. Furthermore, the detection of multiple grades of association forming hierarchical social units in both populations, using multiple approaches, demonstrates the presence of multiple levels of social structure in the patterns of gorilla forest clearing visits. Therefore, in combination, these results strongly suggest the presence of multi-level social structure in western lowland gorilla populations. The well described units of predominantly polygynous family groups and solitary males (Magliocca, Querouil and Gautier-Hion, 1999; Parnell, 2002a; Robbins et al., 2004) form just one level of this overall social structure, with two further levels detected, involving the association of an average of close to two and close to eight solitary males or groups. The presence of solitary males, and all male bachelor groups in addition to family group units, does not represent a dramatic departure from human societies due to the widespread presence of polygyny across human history (Marlowe, 2005).

This analysis takes a very broad approach to categorising association between groups, by using the presence of groups or solitaires at a clearing within a one day period, as justified in the introduction. It does not take account of the different encounter types or whether units were in the same location at the same time. We therefore rely on the assumption that gorillas are aware of the location of others over a fairly large distance (e.g. through auditory communication that can be heard from 2km away (Mirville et al., 2018)) and that this influences their movement decisions. Furthermore, our comparison of association values calculated from presence on the same day, and interactions within 100m demonstrates that our broad approach, enabling a considerably larger sample size and remaining sensitive to potential long range social interactions, still correlates with results for smaller samples for which more fine scale behavioural observations are available. By controlling for the seasonal variation in the rate of all solitaires or groups visiting the clearing we aimed to rule out environmental causes leading to the association patterns observed, leaving the location of other groups as the best explanation for the observed avoidance or association behaviours.

A key characteristic observed in human and other animal social networks is that of homophily or assortativity, where individuals showing similar traits e.g. age, sex or dominance, tend to preferentially associate (Fu et al., 2012). Groups at Lokoué did not appear to associate preferentially with groups of a similar size, suggesting that larger groups which were therefore likely to be more dominant did not choose to associate with one another more than expected. Group size is used here as a predictor of a silverback male's dominance, as group size and dominance are found to strongly correlate in many primate species (Cheney, 1987) and in gorillas, a more dominant male would be likely to attract a larger number of reproductive females, sustaining a larger group. Groups and solitaries did not appear to preferentially associate with those that visited the clearing with a similar frequency suggesting that a higher probability of a co-visit to the clearing, and therefore exposure to each other, did not drive increased social affiliation.

The ability to predict the social units present in the Lokoué population, to some extent, from male kinship data, indicates that, at least within the Lokoué population, the multi-level social structure may have some basis in bonds between male kin. Our results suggest that alliances could be formed between close kin, with higher social levels representing associations between more distant kin such as half-siblings or cousins. This has clear parallels to tribal and clan based human social structure, indicating the potential benefits of gorilla social behaviour as a model for early hominin social evolution, and suggesting the potential for increasingly weak, higher levels of structure in gorilla populations. However, the genetic data used in this analysis is fairly limited, in binary form and relies on a small number of loci. Greater information such as that from pedigree reconstructions will be required to understand how social affiliations vary with differing levels of kinship and between specific relationship types.

The lack of a clear relationship between kinship and group membership in the Mbeli population may be due to the method by which kinship was estimated for this population, or the low sample size of individuals for which kinship data was available. Involuntary transfer of non-adult males and mothers with offspring, between groups (Stokes, Parnell and Olejniczak, 2003), has the potential to cause considerable inaccuracies in the estimation of kinship from behavioural observations which may therefore be obscuring any potential relationship between social structure and kinship in this population. Alternatively, it could be

that, similarly to previous findings on the genetic structure of western gorillas (Bradley et al., 2004; Douadi et al., 2007; Inoue et al., 2013), kinship may be an important component of social structure in some regions (including Lokoué), but too weak to detect or absent in other areas (such as Mbeli).

Silverback males in the Lokoué population (including both solitaries and group-leading individuals) were more likely to return to the clearing, when a related male had also been in the clearing the previous day and when a related male was in the clearing on the day of possible return. This further demonstrates the importance of associations between male kin in influencing movement patterns and the potential for social interaction. It also demonstrates that gorilla groups and solitaries adjust their movement patterns based on those of extra-group individuals, verifying our initial assumption that gorillas are aware of the location of others, and that this influences their movement decisions. This tendency for related males to associate suggests the potential for male kin-affiliation to provide benefits for the defence of either females or food resources. Bais are thought to represent hotspots of gorilla social activity as the high abundance of nutrient rich food resources enables a reduction in feeding competition (Metsio Sienne, Buchwald and Wittemyer, 2014; Magliocca and Gautier-Hion, 2002). However, whilst competition for food is likely to be low, competition for females may be high due to the unusually close proximity of multiple groups and solitaries at the bai. The presence of a related male in the bai could therefore be beneficial by reducing the chances of a female transferring into a new group through cooperative defence between male kin. Further research could therefore investigate the effect of the higher-level social structure detected here, particularly the long-term stability of inter-group male kin bonds on the ability of males to attract and retain females in their groups.

Whilst male kinship predicted higher-level social units at Lokoué, only a small proportion of males within a given social unit were actually related, so it appears likely that male kinship may be only one of multiple factors influencing this structure. Another important driver of this higher-level structure may in fact be female kin bonding. As female gorillas have been found to be more likely to disperse into groups in which another female relative is already present (Arandjelovic et al., 2014; Bradley, Doran-Sheehy and Vigilant, 2007), the potential for female kin-biased behaviours is already evident. With genetic data only available for silverback males, the overall shared kinship between groups could not be investigated and my analyses ignore any potential influence of the kinship of other individuals in the groups.

Silverback male relationships may well have a larger effect on movement patterns than those of any other single individual in the group, as they represent the most dominant individuals in each group, and displays by silverback gorillas are known to often precede group movements (Schaller, 1963; Harcourt, 1979; Stewart et al., 1994a). However, it has been suggested that group movements may be coordinated by vocal signals from many individuals within the group (Stewart et al., 1994b) and it is entirely unknown to what extent the kin relationships between other individuals may influence movement and association patterns, which may represent an important future avenue of research.

Another potential underlying cause for the community structure observed is geography. In human societies, both kinship and geographic distance have strong influences on the formation of communities (Liben-Nowell et al., 2005; Onnela et al., 2011; Dunbar and Spoor, 1995). Despite all gorillas in each study location using the same bai and therefore sharing at least some level of range overlap, the proportion of range shared between core units will likely vary greatly. Therefore, if geography plays a similarly important role for gorilla communities, groups and solitaries may associate more strongly at the bays with those with whom they share a larger proportion of their range. This could be due to a greater tolerance of those individuals with which they often interact, in comparison to relatively unknown groups which may react unpredictably or aggressively and are therefore more likely to be avoided (Mirville et al., 2018). We found no evidence to support this hypothesis from the limited dataset sample of the Lokoué population for which range estimates were available, which indicated that groups and solitaries within the same community did not have significantly closer ranges. Furthermore the lack of preferential association by visit rate also suggests that associations are not strongly influenced by range overlap as groups with overlapping ranges would be expected to have a similar visit rate due to distance discounting (See Chapters 5 and 6). Given the association between geographic distance and kinship detected by Bradley et al. (2004), and our detection of a kin-basis to the social structure, the lack of geographical influence is surprising. However, both these methods are fairly indirect and it is possible that a geographic effect on social structure is present but that these techniques do not have the required power to detect it.

In addition to the potential benefits of the multi-level social system for defence of females or resources, a further potential benefit of these higher-level affiliations could be for foraging. Gorillas feed on many sporadic or irregularly in-season resources such as fruit (Yamagiwa,

Basabose and Kaleme, 2008), which makes the task of predicting food location and abundance somewhat complex. One possible method for overcoming this difficulty could be through cooperative foraging between multiple socially bonded, potentially related groups. If groups communicate the location of good quality food resources to their affiliates, the considerable mutual benefits of increased foraging efficiency through reciprocal altruism (and possibly kin-biased behaviour) could easily overcome the costs to the communicator. This is particularly likely to be the case if, as is often observed, the gorilla group in question moves on to alternate food sources well before consuming the entire available resource. However, the analyses in this chapter only investigate associations at a single, readily-available, predictable resource and therefore investigating the foraging benefits of this social structure require an alternative approach, investigating foraging across gorilla ranges as addressed in Chapter 6.

3.6 Conclusion

These findings demonstrate the presence of a previously unquantified multi-level social structure in western lowland gorilla. By confirming the presence of this structure in two distinct populations these findings suggest that this multi-level social structure may be present species- (or even genus-) wide; although how this structure, present in western gorilla groups with a single dominant male, maps onto the structure present in multi-male mountain gorilla groups is yet to be determined. Without detailed genetic information on all the individual gorillas studied, and information on association patterns across their range it is not possible to determine the precise drivers of the multi-level social structure detected here. However, whilst better understanding the underlying causes and benefits of the higher-level social structure in gorillas identified here may take many years of further study, the importance of male-kin in driving this structure in the Lokoué population is identified.

By demonstrating the presence of kin-based social modules made up of multiple group and solitary core units, clear parallels to tribal and clan based human social structure can be observed. Demonstrating that multi-level social systems are not unique to humans within the ape lineage suggests that a reassessment of the common anthropological hypotheses relating to the evolution of human social structure may be required. The identification of these additional social tiers strongly supports a multi-level approach to understanding gorilla society over traditional group-based approaches and suggests that such an approach in future may enable the detection of further social tiers and increased social complexity in some of our closest evolutionary relatives. The multi-level social structure we detect, however, is observed from only a single region of the gorilla's ranges – the forest clearing, due to the rarity of observing gorilla inter-group interactions within the forest. Further research is therefore required to confirm the extent to which this structure is observed across gorilla ranges, and how it may influence kin-biased behaviour, resource sharing, foraging and movement patterns.

3.7 References

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3.8 Appendices

Appendix 3.1a. Silverback kinship (from genetic data) in SR modules from the Lokoué population for all pairs of units (All), for pairwise associations between two groups (G-G), between a group and a solitary (G-S), and between two solitary males (S-S).

All	Same	Different	G-G	Same	Different
	Module	Module		Module	Module
Related	6	10	Related	4	2
Unrelated	41	125	Unrelated	23	58

G-S	Same	Different	S-S	Same	Different
	Module	Module		Module	Module
Related	2	7	Related	0	1
Unrelated	16	55	Unrelated	2	12

Appendix 3.1b. Silverback kinship (from genetic data) in BP modules from the Lokoué population for all pairs of units (All), for pairwise associations between two groups (G-G), between a group and a solitary (G-S), and between two solitary males (S-S).

All	Same	Different	G-G	Same	Different
	Module	Module		Module	Module
Related	7	9	Related	4	2
Unrelated	41	125	Unrelated	20	61

G-S	Same	Different	S-S	Same	Different
	Module	Module		Module	Module
Related	3	6	Related	0	1
Unrelated	19	52	Unrelated	2	12

Appendix 3.1c. Silverback kinship (from observational data) in SR modules from the Mbeli population for all pairs of units (All), for pairwise associations between two groups (G-G), between a group and a solitary (G-S), and between two solitary males (S-S).

All	Same Module	Different Module	G-G	Same Module	Different Module
Related	5	17	Related	1	4
Unrelated	23	109	Unrelated	6	39

G-S	Same Module	Different Module	S-S	Same Module	Different Module
Related	4	9	Related	0	4
Unrelated	15	53	Unrelated	2	21

Appendix 3.1d. Silverback kinship (from observational data) in BP modules from the Mbeli population for all pairs of units (All), for pairwise associations between two groups (G-G), between a group and a solitary (G-S), and between two solitary males (S-S).

All	Same Module	Different Module	G-G	Same Module	Different Module
Related	8	14	Related	2	3
Unrelated	35	97	Unrelated	9	36

G-S	Same Module	Different Module	S-S	Same Module	Different Module
Related	5	8	Related	1	3
Unrelated	19	49	Unrelated	7	12

Chapter 4: The Evolution of Multi-level Social Structure



Photo by Robin Morrison at Ngaga Research Station, SPAC Foundation Congo

4.1 Abstract

Modern human societies have a complex, hierarchical structure in which lower order units like nuclear families are nested inside increasingly larger units up to the level of nations and multi-national alliances. It has been argued that this multi-level structure evolved independently from other mammalian multi-level societies and after the chimpanzee-human split due to greater recognition of, and bonding between, dispersed kin. However, as demonstrated in chapter 3, western gorillas appear to show a kin-based multi-level structure, suggesting that a key component of human social complexity may have evolved far earlier

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than previously asserted. In this chapter I demonstrate that the sizes of gorilla social units show hierarchical scaling similar to that observed in humans, baboons, whales, and elephants. I then evaluate the potential for kinship to be driving this scaling pattern in gorillas through estimating the number of full-sib and half-sib brothers present within groups using demographic estimates. I then compile information on mating system, male alliance state and multi-level structure across the ape lineage, and carry out ancestral state reconstructions to reassess the likely state of early hominin social structure, in light of the detection of a kin based multi-level social structure in gorillas. My findings suggest that single male groups may have represented the starting point from which multi-level social structure evolved, via increased affiliation between dispersed kin, prior to the human-gorilla-chimpanzee divergence. They also emphasise the previously overlooked importance of gorillas as a model system for human social evolution and suggest that the social brain enhancements observed within the hominin lineage were not necessary to enable human multi-level social structure.

4.2 Introduction

Human social structure is a complex, hierarchical system consisting of multiple social tiers. These range from small family units, up to higher-level political systems, nations and trade networks, involving collaboration and organisation among many individuals. But how did humans transition from small, autonomous groups, to multi-tiered, cooperative, hierarchically nested societies? And when did this happen? One hypothesis is that, the transition to a multi-tiered society in humans was part of a broader trend in mammalian evolution in which brain size increase was associated with enhanced social cognition (Dunbar, 1998). This is suggested to have expanded the number, depth, and complexity of coalitions and alliances (Foley and Gamble, 2009), and is supported by the observation that the mammalian taxa in which multi-level social structure is best-documented (primates, elephantidae and odontocetes) have highly developed neo-cortices (Marino, 2002; Hakeem et al., 2005). These taxa also show a similar scaling pattern in which the size of social groups at each social tier is the same fixed multiple of the size of groups in the next lower tier, such as elephant families, bond groups and clans which increase in size three-fold at each social tier. The presence of this same scaling factor of roughly three, across hierarchical mammalian societies implies that some common underlying mechanism may be at play (Hill, Bentley and Dunbar, 2008). In elephants, as in traditional human societies, social units are strongly based on kinship (Wittemyer, Douglas-Hamilton and Getz, 2005; Grueter et al., 2012), and therefore the potential for reproductive capacity (and hence the mean sizes of family units produced) to drive the common scaling of social tiers, at least in species demonstrating kin affiliation, should be investigated.

Despite these underlying similarities between human social systems and those in other mammalian taxa, anthropologists have relied extensively on comparison between human and chimpanzee societies, using this as evidence that human multi-level social structure evolved after the human-chimpanzee split, and independently from the multi-level societies observed in other animal species (Foley and Gamble, 2009; Chapais, 2013; Kaplan, Hooper and Gurven, 2009; Grueter, Chapais and Zinner, 2012). An extension of the social brain hypothesis has been used to suggest that human multi-level social structure is a unique product of hominin brain evolution, kick-started when early hominins, living in multi-male multi-female (MM-MF) societies homologous to those of chimpanzees (*Pan troglodytes*) and

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bonobos (*Pan paniscus*), evolved a heightened capacity to recognise dispersed kin. Foley & Gamble (2009) hypothesise that nested units of clans and families initially developed within a fission-fusion society, and that heightened kin recognition then enabled the subsequent development of higher-level community structures. Social brain enhancements enabled large alliances of dispersed, related individuals to collaborate and cooperate, which were ultimately extended to even larger networks of reciprocity among non-kin (Dunbar, 2003).

A major foundation of this argument is that of all great apes, only humans have been documented to have a multi-level social system (Grueter, Chapais and Zinner, 2012). However, much of our understanding of ape social structure relies on very limited data on a small number of small populations, in which it is often not possible to investigate higher-level social structure. Chimpanzees and bonobos have fission-fusion social systems (Anderson et al. 2002; Symington 1990), where small transient subgroups form out of the larger closed group. Orangutans (*Pongo*) are far more solitary than other great apes, with adult individuals travelling primarily alone or in the case of reproductive females, with dependent offspring. However, multiple adults often come together to form travel parties, and thus are thought to have an individual-based fission-fusion social structure (Delgado et al. 2000; van Schaik 1999). Whilst modularity can be detected in the short term in both chimpanzee and bonobo societies (Sah et al., 2017), it is argued that the transient nature of chimpanzee and bonobo subgroups and orangutan travel parties mean that these fission-fusion societies do not represent true multi-level societies, which require the association of multiple stable core units to form larger social bands (Grueter, Chapais and Zinner, 2012).

Chimpanzee groups exhibit high levels of territoriality (Watts and Mitani, 2001; Mitani, Watts and Amsler, 2010; Crofoot and Wrangham, 2010), which are likely to prevent the formation of higher-level social structure in this species. However, territoriality is thought to be greatly reduced in bonobos (Parish, De Waal and Haig, 2006), where territories are defended by threats rather than physical violence (Boehm, 2012). Some bonobo groups have overlapping ranges, and cases of peaceful between-group encounters have been observed (Idani, 1990; Furuichi, 2011), suggesting that bonobos may not be territorial after all. These peaceful between-group encounters also suggest the possibility of a higher-level social structure in this species; however data on a far larger number of overlapping groups than currently available would be necessary to investigate this.

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The relative paucity of research on the higher-level social structure of many apes has hindered a broader comparative approach, but the analyses of western gorilla social structure in Chapter 3 provide a much needed assessment of this structure in one of our closest evolutionary relatives. The detection of multi-level social structure in western gorillas brings under considerable doubt the uniqueness of human multi-level social structure within apes and suggests that a rethink of the widely accepted hypotheses on the evolution of human social complexity may be necessary. To assess the level of consistency between human, gorilla and other mammalian multi-level social systems, I investigate the scaling of social unit sizes across three gorilla populations, comparing them with those observed in other mammalian multi-level systems, and examine the potential for kinship patterns to be driving this scaling pattern. I then investigate trends in group structure, mating system and male alliance states across the ape phylogeny to place humans in their wider evolutionary context, discussing potential mechanisms and evolutionary drivers of the multi-level structure and scaling pattern observed.

4.3 Methods

4.3.1 Data

Data on the composition and group structure of three western lowland gorilla (WLG) populations were used for the analyses in this chapter. Two of the populations were those investigated in Chapter 3: The Lokoué data set Levréro (2005), and the Mbeli dataset (data collected during 2010-2015) with a particular focus on the higher-level social units detected in Mbeli dataset C (2014-2015). The third population was an additional bai population, observed at Maya-Nord Bai in the north of the Odzala-Kokoua National Park. The number of solitaires and groups identified at this site in 1996 and 1997 and the age/sex class composition of these groups were described by Magliocca et al. (1999). All sites, data sets and data collection methods are further detailed in Chapter 2.

4.3.2 Community closure

Population accumulation curves for the Mbeli and Lokoué populations were plotted as the cumulative number of unique individuals observed as the sampling period progressed. Group sizes were those reported for the Lokoué dataset in Levréro (2005). For Mbeli, group sizes were estimated as the maximum number of individuals observed in the group, present in the bai during each two year period (Mbeli datasets A, B and C). The mean across all periods for which each group was present was then used as an estimate for overall group size. The cumulative number of individuals was estimated as the sum of the group sizes and the number of solitary males for those that had been observed in the bai within the given number of sampling days.

4.3.3 Scaling

The scaling factor of social unit sizes was investigated using results from the Lokoué and Mbeli C datasets, as well as additional data from the Maya-Nord Bai (Magliocca, Querouil and Gautier-Hion, 1999). The total number of individuals included all gorillas identified in

each bai during the dataset period. Mean mother-offspring unit size and mean group size were calculated as specified in equations 4.1 and 4.2 below.

$$(4.1) \text{ Mean mother-offspring unit size} = (\text{total individuals} - \text{adult males}) \div \text{adult females}$$

$$(4.2) \text{ Mean group size} = (\text{total individuals} - \text{solitary males}) \div \text{number of groups}$$

The mean size of each of the novel social tiers detected in Chapter 3 was calculated by dividing the total number of units by the total number of individuals in the population. These social tiers were not available for the Maya-Nord population due to the lack of available visit data from that study. The log of social unit size at each level was taken. Linear models were run to predict $\log_{10}(\text{social unit size})$ from social level to produce R-squared values and P values. This was done separately for social unit sizes detected by each of the two methods used in Chapter 3 (Method A: hierarchical clustering approach and Method B: modularity resolution varying approach following the approaches described in Chapter 3), and for all three populations separately and then combined whilst controlling for the specific population.

4.3.4 Reproductive drivers of scaling

Published demographic estimates of family composition, group structure and female reproductive capacity were investigated to calculate the estimated number of full-sib (full-sibling) brothers and half-sib (half-sibling) brothers of an individual male gorilla (Breuer et al., 2009; Atsalis and Margulis, 2006; Robbins et al., 2004). Group compositions from the Mbeli population, with age and sex classifications following the method of Breuer et al. (2009), and published group compositions from Lokoué (Levréro, 2005) and Maya-Nord (Magliocca, Querouil and Gautier-Hion, 1999) populations were analysed to determine whether similar estimates were observed within these populations at the time of data collection. To estimate the number of older male half-sibs an individual could bond with, all reproductive groups in which an infant was present were used. The mean number of older male half-sibs was calculated as specified in equation 4.3 by averaging the sum of half the infants, adjusted by mortality rate (Robbins et al. (2004) estimated infant mortality up to 3 years as 36%), half the juveniles and 58.3% of the subadults (males spend 3.5 years classified as subadults in comparison to the 2.5 for females (Breuer et al., 2009)). Blackbacks and

young silverbacks were considered to have left the group by the time an individual reached an age at which any form of bond between them was likely to occur. Using all reproductive groups in which a blackback, young silverback or subadult was present; the number of younger male half-sibs an individual would bond with was also estimated. This included all young silverbacks and blackbacks, 58.3% of subadults and half the juveniles as specified in equation 4.4. Infants were not included as they were considered too young to develop a bond with a blackback or young silverback before their dispersal.

$$(4.3) \text{ Mean number of older male half-sibs} = (0.5 \times I \times S_I) + (0.5 \times J) + (0.583 \times SA)$$

$$(4.4) \text{ Mean number of younger male half-sibs} = YSB + BB + (0.583 \times SA) + (0.5 \times J)$$

Where I = Number of infants

S_I = Infant survival rate = $1 - 0.36 = 0.64$

J = Number of Juveniles

SA = Number of Subadults

BB = Number of blackbacks

YSB = Number of young silverbacks

4.3.5 Ape phylogenies and ancestral state reconstruction

Mating system properties and male alliance size states were reconstructed for ancestral nodes across a great ape phylogenetic tree from the 10k trees project (Arnold, Matthews and Nunn, 2010). Properties in extant taxa at the species level were determined through a thorough review of the literature. Ancestral state reconstruction was carried out using the ‘ace’ function from the ‘ape’ R package (Paradis and Schliep, 2019) using a continuous-time Markov chain model. Traits were fitted with an equal-rates model (“ER”), due to the relatively small number of species present in the phylogeny and therefore the lack of adequate transitions to accurately estimate different rates of transition between different states. The presence or absence of multi-level social structure was plotted on the same ape phylogenetic tree;

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however ancestral state reconstruction was not attempted for this trait due to the lack of knowledge about the presence of multi-level social structure in most ape species. Phylogenies were plotted to provide a broad view of trends across the ape lineage and the evolutionary context to the detection of multi-level social structure in WLGs.

4.4 Results

4.4.1 Community closure

Accumulation curves plotting the cumulative number of individuals observed at Lokoué and Mbeli over the sampling period showed an asymptotic shape (Figure 4.1) demonstrating that the two bai populations represented fairly closed communities. This suggests that the bai population as a whole may represent an important social tier, consistent with the highest level (g6 population) in Binford's classification of traditional human societies (Binford, 2001; Hamilton et al., 2007). This tier was therefore included in subsequent analyses.

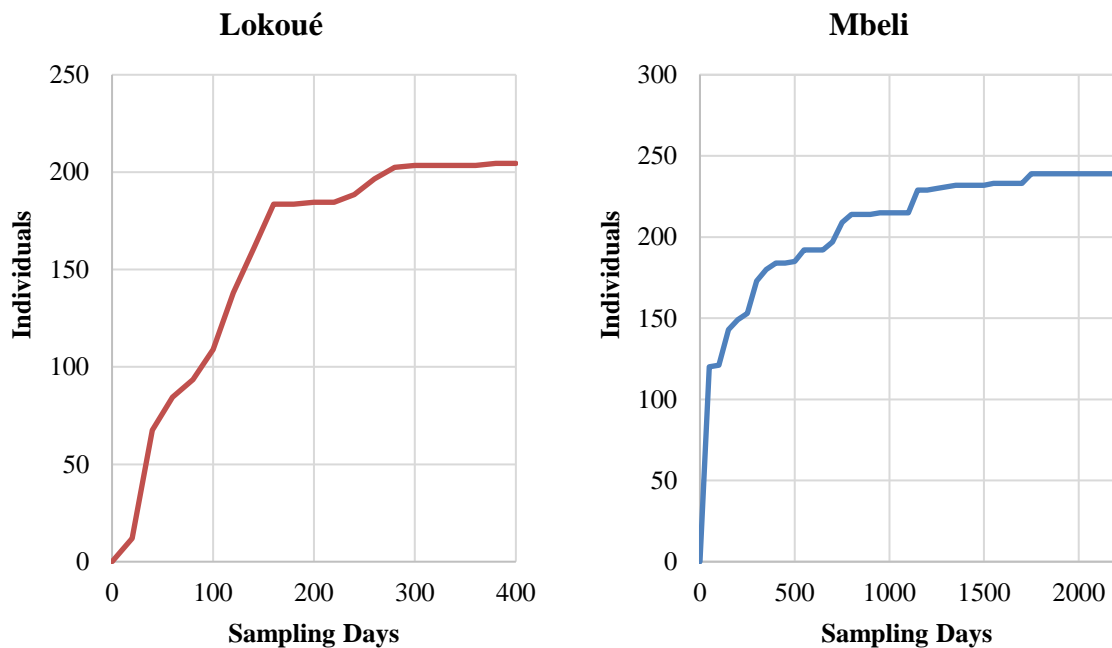


Figure 4.1. Population accumulation curves for Lokoué (red) and Mbeli (blue) across the sampling periods. Cumulative number of individuals estimated as the sum of group sizes and solitaires observed in the clearing within the given number of sampling days. Community closure indicated by asymptotic shape of accumulation curves.

4.4.2 Group size scaling

Mean social unit size at each tier showed high consistency between the three populations (Table 4.1), although fairly high variation in tier 4 and 5 social unit sizes estimated by alternative methods in the same population was observed. Social tiers appeared to roughly follow Binford's classification of traditional human societies (Binford, 2001; Hamilton et al., 2007), as indicated in Table 4.1. The large jump in social unit size between the largest tier detected in Chapter 3 (tier 5 in Table 4.1) and the bai population (tier 7), compared to the low level of variation between the scaling ratios between all other adjacent social tiers suggests that an intermediate social tier may be present between these two. This was not detected using the modularity or hierarchical clustering approaches in Chapter 3, however this may be due to associations at this level being very weak and therefore hard to detect. In the case of hierarchical clustering this may be particularly hard to detect as this tier would represent a very small number of social units in total (roughly 3), and therefore the joining of these 3 social units into one would be very difficult to discriminate from the joining of social units in the previous tier.

Table 4.1. Mean social unit size by social tier across three gorilla populations. Equivalent level in Binford's classification (BC) of traditional human societies (Binford, 2001; Hamilton et al., 2007) indicated (BC: G1-G6). Values for levels 4 and 5 calculated by both methods (Method A: Binomial probability index with hierarchical clustering (level 5) and modularity (level 4) analyses; Method B: Simple ratio index with varying resolution of algorithm (level 5) and modularity (level 4) analyses).

Social Level	BC	Lokoué	Mbeli C	Maya Nord
1 Individual	G1	1	1	1
2 Mother-Offspring unit		2.45	2.67	2.72
3 Group	G2	6.81	8.79	11.19
4 Dispersed extended family group	G3	Method A 9.76	12.94	*
		Method B 11.39	14.67	
5 Aggregated group	G4	Method A 51.25	55	*
		Method B 34.17	44	
6 Sub-population	G5	*	*	*
7 Bai Population	G6	205	220	364

*unknown

When the frequency distribution of group size in each social tier was approximated by an exponential function, under the assumption that an additional sub-population tier was present but undetected, the goodness of fit was extremely high for both Lokoué and Mbeli (Figure 4.2). This scaling pattern was supported regardless of which higher-level tier detection method was used (Appendix 4.1). This indicates that unit size at each social tier increased by a consistent multiplier relative to unit size at the next lower tier. Using Method A, the estimated scaling exponents for the two sites (2.78 and 2.73) were very similar both to each other and that estimated from the nearby site, Maya Nord (3.07), where data on social group and population size but not rates of association are published (Magliocca, Querouil and Gautier-Hion, 1999). Slightly greater variation is observed using Method B (Appendix 4.1), but values across sites and under both methods remain close to the scaling value of three observed across other multi-level mammalian social structures (Hill, Bentley and Dunbar, 2008).

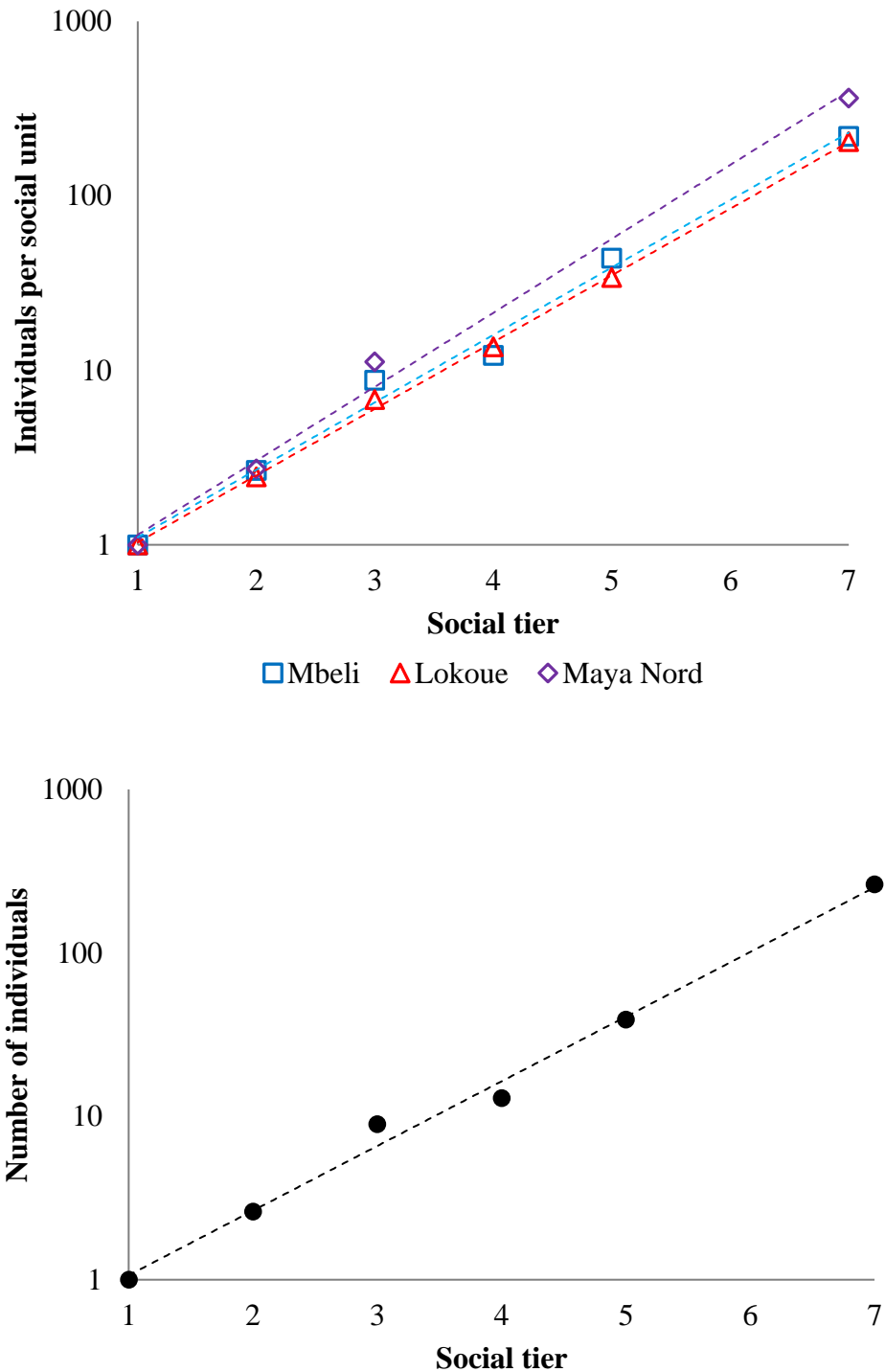


Figure 4.2. Scaling of social unit sizes across 3 gorilla populations where social tier values 1-7 represent G1 (individuals), Mother-offspring units, G2 (family units), G3 (dispersed extended family group), G4 (aggregated group), G5 (Sub-population), and G6 (overall population) using method B. A) for three separate populations Mbeli (blue), Lokoué (red), Maya Nord (purple) with their fitted exponentials shown by dashed lines ($R^2 = 0.996$ (Mbeli) and 0.994 (Lokoué)). B) For the mean of social unit sizes at each level from all populations, with dashed line indicating the fitted exponential (Scaling ratio = 2.70, $R^2 = 0.9911$, $P = 6.366e-10$).

4.4.3 Reproductive drivers of scaling

Analyses in Chapter 3 demonstrated that higher-level social structure had a basis in male kinship. To investigate whether this kinship could be driving the scaling pattern observed, as hypothesized for elephants (Wittemyer, Douglas-Hamilton and Getz, 2005), published demographic estimates of group composition and female reproductive capacity were investigated. Female western gorillas reach sexual maturity at roughly 10 years old (Breuer et al., 2009), at which point they become fertile. This fecundity declines significantly from age 37 (Atsalis and Margulis, 2006), leaving a period of roughly 27 years during which time they may produce offspring. Robbins et al. (2004) estimate the inter-birth interval for surviving births in western gorillas as 4-6 years, which would enable a single female to produce a maximum of between 4.5 and 6.75 offspring throughout their life. Given a 50:50 sex ratio, a female may produce roughly 2-3 male offspring (Table 4.2). However due to mortality, group transitions and variations in fertility this estimate may well be a considerable overestimate.

Table 4.2. Estimated maximum number of male offspring produced by a single female given demographic estimates (Breuer et al., 2009; Atsalis and Margulis, 2006; Robbins et al., 2004) across her lifetime and across a 16 year reproductive period.

Reproductive Years	Inter-birth interval*	Offspring per female	Male offspring per female	Male offspring per female over 16 years
27	4-6 years	$27 \div 6 = 4.5$	$4.5 \times 0.5 = \mathbf{2.25}$	$(16 \div 6) \times 0.5 = \mathbf{1.33}$
		$27 \div 4 = 6.75$	$6.75 \times 0.5 = \mathbf{3.375}$	$(16 \div 4) \times 0.5 = \mathbf{2}$

*of infants surviving to age 3

Male offspring disperse from their groups at roughly 12 years of age, whilst females disperse as sub-adults at roughly 8 years (Robbins et al., 2004). Male offspring will therefore have contact with male full-sibs or half-sibs that are up to 12 years older and 12 years younger if their group remains stable throughout this period. However this contact is likely fairly limited whilst they themselves are infants (up to 4 years) (Breuer et al., 2009), and with those individuals that are still infants when they disperse. This therefore leaves a 16 year period during which individuals could be born with whom they experience high levels of within-

group interaction before their dispersal. During this period their mother is likely to produce a maximum of 2 male offspring (Table 4.2), suggesting that at most, an individual male gorilla is only likely to have interacted considerably with one other male full sibling.

Across the three bai populations, reproductive groups contained an average of 3.53 adult females (Lokoué: 3.2, Mbeli: 3.5, Maya-Nord: 4.0). Robbins et al. (2004) estimated births per adult female per year as 0.19 and infant mortality up to 3 years as 36%. Over a 16-year period, if mortality after 3 years is assumed to be minimal, the average group will produce 6.87 surviving offspring, 3.43 of which would on average be male (Table 4.3). Therefore the estimated number of male paternal half-siblings a male would have close bonds with would be 2.43 (or 3.43 including themselves).

Table 4.3. Estimated maximum number of male paternal half-siblings over a 16 year period using estimates females per group from the bai population group composition data.

Females per group	Births per female per year	Infant mortality	Offspring per group (16 yrs)	Male offspring per group (16 yrs)
3.53	0.19	36%	$3.53 \times 0.19 \times 0.64 \times 16 = 6.87$	3.43

The number of male half-sibs was also estimated from bai group compositions themselves. Using all reproductive groups in which an infant was present, across all three populations, the mean number of older male half-sibs an individual could potentially bond with was estimated as 2.14. Using all reproductive groups in which a blackback, young silverback or subadult was present, the mean number of younger male half-sibs an individual could potentially bond with was estimated as 2.20 across groups and populations. Therefore the total expected number of socially bonded male half-sibs within a group in these populations was 4.34, if these groups remain stable until that infant reaches adolescence.

4.4.4 Ape social trait ancestral state reconstructions

Ape mating systems are highly variable, both within and among species. The mating systems discussed here primarily refer to the social mating system rather than the underlying genetic mating system (accounting for extra-pair/group mating). However, analysis across mammalian societies suggests a strong association between social and genetic mating system, with limited incidence of extra-pair mating (Clutton-Brock and Isvaran, 2006; Lukas and Clutton-Brock, 2013). Orangutan (*Pongo*) females were originally thought to mate cooperatively with a single dominant male in their range, with non-dominant (unflanged) males only able to mate with these females by force, suggesting a preferentially polygynous mating strategy (from the females perspective) (Utami Atmoko et al., 2009). Orangutans are known to form short-term monogamous consortships of up to a month, but on rare occasions extra-consort copulations have been observed to take place during this time both between flanged males in the consortship and other females, and between females and other unflanged males when in consortship with a flanged male. Only unflanged males have not been observed to have extra-consortship copulations (Utami Atmoko et al., 2009). Overall this suggests a mating system that is variable between polygyny and promiscuity with only brief periods of monogamy.

In contrast, whilst consortships also occur in the *Pan* genus, the mating system overall is found to be highly promiscuous (Tutin, 1979; Furuichi, 2011), although more dominant males typically gain greater mating opportunities and have higher reproductive success (Wroblewski et al., 2009). Gorilla species are highly polygynous, with limited mating opportunities for non-dominant males even in multi-male mountain gorilla groups (Bradley et al., 2005; Stoinski et al., 2009), whilst gibbons follow a primarily monogamous mating system (Fuentes, 2000). Finally, modern human societies are predominantly classified as monogamous although polygyny is also observed widely (Walker et al., 2011).

Maximum likelihood ancestral state reconstruction of ape mating systems suggested that whilst the ancestral states of ape genera can be fairly conclusively determined, no single mating system is strongly supported in the earlier ancestral nodes (Figure 4.3). Furthermore, the best supported mating system in the common ancestor of great apes is highly dependent on how orangutans are categorised (Figure 4.3a and Figure 4.3b). Discrete categorisation of mating systems is clearly an oversimplification in many ape species, further obscuring the identification of the mating systems present at ancestral nodes.

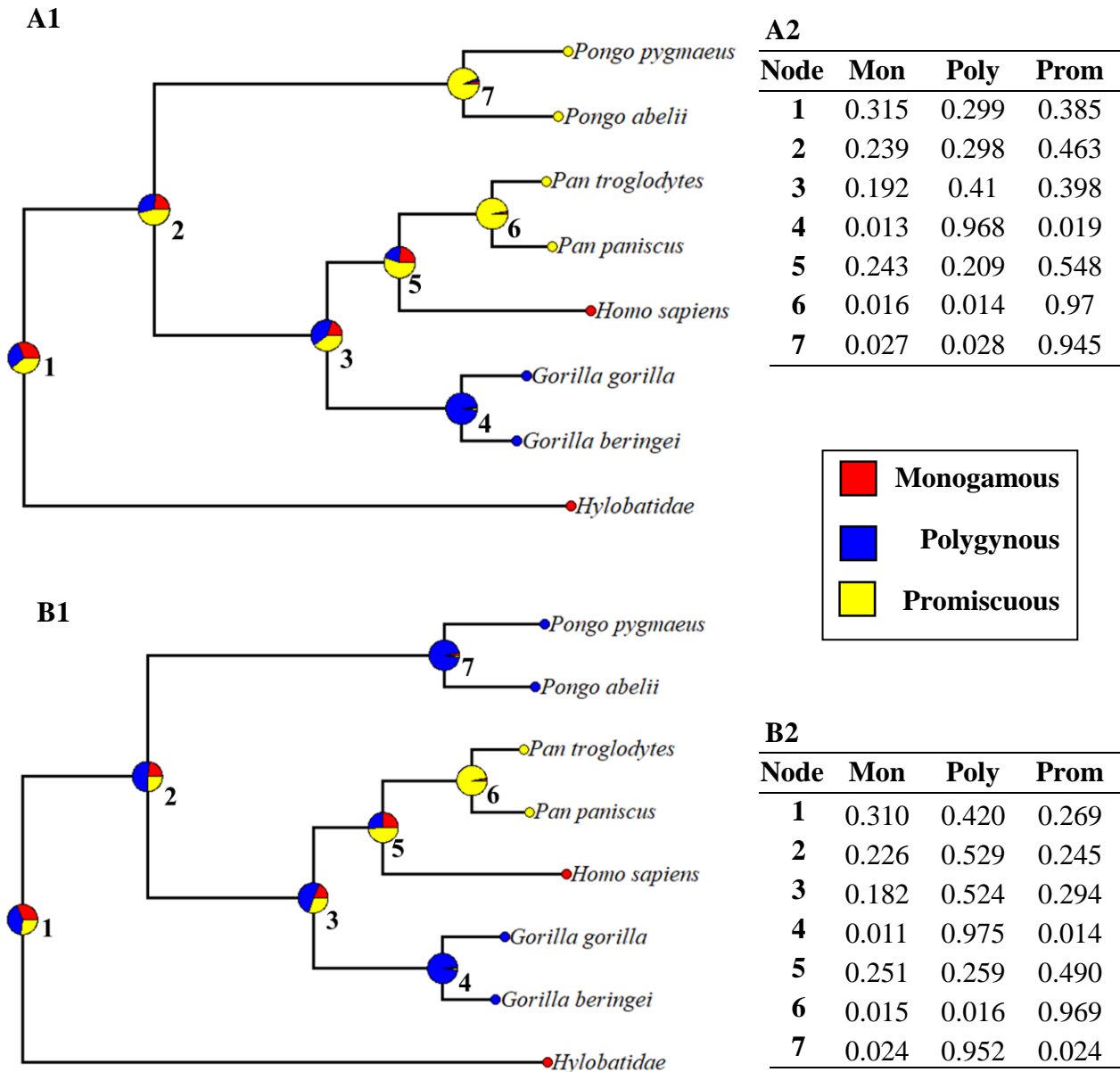


Figure 4.3. Ancestral state reconstruction of mating systems in apes (Utami Atmoko et al., 2009; Tutin, 1979; Furuichi, 2011; Bradley et al., 2005; Fuentes, 2000) A) when orangutans are classified as promiscuous (accounting for the social preferences of females) and B) when orangutans are classified as polygynous (accounting for the genetic mating system due to forced matings by males). A1 and B1 show phylogenies with empirical Bayesian posterior probabilities of monogamy (red), polygyny (blue) and promiscuity (yellow) at each internal node (1-7) indicated by pie chart, and trait of extant species indicated by coloured circle at tip. A2 and B2 show precise values for empirical Bayesian posterior probabilities for each mating system (Mon=monogamous, Poly=polygynous and Prom=promiscuous) for internal nodes (1-7) as indicated in A1 and B2.

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Alternatively, if we focus on the size of alliances of males cooperating to control access to females (the number of socially bonded males within a single, reproductive, social group), a more consistent pattern can be observed across the ape lineage (Figure 4.4). Single male reproductive groups are the dominant theme in gibbons, orangutans, western gorillas and in human hunter gather societies, where less than 10% of reproductive units involve cooperation between more than one male (most often two) (Fuentes, 2000; Singleton and Van Schaik, 2002; Yamagiwa, 1983; Walker et al., 2011; Breuer et al., 2010). These taxa were therefore all scored as predominantly single male. Communities in both species of the genus *Pan* are composed of alliances of multiple cooperating males (Kalpers et al., 2003; Stanford, 1998), and these were therefore scored as multi-male.

Eastern gorillas (*G. Beringei*) posed a problem, as in the mountain gorilla subspecies (*G.b. beringei*) alliances of multiple cooperating males are observed in about 40% of reproductive groups, whilst reproductive groups in the lowland subspecies (*G.b. graueri*) are predominantly single male (Yamagiwa, Kahekwa and Basabose, 2003). Overall the most common alliance state observed in this species was single male and it was therefore scored as such for the purposes of ancestral state reconstruction. This however made a considerable difference to the reconstruction of ancestral states as can be observed by comparing Figure 4.4 with Appendix 4.2. Ancestral state reconstruction demonstrated that single male alliances were likely to be the ancestral state of great apes, with strong support for single male alliance states at all internal nodes except for the common ancestor of the *Pan* genus (Figure 4.4, node 6).

As discussed in the introduction, whilst multi-level social structure was previously thought to be absent in all non-human ape species, with multi-level social structure evolving fairly late in human evolution, the detection of this structure in western gorillas casts this hypothesis into doubt. Multi-level social structure is expected to be absent in the *Pan* genus due to high territoriality (Watts and Mitani, 2001; Mitani, Watts and Amsler, 2010; Crofoot and Wrangham, 2010; Parish, De Waal and Haig, 2006), however this has not been confirmed. The only ape species for which multi-level social structure has been investigated are humans and western gorillas and therefore meaningful ancestral state reconstruction could not be attempted for this trait. Instead, known, suspected but unconfirmed, and unknown states of the trait were plotted across the ape phylogeny (Figure 4.5).

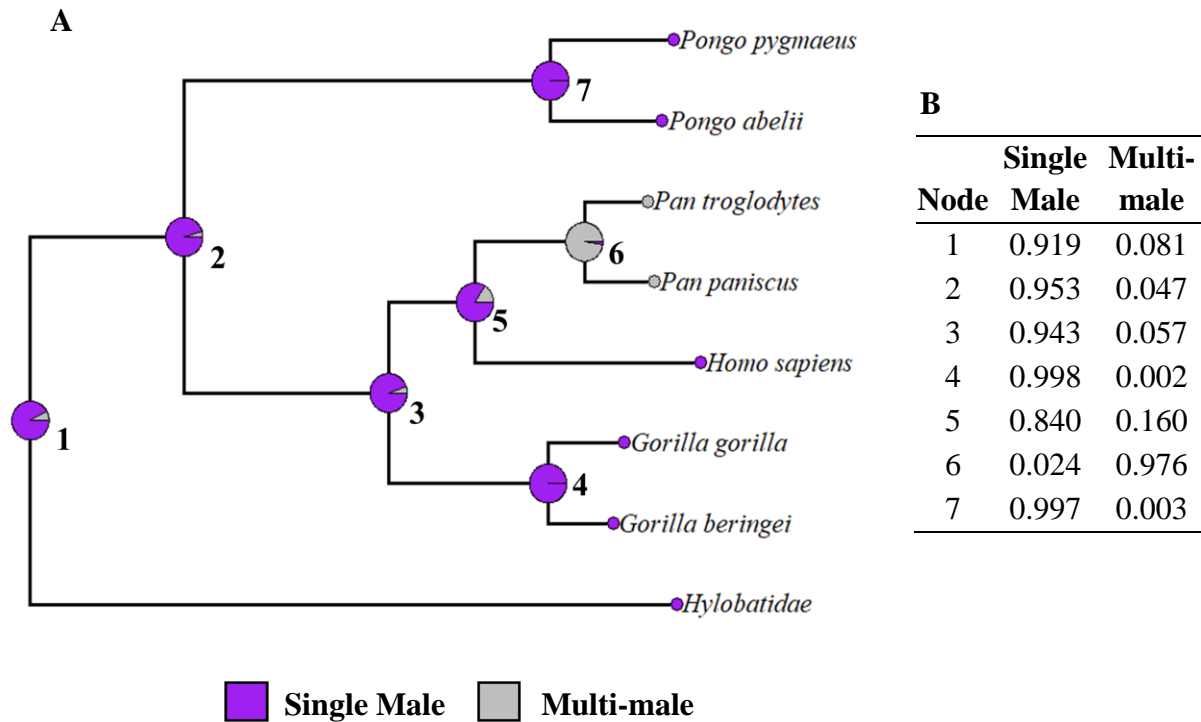


Figure 4.4. A) Ancestral state reconstruction of male alliance size in apes (Fuentes, 2000; Singleton and Van Schaik, 2002; Yamagiwa, 1983; Walker et al., 2011; Breuer et al., 2010; Kalpers et al., 2003; Stanford, 1998; Yamagiwa, Kahekwa and Basabose, 2003), with empirical Bayesian posterior probabilities of single male alliances (purple) and multi-male alliances (grey) at each internal node (1-7) indicated by pie chart, and the trait of extant species indicated by coloured circle at tip. B) Precise values for empirical Bayesian posterior probabilities for alliance size state for internal nodes (1-7) as indicated in A.

Due to the likely lack of multi-level social structure in chimpanzees, the *Pan* genus has been scored with multi-level social structure being potentially absent (Figure 4.5 dashed black line). Humans and western gorillas have been scored with multi-level social structure being present, and eastern gorillas have been scored with multi-level social structure being potentially present (dashed green line), as its presence in the very ecologically similar and closely related western gorilla suggests the likelihood of its presence throughout the genus. The presence of multi-level social structure in orangutans and gibbons has not been investigated, and whilst it has been largely assumed to be absent in these taxa, it remains unknown and is therefore scored as such. Figure 4.5a depicts the hypothesised states of ancestral nodes if multi-level social structure evolved in a common ancestor of gorillas and humans, prior to their divergence, whilst figure 4.5b depicts the hypothesized states of

ancestral species under the theory that multi-level social structure evolved late in human evolutionary history as hypothesised by Foley and Gamble (2009).

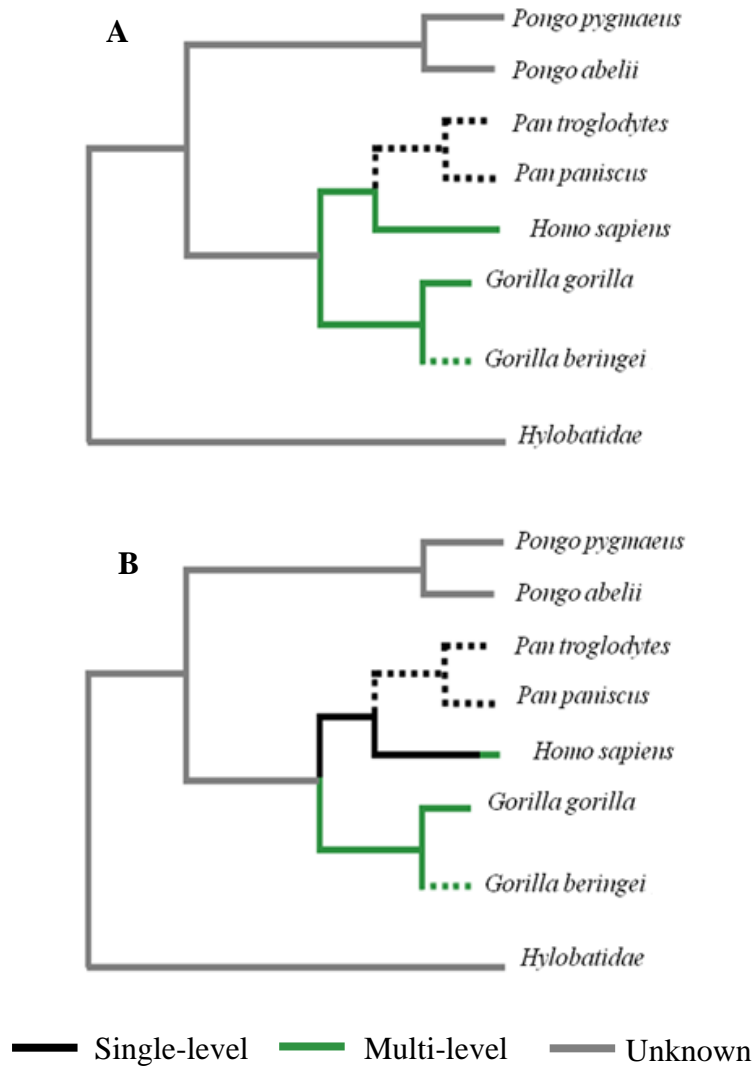


Figure 4.5. Presence of multi-level social structure in ape species: absent (black), present (green), and unknown (grey) plotted on a phylogeny of apes (Arnold, Matthews and Nunn, 2010). Suspected but unconfirmed traits indicated by dashed lines. A) Transitions required under our proposed model of social evolution and B) Transitions required under the assumption that multi-level social structure evolved late in the hominin lineage.

4.5 Discussion

4.5.1 Scaling

The additional tiers of western gorilla social structure identified in Chapter 3 correspond closely to those of other taxa with multi-level social structure. The first order of multi-unit associations detected in Chapter 3 map closely to tier g3 (dispersed extended family group) in Binford's classification of traditional human societies (Binford, 2001; Hamilton et al., 2007), where g1 and g2 represent respectively, individuals and family groups. They also resemble baboon "clans" or "gangs", elephant "bond groups", and dolphin "first order alliances" (Hill, Bentley and Dunbar, 2008). The second tier of multi-unit associations we detected map to Binford's g4 (aggregated group), baboon "bands", elephant "clans", and dolphin "second order alliances". The potential for Binford's tier g5 (sub-population), is suggested by the periodic aggregations observed at resource hotspots, and the tendency for many gorilla groups to converge on places like Mbeli during super-annual "mast" fruiting events, where up to 10 groups have been observed feeding in the clearing on a single day (Walsh et al., 2007). But it appears likely that the observation days in the datasets were too few to provide adequate statistical power for detecting this sub-population tier in Chapter 3. Community closure consistent with Binford's tier g6 (population) is indicated by the asymptotic new group accumulation curves for Lokoué and Mbeli (Figure 4.1). Gorillas also appear to exhibit a social tier observed in humans and referenced by animal ecologists but omitted by Binford's classification, the preferential affiliation within mother-offspring units (Nowell and Fletcher, 2007; Watts and Pusey, 2002). Previous analyses of gorilla social systems have focussed on the group level of social structure alone, however our detection of two novel social tiers in Chapter 3, combined with the previously known tiers of mother-offspring unit and group unit, brings the number of empirically confirmed tiers of social structure in western gorillas to 4, with two further tiers (sub-population and population) supported but not confirmed.

The scaling ratio of roughly 2.7 observed between gorilla social tiers was highly consistent both between the different gorilla populations, and with that observed in other multi-level mammalian species (Hill, Bentley and Dunbar, 2008). The slightly lower scaling size compared to other multi-level mammalian species could be explained by a marginally lower demographic rate or higher mortality from poaching, habitat loss and disease (Köndgen et al.,

2008), that produces fewer potential kin associates. Kaplan et al. (2009) suggest that much of the band-based human social structure can be explained by human's unique collaborative resource production; however the presence of above-group social units in many other animal societies indicates that collaborative resource production is either not a requirement in order for this to evolve, or not uniquely human. For example the cooperative herding of prey by orcas (Smith et al., 1981), another species with multi-level social structure could be considered closely comparable. Therefore, investigation of the potential for cooperation within the higher-level social tiers of western gorillas, such as through cooperative foraging, should be a key area of research to pursue in the future. The similarities between human social structure and the levels of gorilla social structure we have detected here, strongly argue that there is continuity between human and gorilla social complexity. That, rather than considering human social complexity as a unique product of hominin brain evolution, it must be considered in its broader evolutionary context through comparison with other apes.

4.5.2 Reproductive drivers of scaling

In human, elephant, and now gorilla society, kinship is thought to be a fundamental component of the multi-level structure (Wittemyer, Douglas-Hamilton and Getz, 2005; Grueter et al., 2012). One hypothesised mechanism of the common scaling ratio is that if both human and elephant females have roughly three offspring of the sex that most strongly defines the social interactions (males in primarily patriarchal human societies and females in matriarchal elephants), that this reproductive capacity could be driving the scaling of patterns of association through kinship. Due to the polygynous groups western gorillas live in, individuals will grow up in the same social group as both full-siblings and paternal half-siblings and affiliations developed during this period could represent the foundation for the observed multi-level social scaling.

If a female gorilla remained in the same group for the entirety of her fertile years, she could produce roughly 2-3 male full-siblings. This fits very well with the scaling ratio of gorilla social tiers and therefore could provide a feasible explanation of how this scaling ratio comes about, with full-sib male maternal siblings (brothers and their respective groups) forming social tier 4 (dispersed extended family groups), with the next social tier representing associations between cousins. However, due to mortality and group transitions, the average number of brothers is likely far lower than 2-3 and therefore it seems unlikely that

associations between male full-siblings (and the groups they might lead) could be responsible for the community structure we have detected.

Male paternal half-siblings, in comparison, may be a more likely cause of the kin-based above-group tier. The number of socially bonded male half-siblings was estimated as 3.43 per group using estimates of birth rate and mortality from Robbins et al. (2004), or 4.34 using the bai group composition data. These estimates only consider males present in a group within the time an individual gorilla spends in their natal group, however some groups remain stable over a longer period than this. Therefore half-siblings that spent little time in the group together may still be bonded through sharing close bonds with a third half-sibling of intermediate age. In contrast, some groups may disintegrate prior to a male reaching maturity resulting in the male joining a non-breeding group or becoming solitary at a far earlier age, leading to a reduced number of bonded half-siblings. This was estimated to occur for 39% of western lowland gorilla males (Robbins et al., 2016), however the strength of this effect would vary depending on how long before reaching maturity this occurred. Despite the roughness of our estimate, when factoring in the potential for mortality or migration out of the bai population, the estimated values of 3.43 or 4.34 half brothers per group could feasibly be responsible for the scaling value of 2.7 detected here. The first level of associations between groups and solitaries would represent half-brothers, with the next social tier representing affiliations between the sons of silverback males that were half-brothers and so on.

Whilst kinship scaling with half-siblings provides a nice story to explain the multi-level structure detected, the detection of a kin-basis to the social structure is based on only a subset of gorilla males for which genetic data is available, at a single study site. In addition, whilst the genetic analysis detects a significant association between social unit and kinship, it also detects a large proportion of un-related group males in the same social unit and related males in different social units (Chapter 3 Appendix 3.1). Furthermore these reproductive rates may well not be conserved across mammalian multi-level social systems and therefore may not provide the best explanation for the underlying basis to this conserved scaling pattern. Kinship scaling is therefore provided as a potential hypothesis to be investigated by further study. This could be done through higher coverage genetic sampling of a population, including both males and females, to determine the importance of kinship to social interactions between individuals in different groups. However, kinship is likely to be only

one of many factors determining the overall social structure and understanding the various mechanisms underlying a social structure is highly complex. In humans, social networks are strongly influenced by kinship, geography, homophily, and many other factors beside (Liben-Nowell et al., 2005; Onnela et al., 2011; Dunbar and Spoor, 1995), and we are still far from fully understanding the numerous factors influencing social structure even within our own species (Boardman, Domingue and Fletcher, 2012).

4.5.3 Ape social evolution

Hypotheses relating to early hominin social systems are greatly reliant on comparison with *Pan troglodytes* (Sayers and Lovejoy, 2008), in part due to the relative lack of information on the higher level social structures of other highly related ape species, crucially the bonobo and both western and eastern gorilla species. By collating current research on the mating systems, male alliance states and multi-level social structure for ancestral state reconstruction I aimed to provide a more informed discussion of the evolution of hominin social structure, particularly with regards to multi-level complexity.

As demonstrated in Figure 4.3, ape mating system properties are highly diverse between species and appear to show a high degree of plasticity within species. This makes any reliable reconstruction of the ancestral state in apes or mating systems within early hominins extremely difficult from a comparative approach. Comparison with chimpanzees has led to the common hypothesis that the ancestral human state was one of promiscuous mating in a MM-MF group, from which the current states of polygyny and monogamy in modern humans evolved relatively recently (Foley and Gamble, 2009; Chapais, 2013). This is supported to some extent by the findings of Shultz et al. (2011) that monogamous systems in primates have primarily evolved from MM-MF groups. My ancestral state reconstructions also suggest that whilst a polygynous state is best supported in the common ancestor of African apes, there is marginally more support for promiscuity in the common ancestor of humans and chimpanzees (Figure 4.3). However a clear hypothesis on the ancestral mating system of humans is obscured by the high variability of strategies across apes. Broader analysis of mating strategies across mammals (Lukas and Clutton-Brock, 2013), that ensured that monogamously mating species that lived in social groups with non-breeding offspring were classified as monogamous rather than “group-living”, finds that in contrast to Shultz et al. (2011), social monogamy appears to have largely evolved from an ancestral state of solitary

females, where male's ranges overlap with those of multiple females. Due to the presence of social groups including multiple reproductive females in all non-human African apes, Lukas & Clutton-Brock (2013) suggest that this was likely observed in the hominin ancestor.

However, this does not discriminate between the possibility of MM-MF social groups such as those observed in chimpanzees, or single-male multiple-female polygynous groups such as those in western gorillas, where the key difference between these two polygamous mating systems relates to the number of males cooperating to control access to females.

If we focus only on the size of alliances of males cooperating to control access to females, a more consistent pattern can be observed across apes, with broad support for single males defending a female (or females) at all internal nodes prior to the *Pan* genus (Figure 4.4).

Alliance size also relates more generally to the origins of higher-level human cooperative networks, which tend not to hinge on the pattern of mating between males and females. In order for early hominins to have had multi-male groups, three evolutionary transitions are required: transitions from single to multi-male in the mountain gorilla sub-species and the *Pan/Homo* common ancestor, and a reversal back to single-male groups suggested to have taken place at roughly 1myBP (Foley and Gamble, 2009). In contrast, if the *Pan/Homo* common ancestor is reconstructed as single male, only two transitions are required: single male to multi-male in both mountain gorillas and *Pan* (Figure 4.4).

Given the presence of multi-level structure in both humans and gorillas, and its relatively rare occurrence across mammalian species, it appears most parsimonious that this social complexity evolved prior to their divergence. The predominance of single male reproductive groups in humans is also likely to have been inherited from the common ancestor of all apes, rather than replaced by territorial MM-MF structure in the most recent common ancestor of chimpanzees and humans then regained somewhere in the hominin lineage. Therefore, these ancestral single male groups may have represented the starting point from which multi-level social structure evolved prior to the human-gorilla-chimpanzee divergence, via increased affiliation between dispersed kin. Given that gorillas and humans also share characters such as a matrix of evenly spaced, overlapping home ranges and long-tailed distributions of social contact at resource hotspots (Walsh et al., 2007) (Chapter 5), they appear to represent an excellent model system for human social evolution, with clear advantages over the more commonly used chimpanzee (Foley and Gamble, 2009; Chapais, 2013). However, as primate social systems are so plastic within and variable between species, it seems imprudent to lean

Chapter 4: The Evolution of Multi-level Social Structure

too heavily on the states of extant taxa when drawing conclusions about distantly related early hominins. Rather, the key point is that if we explicitly define “complexity” as nested hierarchical multi-level structure, then the social brain enhancements of the hominin neocortical explosion do not appear necessary to explain human social complexity.

4.6 Conclusion

A major component of humanity's complex social structure, and arguably the core of our human society, is the extent of higher level social tiers, such as nations, uniting huge numbers of weakly related or entirely unrelated individuals in cooperation. The results in this, and the subsequent chapter demonstrate extensive, previously overlooked similarities between human and gorilla social systems, suggesting that the social brain enhancements observed within the hominin lineage were not necessary to enable human social complexity. Extensive comparison between humans and the *Pan* genus has been used to suggest that the evolution of complex, between-group social interactions and multi-level social structure, occurred after the chimpanzee-human split. However, the presence of a kin-based, multi-tiered social structure in gorillas following a common scaling structure suggests that fundamental elements of human social complexity may have far deeper evolutionary roots than previously assumed. The extreme territoriality observed in chimpanzees (Watts and Mitani, 2001; Mitani, Watts and Amsler, 2010) suggests that higher-level associations are unlikely to be occurring in this species, however the range overlap and peaceful between-group encounters observed in bonobos (Idani, 1990; Furuichi, 2011) combined with the findings here, suggest that the presence of a multi-level social system in this species should not be ruled out. Whilst my findings suggest reproductive rates could feasibly be driving the conserved scaling pattern observed in gorillas and possibly other multi-level mammalian social structures, this remains to be confirmed. However, the detection, yet again of this common scaling factor in another mammalian species, this time in one of our closest evolutionary relatives, suggests that the underlying mechanisms leading to the emergence of humanity's supposedly unique social complexity may have far deeper evolutionary origins than previously thought. Peering more deeply into our evolutionary past will therefore be crucial to determining when key transitions in social evolution took place, and ultimately the true extent of human social uniqueness.

4.7 References

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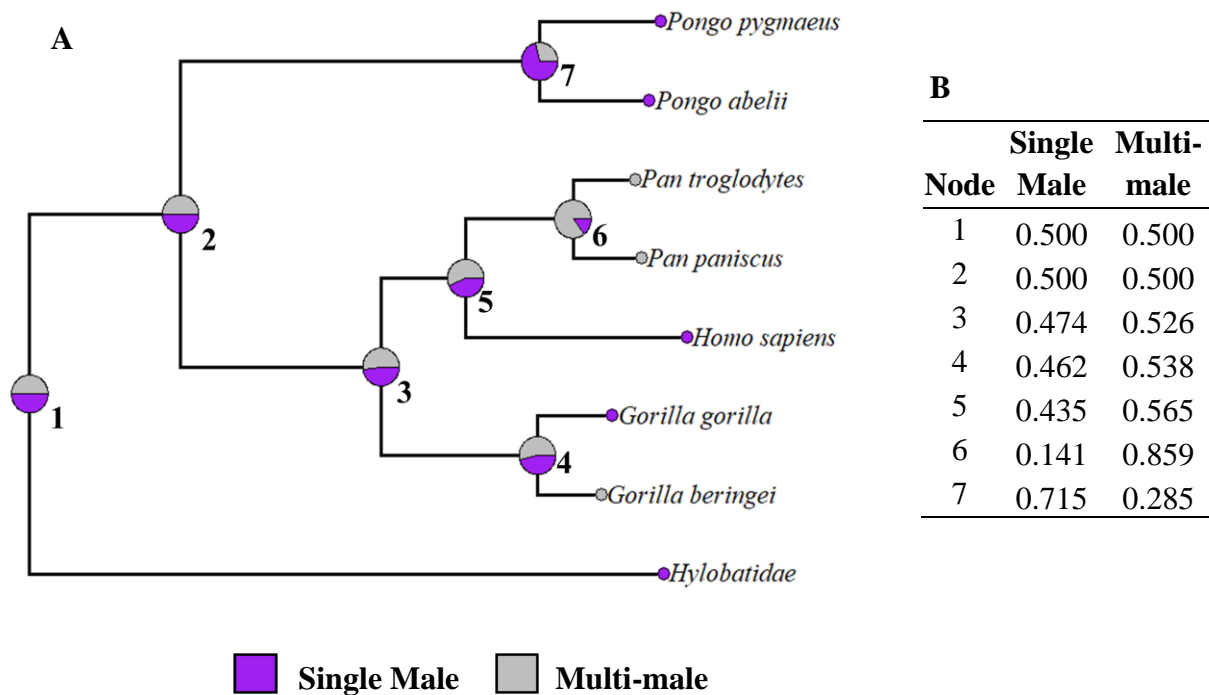
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4.8 Appendices

Appendix 4.1. Scaling statistics across three gorilla populations and for all combined, using social unit sizes calculated by both methods. Method A: Binomial probability index with hierarchical clustering and modularity analyses; Method B: Simple ratio index with varying resolution of algorithm and modularity analyses.

	Method A			Method B		
	Scaling Ratio	R squared	P	Scaling Ratio	R squared	P
Lokoué	2.78	0.984	9.91e-05	2.47	0.996	5.71e-06
Mbeli	2.74	0.987	6.12e-05	2.57	0.994	1.43e-05
Maya Nord	3.07	0.993	0.00369	3.07	0.993	0.00369
Combined	2.83	0.988	2.90e-09	2.65	0.994	8.02e-11

Appendix 4.2. A) Ancestral state reconstruction of male alliance size in apes (Fuentes, 2000; Singleton and Van Schaik, 2002; Yamagiwa, 1983; Walker et al., 2011; Breuer et al., 2010; Kalpers et al., 2003; Stanford, 1998; Yamagiwa, Kahekwa and Basabose, 2003), when eastern gorillas (*Gorilla beringei*) are classified as multi-male, due to the presence of multiple adult males in roughly 40% of reproductive units (Yamagiwa, Kahekwa and Basabose, 2003). Empirical Bayesian posterior probabilities of single male alliances (purple) and multi-male alliances (grey) indicated at each internal node (1-7) by pie chart, and the trait of extant species indicated by coloured circle at tip. B) Precise values for empirical Bayesian posterior probabilities for alliance size state for internal nodes (1-7) as indicated in A.



Chapter 5: Disease Transmission through the Lokoué Bai Gorilla Social Network



Photo: Mbeli Bai Study, WCS Congo

5.1 Abstract

Forest clearings represent important social hubs for the critically endangered western gorilla. Mineral-rich vegetation at these sites attracts gorilla groups and solitary males from considerable distances and they therefore represent potential hotspots for disease transmission. Gorillas are hypothesized to follow distance-discounting rules, such that groups with home ranges closest to forest clearings visit most frequently. This could drive a long-tailed contact structure with many weakly connected groups, from more distant home ranges, and smaller numbers of highly connected groups with nearby home ranges. If contact patterns at these clearings follow a long-tailed distribution, this could cause super-spreading transmission dynamics, enabling the rapid transmission of disease. To test for this, I used social network analysis of same-day visits, to investigate contact structure at Lokoué Bai. Results demonstrated a long-tailed contact distribution where a small number of individuals were responsible for a large proportion of connections in the social network (degree) and a

large proportion of connections to other highly connected individuals (eigenvector centrality). Solitary males exclusively represented the highest 4% of values across all contact metrics. Gorillas with nearby home ranges and higher visit rates were more connected, suggesting that they may represent important targets for disease intervention strategies, and that distance-discounting may be driving the underlying contact distribution. A yaws (*Treponema pallidum*) outbreak, present in the population at the time of data collection, did not transmit predictably by social contact alone, as individuals in larger social groups were not more likely to be infected, and yaws was not more prevalent in groups that were more central to the network. Whilst the extreme long-tailed distributions necessary for super-spreading could not be conclusively confirmed, data were consistent with a super-spreader structure, suggesting that clearings may act as important transmission hubs for disease. The correlation between contact rate and home range distance suggests that this long-tailed contact distribution is driven by spatial dynamics and that disease intervention strategies targeting gorillas with nearby home ranges, particularly solitary males, may be most effective for limiting the spread of disease.

5.2 Introduction

Infectious disease has now joined poaching and habitat loss as one of the major threats to the critically endangered western gorilla (Ryan and Walsh, 2011). In Gabon, infectious disease has contributed to the decline of ape populations by over a half in a 17 year period (Walsh et al., 2003), whilst in the Republic of Congo, Ebola haemorrhagic fever caused the deaths of an estimated 5500 gorillas in a 2700 km² study area alone between 2002 and 2003 (Bermejo et al., 2006). Treatments and vaccines to prevent the decline in populations of endangered apes are in development (Warfield et al., 2014; Capps and Lederman, 2015; Walsh et al., 2017). However, efficiently controlling disease requires a better understanding of the structure of gorilla social networks and the dynamics of disease transmission through these networks.

Whilst traditional epidemiological models assume the random movement and interaction of individuals, there is an abundance of evidence (as discussed in Chapter 1) demonstrating the considerable influence of social structure on the transmission of disease. The gorilla social structure described in previous chapters of this PhD demonstrates that the movement and interaction patterns taking place in western gorilla populations have a non-random structure, which needs to be accounted for in any model of disease transmission in this species. In addition to accounting for the overall social structure, the stability of social affiliations demonstrated in Chapter 3 suggests that it may be possible for future interactions to be predicted from past interactions, enabling the potential to include social network information on specific individuals or groups, when controlling disease outbreaks or predicting future disease transmission in monitored populations.

As well as providing a description of the overall social structure of a population, network analysis has enabled a far greater understanding of how social structure influences disease transmission, in both human and animal networks (Eubank et al., 2004; Sah et al., 2017). In chimpanzee populations, network analysis has identified adult females and juveniles with large families, as highly central to networks. Those individuals are therefore more likely to be responsible for a larger proportion of disease transmission, and thus represent important potential targets for disease intervention strategies (Rushmore et al., 2013). Social structure has already been observed to greatly influence disease transmission and population decline in western gorillas during the Ebola outbreak in the Lokoué gorilla population. During this

catastrophic outbreak, greater mortality was observed for individuals in groups, with mortality rates of 97% (CI:92-98%), compared to 77% (CI 62-78%) in solitary males (Caillaud et al., 2006). This was hypothesized to cause an even slower population recovery than expected, by biasing the population towards solitary males and reducing the reproductive capacity of the population. Understanding the way in which rates of contact vary for certain demographics within a population can therefore be vital for predicting which individuals are at greatest exposure to disease, how a disease will spread, and the long term implications for population recovery.

As discussed in Chapter 1, the distribution of contacts in a network can have a dramatic influence on the speed at which a disease transmits through a population. In networks where contact degree distributions follow a long-tailed power-law distribution, a small number of highly connected individuals known as super-spreaders can be responsible for a high proportion of transmission events, enabling transmission to occur much more rapidly (Lloyd-Smith et al., 2005). If contacts in gorilla networks follow this distribution it would suggest that they are at high risk of explosive disease outbreaks. However, it also suggests a potential solution. Targetted vaccination of super-spreader individuals (or those likely to be super-spreaders) could dramatically reduce disease transmission if they can be identified. Alternatively if super-spreaders cannot be easily identified, the approach of Cohen et al. (2003) could be used whereby highly connected individuals are identified by selecting from an initially randomly chosen individual's contacts, as highly connected individuals are more likely to be contacts.

Many western gorilla food resources (such as fruit, flowers, ants, termites, or roots) are present in limited quantities and widely dispersed (Goldsmith, 1999; Nishihara, 1995). This may lead to considerable competition and therefore avoidance, such that gorilla groups come into contact with each other at these sites less than expected by chance (Seiler et al., 2018) (See Chapter 6). In contrast, forest clearings (known locally as *bais*) represent a superabundant resource of aquatic vegetation with high nutritional value (Metsio Sienne, Buchwald and Wittemyer, 2014; Magliocca and Gautier-Hion, 2002) for which there is therefore thought to be very little competition. Gorilla groups are known to be attracted from considerable distances and show active association with one another, potentially due to the relaxation of feeding competition (Levréro, 2005). Forest clearings therefore represent key social hubs at which a large proportion of inter-group encounters are likely to take place, and are therefore potentially important targets for disease intervention (Parnell, 2002a; Benavides

et al., 2012). Furthermore, the interactions at these locations can occur between groups from different regions that may not interact at all in their usual ranging patterns. This breaks down the spatial clustering of interactions from limited home range overlap, potentially enabling more rapid transmission across the landscape and more explosive outbreak dynamics (Walsh, 2013). Simulations of human contact networks by Scoglio et al. (2010) demonstrated that randomly vaccinating 10% of the population visiting one of the most popular locations reduced the epidemic size by 19%, clearly quantifying the importance of activity hotspots for disease transmission and therefore intervention. However, intervention at these clearings need not be random, and if informed by network structure (e.g. targeted intervention of super-spreaders) could potentially provide even greater reductions in disease transmission, especially if key individuals or demographics can be identified.

One potential driver of long-tailed contact distributions at these resource hotspots could be the distance-discounting methods by which gorillas choose which resource hotspots to visit. Parnell (2002b) suggested that variation in the frequency with which different gorilla groups visit a forest clearing may in part be explained by the distance of those groups' home ranges from the forest clearing, with groups that must travel further from the core areas of their home range, to reach the clearing, visiting less frequently. As the area within a given distance of a clearing increases non-linearly ($\text{area} = \pi \times r^2$) (Figure 5.1c), if gorilla ranges are distributed evenly across space, the number of groups with a given visit rate would be expected to increase with decreasing visit rate. This would be expected to continue up to a cut-off, at which point the distance required to reach the forest clearing would no longer be worth the potential benefits of visiting that site (Trapanese, Meunier and Masi, 2018). This would lead to a large number of rare-visiting groups and a gradually decreasing number of groups that visit more often (Figure 5.1). However, this would not necessarily lead to a long-tailed distribution of contact rates, as the relationship between the number of groups and a given visit frequency would depend on the precise distance-discounting rules used by gorillas. If the rate at which a group visited the forest clearing declined linearly with the distance of their home range centre, a visit rate distribution similar to that of Figure 5.1a would be observed, where area would scale relatively with frequency (the number of groups whose home range centre's were located within that area), and home range distance would scale with visit rate.

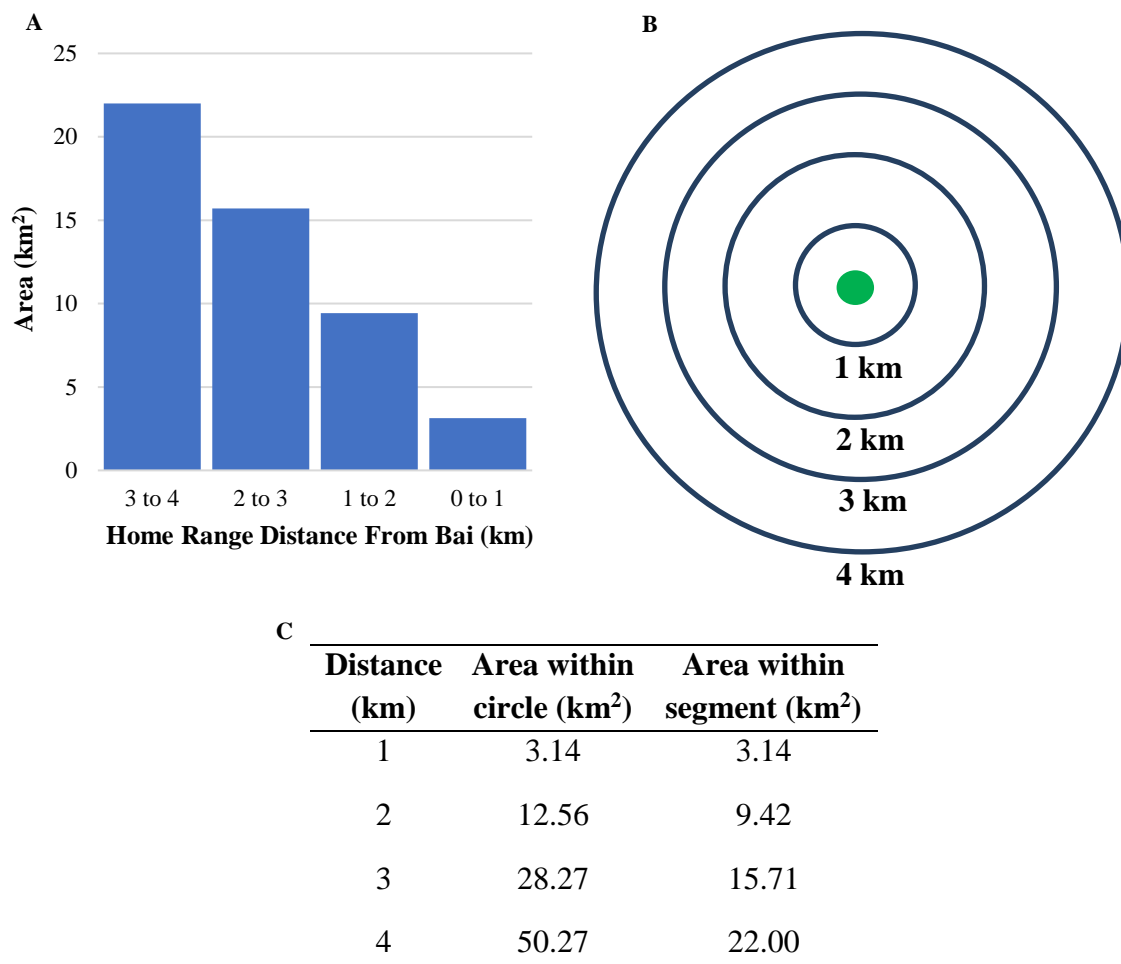


Figure 5.1. Area of potential gorilla home range habitat, with distance from the forest clearing. A) Bar plot of area within a given 1 km width segment, with distance from the forest clearing. B) Plot of 1 km width segments of increasing distance from the forest clearing (represented as a green circle). C) Area within a given distance of the forest clearing (area within circle) or within a given 1 km width segment (area within segment).

Alternatively, visit patterns to forest clearings could be influenced by social factors such as affiliations between groups or the relative size or dominance of groups. As demonstrated in Chapter 3, gorillas show biases in their visit patterns to these forest clearings, which appears to occur through active associations between affiliated groups. If certain groups are more “popular”, or strongly affiliated with a larger number of other groups, this could lead to higher contact rates for these groups, as other groups bias their movement patterns in order to visit the clearing at the same time as them. However, biases in visit patterns could also occur through active exclusion of smaller, less dominant groups (e.g. through physical or vocal threats). This could lead to dominant groups being able to visit more often and therefore

being more central to the network structure. A further option is that larger groups may be more reliant on the super-abundant resources represented by these forest clearings, as smaller food sources such as fruiting trees or termite mounds may be less able to adequately support larger groups. This mechanism would also lead to larger groups visiting more often and therefore having the potential to be much more central to the network structure.

Given the rapid decline of gorilla populations due to infectious disease (Walsh et al., 2003; Ryan and Walsh, 2011), a better understanding of social structure in gorillas through network analysis could provide highly beneficial insights for disease prediction, management and prevention. Past studies of social interactions in gorillas have concentrated primarily on within-group social dynamics, but we know little about what is most important to the spread of diseases like Ebola: the between-group social dynamics. Here I use social network analysis to test for the presence of long-tailed super-spreader structure in the pattern of contacts at Lokoué clearing. I then investigate the potential for ranging dynamics and dominance or group size as mechanisms behind the contact rate distributions observed. By focusing on inter-group and solitary contacts I assess the feasibility of detecting those likely to be responsible for considerable transmission between these social units, and discuss how this could inform effective conservation strategies.

5.3 Methods

5.3.1 Data

This chapter uses the Lokoué Bai dataset described in Chapter 2 with additional yaws outbreak data from Levréro et al. (2007) and Levréro's PhD thesis (2005). Both visit data and yaws infection status were recorded at this site simultaneously between April 2001 and September 2002. Using the Lokoué Bai visit data, visit rates were calculated as the total number of visits by gorilla units (groups or solitary males) during the 409 day study period. Social units were classified as either reproductive groups (RGs) (N=24), which contained at least one adult female and at least one adult male, non-reproductive groups (NRGs) (N=3) which contained multiple individuals but no adult females, or solitary males (S) (N=21) which represented a single adult or young adult male gorilla that moved independently from others. The classifications used were those reported by Levréro (2005).

5.3.2 Networks and centrality metrics

Two networks were generated using the Igraph R package (Csárdi and Nepusz, 2006). The first used pairwise co-visit number – the total number of days on which a pair of units were recorded in the clearing on the same day. The second network was generated using the simple ratio (SR) association index values as described in Chapter 3. Network centrality metrics: weighted degree, eigenvector centrality, and betweenness from both networks were calculated using the Igraph R package (Csárdi and Nepusz, 2006). Correlations between centrality metrics in each network were investigated using Pearson's product moment correlation. Whilst betweenness is often used to investigate the potential for disease transmission, due to its estimation of the importance of individuals in connecting different regions of the network (Silk et al., 2017), it was not analysed in considerable depth here. This is in part due to the proportion of nodes for which betweenness was estimated as 0, therefore providing very little information, and also due to the fact that nodes in these networks represented gorilla groups or solitary males and therefore, connections between these nodes already represented connections between multiple individuals. The more local centrality metrics of weighted degree and eigenvector centrality were therefore investigated in greater

depth as they included both direct connections between individuals in differing groups, and also indirect connections via other group members.

5.3.3 Modelling distributions

Distributions of visit rate and network centrality metrics for the raw co-visit network were investigated using the `powerLaw` package (Gillespie, 2014). Power law, exponential and poisson distributions were fitted to discrete variables (visit rate and weighted degree), whilst power law and exponential distributions were fitted to continuous eigenvector centrality values. A maximum likelihood estimator bootstrapping approach was used to assess whether given values could have come from each distribution type by Kolmogorov-Smirnoff test. If multiple distributions could not be excluded, model fit was compared using Vuong's test. Long-tailed distributions were not investigated for network metrics from SR networks as plotting values demonstrated that long-tailed distributions would not be a good fit. Normal Q-Q plots were used to demonstrate that values were close to those expected under a normal distribution.

5.3.4 Predicting centrality

Kolmogorov-Smirnoff tests were used to determine whether reproductive groups and solitaries had significantly different centrality or visit rate values. Modified signed-likelihood ratio tests (Krishnamoorthy and Lee, 2014; Marwick and Krishnamoorthy, 2018) were used to determine whether reproductive groups and solitaries had significantly different coefficients of variation. Non-reproductive groups were not investigated given the low sample size of 3. The relationships between home range distance and visit rate, raw weighted degree, raw eigenvector centrality and group size were investigated using Pearson's Product Moment Correlation. The relationships between visit rate and all centrality metrics were investigated using Pearson's Product Moment Correlation.

5.3.5 Sub-sample networks

The dataset was split into 10 non-overlapping 40-day sub-samples. Visit rates were calculated for all gorilla units across these 10 sub-samples and networks were constructed from the

number of same-day visits occurring within a 40-day sub-sample window. Weighted degree of nodes (gorilla units) from these networks was calculated using the Igraph R package (Csárdi and Nepusz, 2006). Distributions of visit rate and weighted degree values across all sub-samples were modelled as described above.

5.3.6 Predicting yaws transmission

Yaws (*Treponema pallidum*) is a chronic bacterial infection found in humans and non-human primates in tropical regions. It leads to skin and bone lesions and is transmitted via skin contact with lesions or through flies that come into contact with wounds (Levréro et al., 2007). Binomial logistic regressions were used to investigate the relationship between group size and yaws infection status at Lokoué Bai, both for individuals and for groups as a whole. The infectious status of groups was scored as 1 for all groups containing any individual observed to be infected with yaws (presence of lesions) over the study period by Levréro et al. (2007), and 0 for all groups that were not observed to contain any infected individuals. The proportion infected for groups was calculated as the proportion of total group members that were observed by Levréro et al. (2007) to be infected with yaws at any point during the study period. Binomial logistic regressions and logistic regressions were used to investigate whether network metrics or visit rate could predict yaws infection.

5.4 Results

5.4.1 Distribution of visit rates

To investigate the potential for super-spreading structure at forest clearings, the distribution of visit rates was plotted (Figure 5.2a). Model fit using maximum likelihood bootstrapping demonstrated that a power law distribution could not be ruled out (KS goodness of fit = 0.138, $p=0.221$), however that was also the case for exponential (KS goodness of fit = 0.079, $p=0.926$) and poisson (KS goodness of fit = 0.076, $p=0.932$) distributions (Figure 5.2b). This suggests the potential for super-spreader structure in the social interactions taking place within clearings. Comparison of power law and exponential model fit suggested an exponential distribution was a marginally better fit but not significantly so (Vuong's Test: $R=-1.608$, $p=0.108$). Power law and poisson distributions were found to fit the data roughly equally as well (Vuong's Test: $R = -0.011$, $p = 0.992$). Solitaries were responsible for the majority of the highest visit rates, however visit rate values (KS test: $D = 0.24405$, $p = 0.51$) and coefficients of variation (MSLRT = 3.13, $p=0.0768$) were not significantly different between solitaries and reproductive groups.

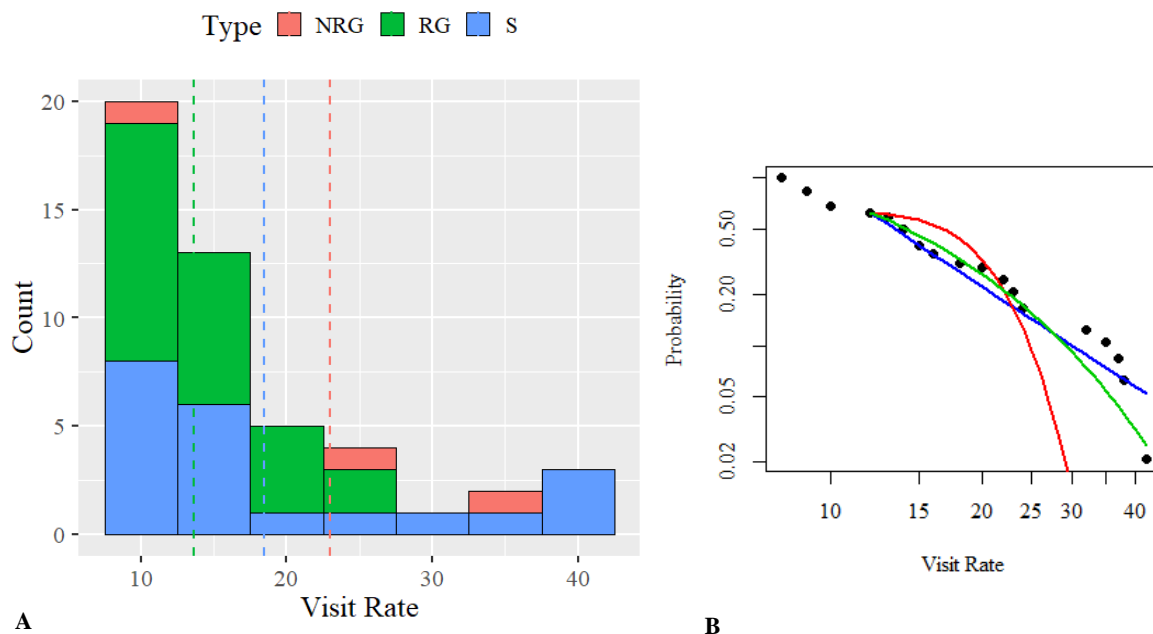


Figure 5.2. The distribution of visit rate values. A) Histogram of visit rates by social unit type. Non-reproductive groups (NRG) in red, reproductive groups (RG) in green and solitaries (S) in blue. Means of visit rate by social unit type indicated by dashed line in respective colour. B) Probability of a group or solitary having a given visit rate value with fitted power law (blue), exponential (green) and poisson (red) curves.

5.4.2 Centrality metric correlations

Two local centrality metrics (weighted degree and eigenvector centrality) and one global centrality metric (betweenness) were calculated for both the raw visit network and the simple ratio (SR) network. All metrics correlated significantly with one another in both networks, with correlations suggestive of a medium to low level of modularity in social networks (Table 5.1).

Table 5.1. Correlations between two local centrality metrics (WD=weighted degree and EC=eigenvector centrality) and one global centrality metric (B=betweenness), for a) the SR network and b) the raw visit network, for group and solitary co-visits at Lokoué Bai. Correlations calculated by pearson correlation coefficient and shading indicating strength of the correlation (low-light yellow to high-dark red). All correlations produced p-values of <0.05.

A				B			
WD	EC	B		WD	EC	B	
	0.982	0.435	WD		0.985	0.382	WD
		0.364	EC			0.31	EC
			B				B

5.4.3 Centrality distribution in bai co-visit network

Local centrality metrics were investigated in the simple ratio social network constructed from the number of days on which pairs of social units visited on the same day (modularity of network = 0.140). For weighted degree a power law distribution could not be ruled out (KS goodness of fit = 0.135, p=0.167), but neither could exponential (KS goodness of fit = 0.082, p=0.826) or poisson (KS goodness of fit = 0.178, p=0.523) distributions (Figure 5.3). Model comparison suggested that an exponential distribution was a better fit than a power law but not significantly so (Vuong's Test: R=-1.322, p=0.186), and that a power law distribution was a better fit than a poisson distribution (Vuong's Test: R=1.923, p=0.054).

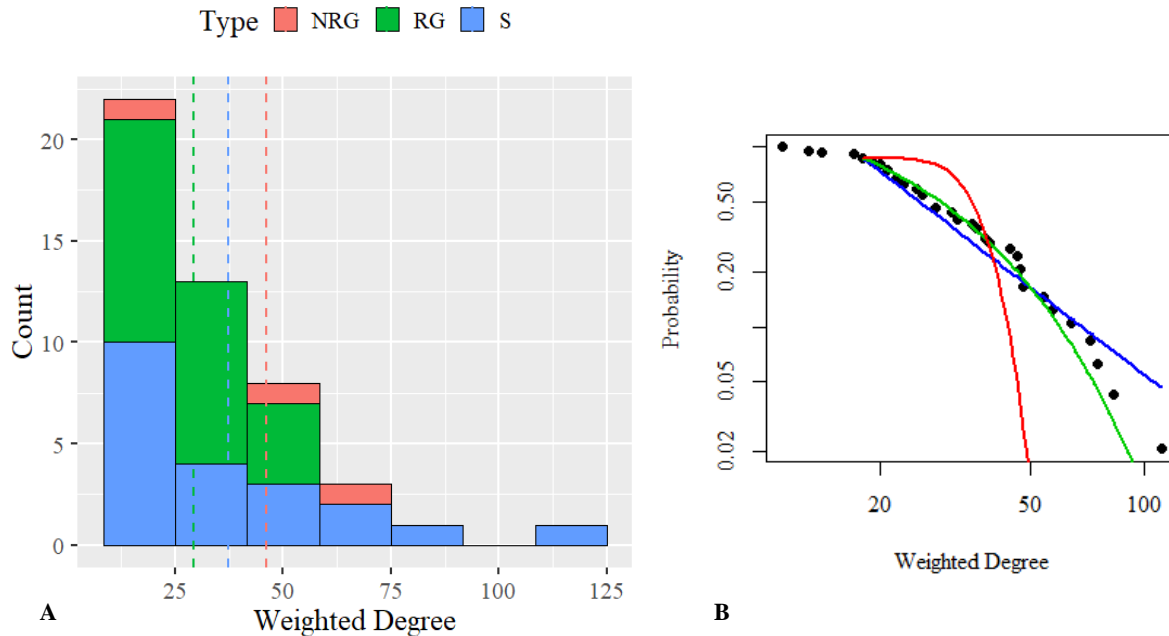


Figure 5.3. The distribution of weighted degree values from the network constructed from same-day visit values. A) Histogram by social unit type. Non-reproductive groups (NRG) in red, reproductive groups (RG) in green and solitaries (S) in blue. Mean of weighted degree by social unit type indicated by dashed line in respective colour. B) Probability of a group or solitary having a given weighted degree with fitted power law (blue), exponential (green) and poisson (red) curves.

A power law distribution was again a plausible hypothesis for eigenvector centrality (KS goodness of fit = 0.141, $p=0.172$), but an exponential distribution could be ruled out (KS goodness of fit = 0.156, $p=0.037$) (Figure 5.4). Poisson distribution could not be fitted to continuous eigenvector centrality values. Model comparison showed that a power law was a marginally better fit than an exponential distribution but not significantly so (Vuong's Test: $R=0.429$, $p=0.668$). Solitaries again represented the majority of the most highly connected individuals, showing greater coefficient of variation than reproductive groups (weighted degree: MSLRT=5.89, $p=0.0152$, eigenvector centrality: MSLRT=5.51, $p = 0.0189$); however values themselves were not significantly different between reproductive groups and solitaries (KS test: weighted degree: $D = 0.2381$, $p = 0.5493$, eigenvector centrality: $D = 0.31548$, $p = 0.1704$).

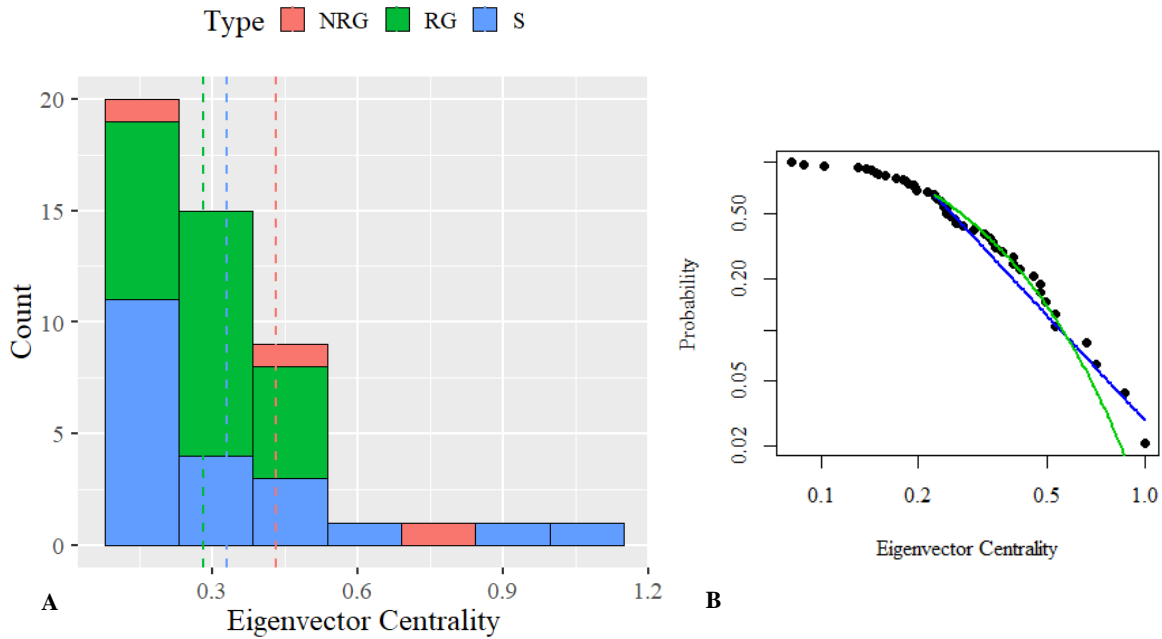


Figure 5.4. The distribution of eigenvector centrality values from the network constructed from same-day visit values. A) Histogram by social unit type. Non-reproductive groups (NRG) in red, reproductive groups (RG) in green and solitaries (S) in blue. Mean of weighted degree by social unit type indicated by dashed line in respective colour. B) Probability of a group or solitary having a given eigenvector centrality with fitted power law (blue) and exponential (green) curves.

5.4.4 Centrality distribution in the network of social affiliation

SR association index values were calculated to estimate the levels of active association between groups or solitaries, after controlling for visit rate. Networks from these values were therefore an estimate of the social affiliation between groups and solitaries (social units), as any effect of spatial dynamics on visit frequency was removed (modularity of network = 0.170). Network metrics from the SR network did not show the same heavy-tailed distributions, instead following a normal distribution fairly closely (Figure 5.5). This suggests that social affiliations are not responsible for the heavy-tailed contact distributions occurring at Lokoué Bai. As spatial effects are likely to be specific to the bai itself, whilst social affiliation between units could be expected to remain fairly constant across ranges, any super-spreader effect may to some extent be limited to the specific location and not be observed throughout gorilla ranges. Solitaries still represented the majority of the most highly connected individuals in the SR network but did not have significantly greater coefficient of variation

(weighted degree: MSLRT=2.59, $p=0.107$, eigenvector centrality: MSLRT=3.12, $p = 0.0776$) or centrality values than reproductive groups (KS test: weighted degree: $D = 0.215$, $p = 0.590$, eigenvector centrality: $D = 0.215$, $p = 0.590$).

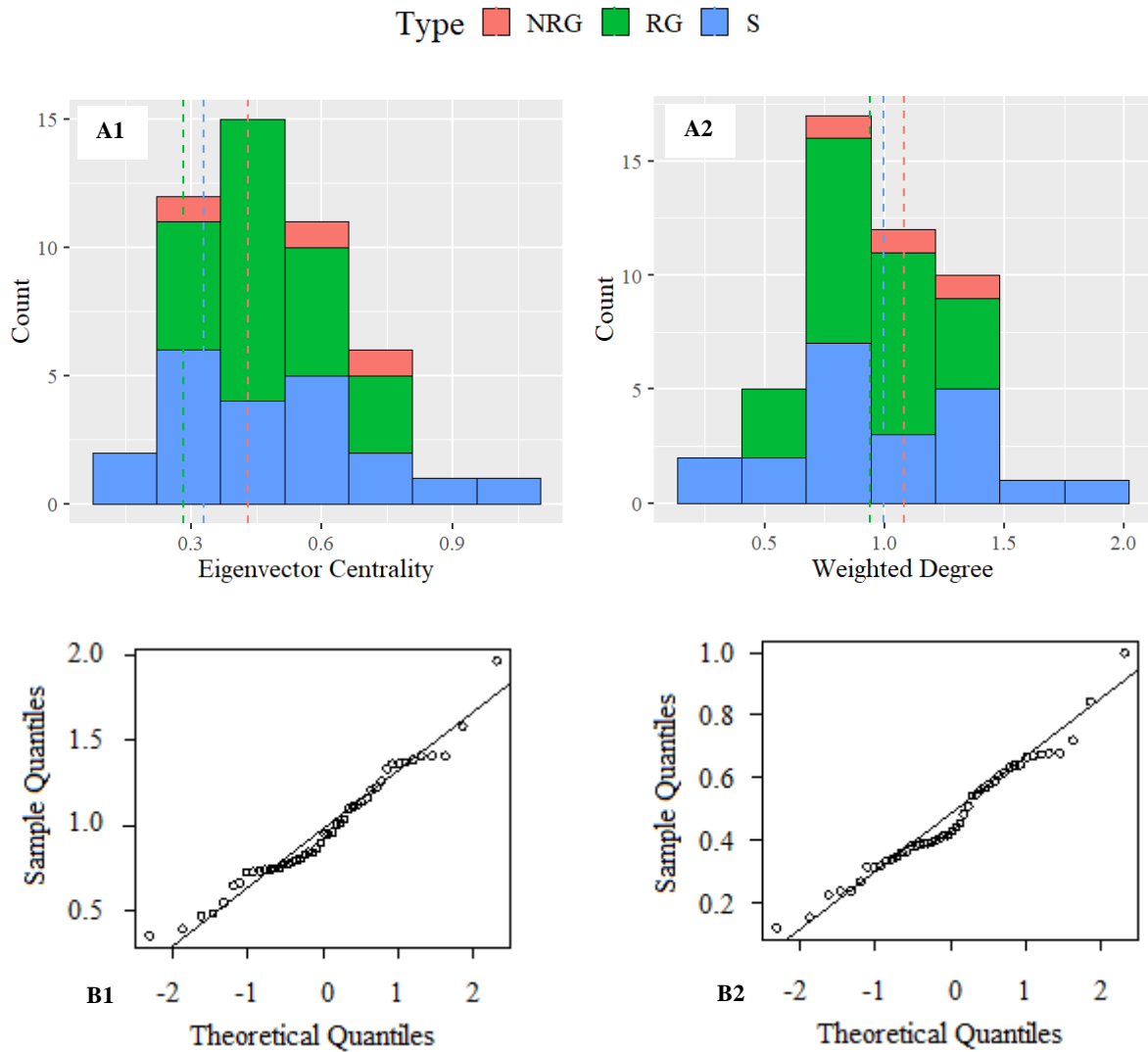


Figure 5.5. A) Histograms of 1) weighted degree and 2) eigenvector centrality values from the network constructed using SR associations from same-day visits. Non-reproductive groups (NRG) in red, reproductive groups (RG) in green and solitaries (S) in blue. Mean of network metric by social unit type indicated by dashed line in respective colour. B) Normal Q-Q plots of 1) weighted degree and 2) eigenvector centrality values from the network constructed using SR associations from same-day visits.

5.4.5 Spatial predictors of network centrality

Using published home range estimates (Levréro, 2005), the relationship between home range distance from the bai and visit rate was investigated. Visit rate decreased the further away a group's home range was from the bai (Figure 5.6), and gorillas appeared to be following a linear distance-discounting rule (Pearsons Product Moment Correlation: $t = -5.30$, $df = 8$, $p = 7.30e^{-4}$). Although, with a small sample size of only 9 groups of known home range, there is a considerable level of uncertainty surrounding the precise discounting relationship. This same negative correlation was observed between home range distance and both network metrics from the raw co-visit network (Pearsons Product Moment Correlation: Weighted degree: $t = -3.39$, $df = 8$, $p = 9.46e^{-3}$. Eigenvector centrality: $t = -2.87$, $df = 8$, $p = 0.021$) demonstrating that gorillas living closest to the clearing were likely to be highly central to the network and responsible for the highest proportion of transmission events (Figure 5.6). Network metrics from the SR association network did not show a significant correlation with home range distance from the bai (Pearsons Product Moment Correlation: Weighted degree: $t = -1.70$, $df = 8$, $p = 0.127$. Eigenvector centrality: $t = -1.40$, $df = 8$, $p = 0.200$).

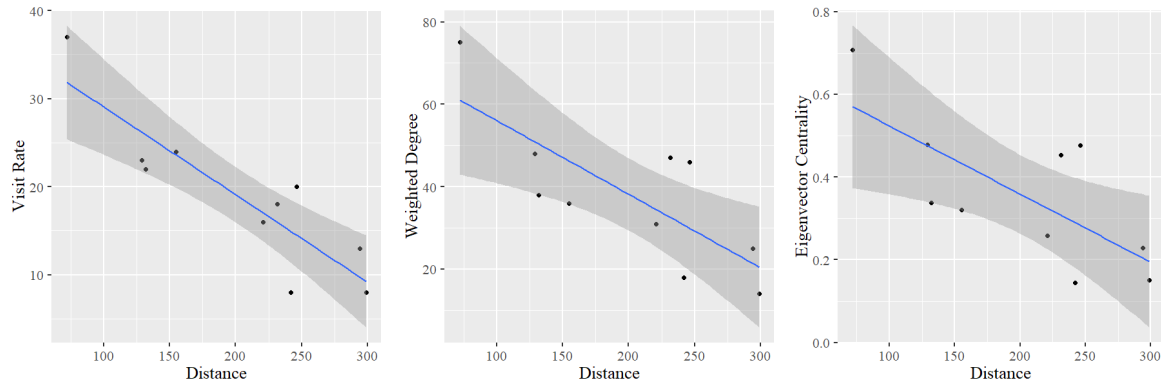


Figure 5.6. Linear decline in visit rate and raw co-visit network metrics (weighted degree and eigenvector centrality) with increasing distance of a gorilla group's home range from the bai. Distance measured in pixel distance from home range estimate diagram (Levréro, 2005). Plots show fitted linear model with 95% confidence intervals.

As home range estimates weren't available for any solitaires, were only available for a limited number of groups, and are rarely known for many (if any) visitors to other resource hotspots, the relationship between visit rate and network metrics was investigated. As visit rate correlated strongly with home range distance from the bai, and is hypothesized to be a

major cause of visit rate variation due to common distance discounting rules, I investigated whether social units with higher visit rate, were also more connected in the social networks. Visit rate strongly predicted both weighted degree and eigenvector centrality from the raw co-visit network (respectively $p < 2.2e-16$ and $p = 6.4e-16$). This relationship was also observed for weighted degree and eigenvector centrality metrics from the SR network, although with considerably greater residual variance ($p = 3.2e-07$ and $p = 6.3e-06$) as shown in Figure 5.7.

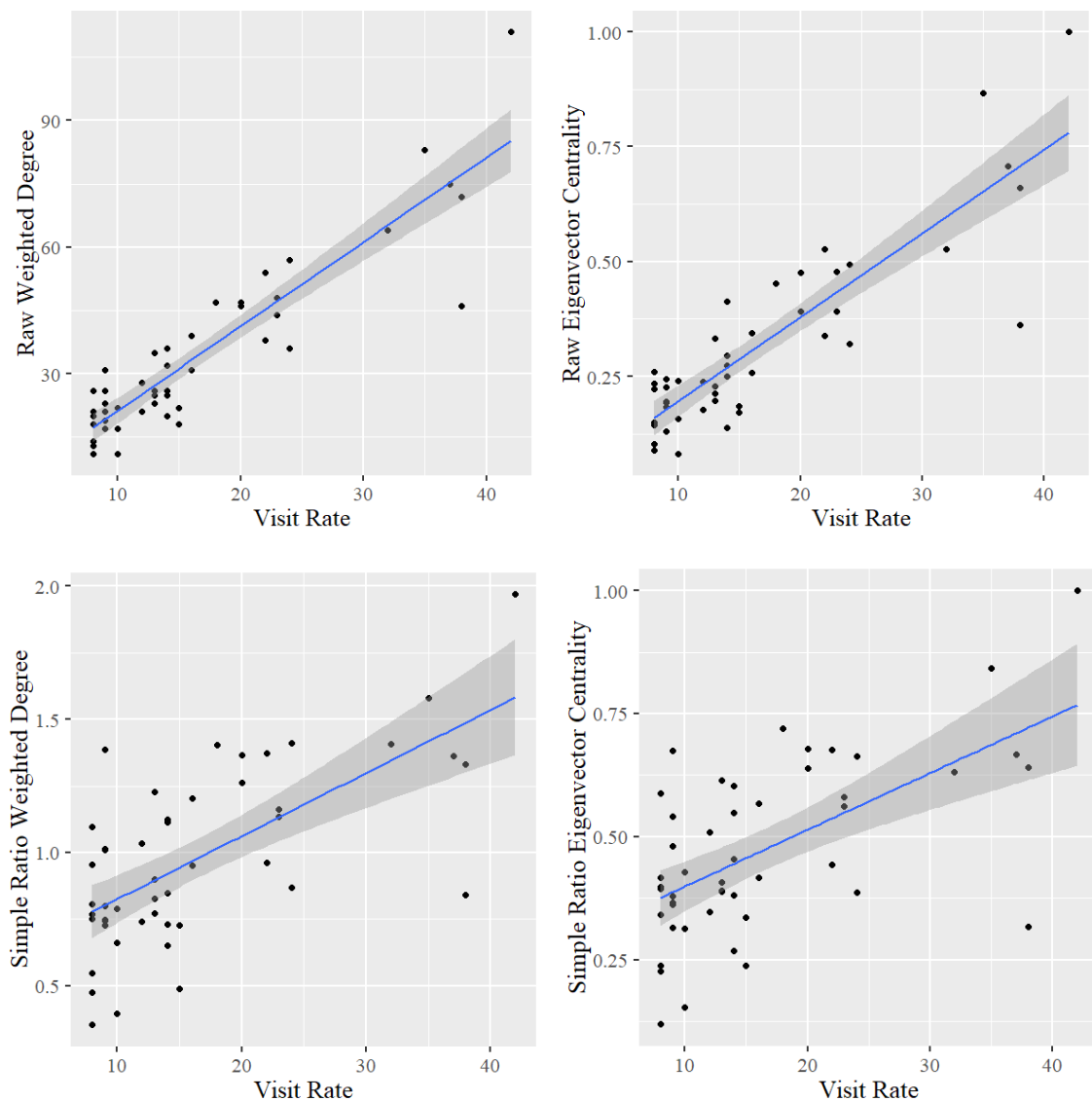


Figure 5.7. Visit rate correlated with weighted degree ($t=14.8$, $df=46$, $p < 2.2e-16$) and eigenvector centrality ($t=12.1$, $df=46$, $p=6.4e-16$) when using raw covisit values. When using the SR association index, visit rate still correlated with weighted degree ($t=5.8$, $df=46$, $p=3.2e-07$) and eigenvector centrality ($t=5.1$, $df=46$, $p=6.3e-06$) using Pearson's product moment correlation. Plots show fitted linear model with 95% confidence intervals.

5.4.6 Social predictors of network centrality

There was no correlation between group size and visit rate ($t = 1.0469$, $df = 22$, $p\text{-value} = 0.3065$) suggesting that larger, potentially more dominant groups were not more likely to have home ranges closer to the bai or to visit more often. There was also no correlation between group size and network metrics in either the raw visit network or SR network (Figure 5.8), demonstrating that groups of larger size and potential higher dominance were unlikely to be responsible for a higher proportion of transmission events.

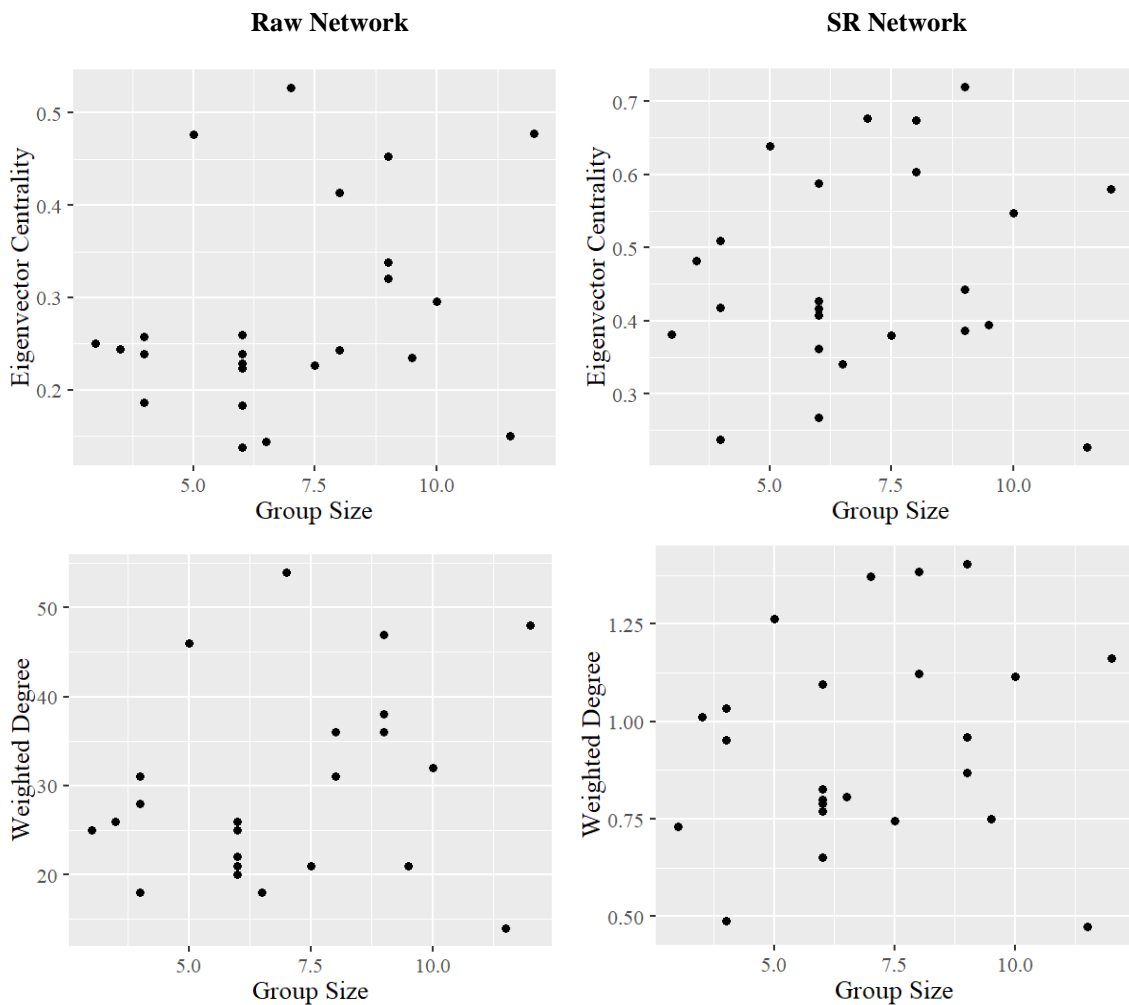


Figure 5.8. Group size plotted against network metric for both raw co-visit and SR networks. No relationship was observed between any network metric and group size.

5.4.7 Sub-sample networks

To investigate whether the underlying distributions could be better distinguished over a shorter time period, the dataset was split into ten 40-day windows. This timescale also relates more closely to the timescale over which a highly-contagious disease might spread through a gorilla population. The distribution of visit rate values from all units over each of the ten time windows was combined and plotted (Figure 5.9). As each value from the same unit from different time periods did not represent independent data points, no comparison between unit type was attempted. Despite the increased sample size and shorter time period, model fit using maximum likelihood bootstrapping demonstrated that neither a power law distribution (KS goodness of fit = 0.051, $p=0.094$), an exponential distribution (KS goodness of fit = 0.024, $p=0.615$), or a poisson distribution (KS goodness of fit = 0.049, $p=0.595$), for the number of visits over a 40-day period could be ruled out. A power law distribution was not a significantly better fit than either an exponential distribution (Vuong's Test: $R=-1.15$, $p=0.252$) or a poisson distribution (Vuong's Test: $R=0.908$, $p=0.364$).

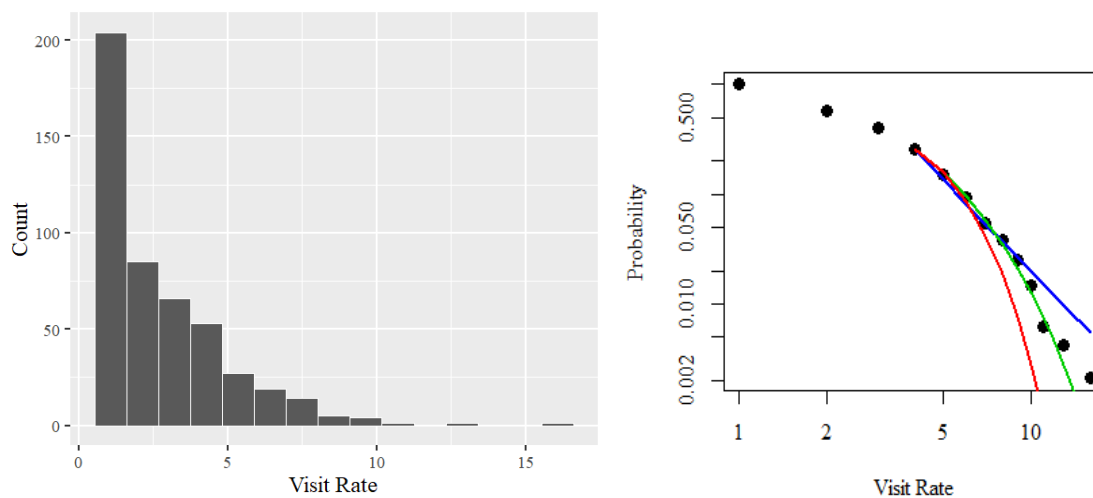


Figure 5.9. A) The distribution of visit rates by gorilla units during ten 40-day sampling windows. B) The probability of a unit having a given visit rate with fitted power law (blue), exponential (green) and poisson (red) curves.

Model fitting of the distribution of weighted degree values from 40-day networks (Figure 5.10) also demonstrated that a power law distribution (KS goodness of fit = 0.075, $p=0.607$), an exponential distribution (KS goodness of fit = 0.032, $p=0.617$) and a poisson distribution (KS goodness of fit = 0.058, $p=0.827$) could not be ruled out. A power law distribution was not a significantly better fit than an exponential distribution (Vuong's Test: $R=-0.809$,

$p=0.418$) or a poisson distribution (Vuong's Test: $R=0.191$ -, $p=0.848$). Eigenvector centrality was not investigated due to the sparsity of connections in the 40-day networks.

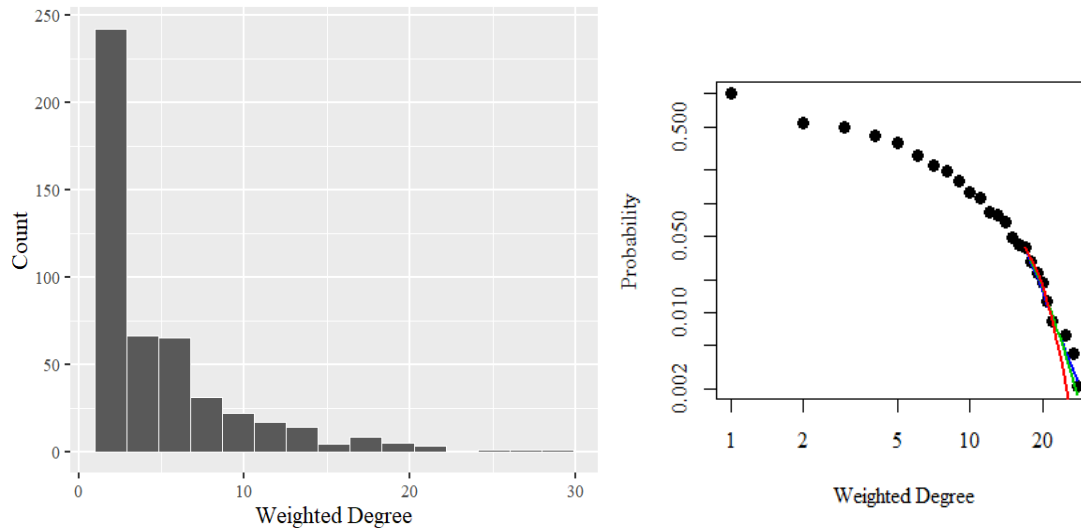


Figure 5.10. A) The distribution of weighted degree values from networks generated from 40-day sampling windows. B) The probability of a given weighted degree with fitted power law (blue), exponential (green) and poisson (red) curves.

5.4.8 Predicting yaws transmission

During the outbreak of yaws (*Treponema pallidum*), a chronic bacterial infection, that took place at Lokoué Bai, larger groups were more likely to contain an infected individual (binomial logistic regression: 0.451, $p = 0.0259$), but an individual's likelihood of infection did not increase with group size (binomial logistic regression (BLR): 0.0376, $p = 0.488$) (Figure 5.11). The visit rate of a group to the bai did not predict their infectious status (BLR: 0.001, $p = 0.981$) or the proportion of infected individuals in a group (logistic regression (LR): 0.007, $p = 0.205$). Neither weighted degree from raw (infection status: BLR: $1.79e^{-4}$, $p = 0.995$. proportion infected: LR: 0.00369, $p = 0.154$) or SR network values (infection status: BLR: -0.708, $p = 0.662$. proportion infected: LR: 0.109, $p = 0.45$) predicted group infection status or proportion infected. This was also the case for eigenvector centrality values from raw (infection status: BLR: 0.217, $p = 0.944$. proportion infected: LR: 0.198, $p = 0.472$) and SR networks (infection status: BLR: -1,248, $p = 0.686$. proportion: LR: 0.198, $p = 0.472$).

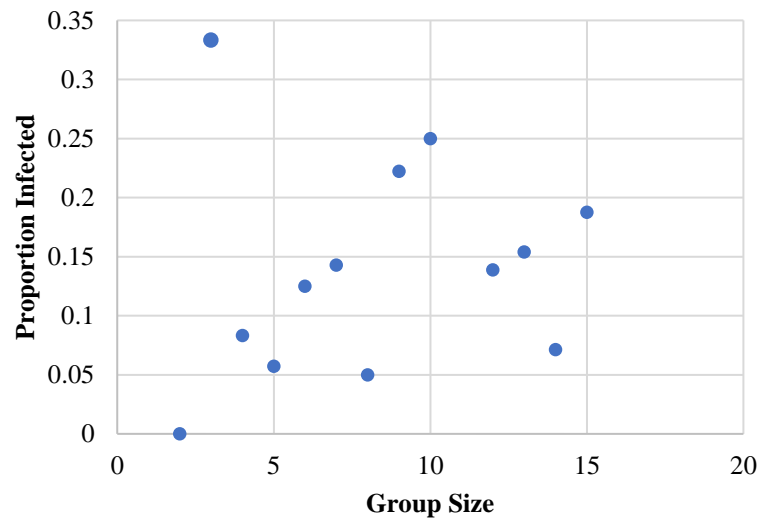


Figure 5.11. Proportion of infected individuals for a given group size.

5.5 Discussion

5.5.1 Super-spreading structure

A super-spreading structure was broadly supported in the analysis of the distribution of visit rates and both centrality metrics based on raw co-visit values, as a power law distribution could not be ruled out. However, the analyses could not distinguish between alternative heavy-tailed distributions, with similar support seen for the presence of an exponential distribution. Given the necessarily small number of super-spreaders in a given population, ruling out alternative heavy-tailed distributions in the structure of contacts between gorilla groups and solitaries is very difficult, as even with the fairly large sample of individuals at Lokoué Bai, that still only represented 27 groups and 21 solitaries making a total of 48 independent units. Super-spreaders, by definition make up a very small component of the overall population so with sample sizes of <100 it is difficult to distinguish between alternative heavy-tailed distributions.

Despite this, the distributions of visit rate and both raw network values (weighted degree and eigenvector centrality) showed considerable heterogeneity appearing to follow either an exponential or power law distribution, whilst a poisson distribution was broadly rejected. Although the best fitting distributions could rarely be distinguished, even after combining multiple smaller sub-samples, the data followed a heavy-tailed distribution. This indicates that there were a small number of individuals at Lokoué Bai with high centrality, that appeared to come into contact with a considerably larger proportion of the population. They represent potentially important target individuals for disease intervention strategies.

Both local centrality measures: weighted degree (the sum of the weight of connections a solitary or group has in the network, also known as strength) and eigenvector centrality (how connected a solitary or group is to other highly connected individuals) are thought to be greatly important to an individual's potential to transmit disease. Both metrics showed very similar heavy-tailed distributions. Individuals with a high degree are more likely to contact a large number of individuals to whom they can potentially transmit, however this metric is somewhat limited by not taking into account secondary connections and only providing information on the immediate neighbourhood of an individual (Silk et al., 2017). Eigenvector centrality does take those secondary connections into account to provide a less local metric,

potentially providing a better measure of how important an individual would be for the onward spread of infection. Both weighted degree and eigenvector centrality both still represent fairly local estimators which may not represent the best measures of transmission capacity in strongly sub-structured populations. However, despite the detection of significant modularity in forest clearing gorilla populations relative to randomised datasets (Chapter 3), this modularity still represents fairly weak sub-structuring at the above-group level compared to the extreme level of modularity observed for example within gorilla groups where the vast majority of social interactions take place. The fairly low modularity values of 0.140 and 0.170 for raw co-visit and SR inter-group networks respectively, are well below the suggested 0.3 cut-off of a highly sub-structured population (Whitehead, 2008). Furthermore, local centrality measures showed strong correlations with each other and the more global betweenness centrality metric. This demonstrates that these networks have limited sub-structuring, suggesting that the local centrality metrics should provide a better estimate of the transmission potential of a solitary or group as a whole, rather than a global metric (Appendix 5.1).

The network from the SR association index, which calculated the proportion of visits during which gorilla groups or solitaries visited at the same time, did not follow the same heavy-tailed distributions as those generated from the actual number of co-visits. This association based network was generated to estimate active associations between groups and solitaries after accounting for visit rates and therefore to be predictive of the social associations between units. In contrast, the network based on raw values was more likely to be predictive of actual disease transmission taking place within the bai, as it was based on the observed contact pattern (where contacts represented visits to the clearing on the same day). The lack of a heavy-tailed distribution of centrality metrics from the SR network suggests that super-spreading structure is not caused by social dynamics and therefore is unlikely to be present across gorilla ranges. Instead, it is likely to be a result of spatial dynamics and therefore associated with key hotspots such as forest clearings.

5.5.2 Centrality differences by unit type

Solitary silverback males were consistently over-represented in the highest visit rate and centrality metric values. Whilst value distributions weren't significantly different between reproductive groups (RGs) and solitaries, solitaries had higher coefficients of variation for

both centrality metrics, and represented the top two highest values across all three variables. This suggests that solitary males in particular have the potential to act as super-spreaders enabling rapid transmission between groups. One possible reason for the lower variation in centrality values for RGs compared to solitary males could be the averaging effect of having multiple individuals. Whilst silverback males are thought to be the major decision making force in gorilla movement patterns, due to the predominance of females transferring multiple times within their lifetimes, silverbacks may well be under pressure to factor in the decisions of other group members (Stokes, Parnell and Olejniczak, 2003). It is also likely that the presence of young offspring may limit the distance travelled by groups relative to solitary males, leading to lower variation.

The high super-spreader-like values of centrality observed for a number of solitary male individuals, do not however directly demonstrate their super-spreader status for all diseases. Presence in the clearing on the same day may be an important factor enabling the transmission of certain diseases (e.g. diseases transmitted through urine, faeces, or saliva) but is unlikely to be an accurate estimate of the physical contact or close proximity required for the transmission of many other diseases. Interactions between group-living individuals and solitary males that enable transmission may be considerably reduced relative to inter-group interactions as group-solitary encounters are thought to represent potential instances of mating competition where solitary males can attempt to entice females away. Supporting this, Levrero (2005) found solitary-group interactions occurred during a smaller proportion of co-visits, were of shorter duration, occurred at greater distances apart (median = 50m) and were considerably more agonistic than interactions between groups. Therefore whilst solitary males may represent some of the most connected individuals from a co-visit perspective, whether or not this holds true from a disease transmission perspective may be highly dependent on the mode of transmission of the disease. Reduced interaction at close proximity may well prevent these solitary males being important for the transmission of diseases where close proximity or physical contact are required. Although, agonistic contact between males was more likely during group-solitary encounters when they did occur (Levrero, 2005), relative to inter-group encounters, potentially providing an important transmission route.

Non-reproductive groups (NRGs) reliably had the highest visit rate and centrality metric means across networks, suggesting that these groups may be most strongly connected. However, as only 3 NRGs were present in the bai population, it was not possible to determine

whether this more central network position is a trait of NRGs generally or just a considerable proportion of the small number of NRGs present at Lokoué Bai.

5.5.3 Do spatial dynamics lead to super-spreading?

Visit rate declined significantly with the estimated distance of a group's home range from the forest clearing, supporting the hypothesis that gorillas follow distance-discounting rules in their foraging patterns (Chapter 6), and that this influences the pattern of their visits to forest clearings (Parnell, 2002b). Spatial dynamics are therefore likely to be responsible in part for the heavy-tailed distribution of visits, due to a small number of close-living gorillas visiting very often and the majority visiting fairly infrequently due to the greater distances they would need to travel to reach the resource (Figure 5.1). Whilst the distance-discounting rule applied appeared to follow a linear relationship, the small number of groups for which home range estimates were available meant that the precise relationship could not be investigated. More detailed range estimates for a larger number of groups will be necessary in order to better understand the cognitive rules used and the underlying relationship between distance and visit probability.

Both centrality metrics from the co-visit network and the SR network were predicted by estimated home range distance, demonstrating that the close-living regular visitors were likely to be responsible for a higher proportion of transmission. This relationship in the co-visit network metrics suggests that close-living groups have the potential to act as super-spreaders through transmission taking place at the bai. The strong correlations between distance and visit rate, and visit rate and centrality metrics support the hypothesized mechanism that gorillas with closer ranges visit more often, causing them to be more connected in the network, with the potential to act as disease super-spreaders by connecting infrequent visitors with more distant home ranges. Therefore biased targetting of more frequent bai visitors may enable more efficient disease intervention when interactions are comparatively rarer outside the bai.

No correlation between home range distance and centrality was observed in the SR network demonstrating that whilst groups living in close proximity to the bai may act as super-spreaders at the bai itself, they are unlikely to act as super-spreaders across their ranges (if social association patterns within the bai are representative of patterns across their ranges). However, visit rate did correlate with centrality metrics in the SR association network (although less significantly than the raw network), suggesting that the lack of significance

from home range distance may be due to the reduced sample size ($n=9$ for home range distance compared to $n=48$ for visit rate). The correlation between visit rate and centrality in the association network is unexpected as the overall number of visits is controlled for. However it is possible that positive reinforcement of social bonds, through increased chance encounters with groups that visit more often, could lead to those regular bai visitors having stronger and more numerous associations (Rivera, Soderstrom and Uzzi, 2010), and therefore being more central in the network.

These results suggest that both close-living solitary males and groups may represent key vaccination targets. But are all members of a group equally important to vaccinate? To understand which group members are likely to be most important for transmission to individuals outside their group, finer scale data on inter-group interactions is required, at least for diseases that transmit most easily through close-contact situations. Diseases that can transmit through common space use alone are unlikely to show high transmission variability from different individuals in the group. Another factor to take into account is whether the dispersal of individuals between groups, may represent a stronger transmission risk than inter-group contacts. If sustained close-contact interactions are necessary, inter-group contact may not be close enough or common enough to cause a significant transmission risk in comparison to infected individuals that transfer from an infected group to an uninfected group, exposing a new set of individuals to the disease threat. Those reaching sexual maturity within their natal groups, particularly females, may represent clearly identifiable individuals worth targetting for the prevention of disease transmission where sustained close-contact is necessary for transmission.

5.5.4 Do social dynamics lead to super-spreading?

The results did not provide any support for the hypothesis that larger, potentially more dominant groups would be more connected in the social network. The size of a group did not correlate with their centrality (weighted degree or eigenvector centrality) for either the co-visit network or the SR network. So, whilst a single infected individual would be able to transmit a disease to a larger number of individuals easily if they were in a larger group, that group would not be significantly more likely to come into contact with a greater number of other groups or solitaries. Therefore group size is likely to be important for transmission below the group level but not at the above-group level. Indeed, at the above-group level it

could even be suggested that targetting smaller groups and solitaires may be the most economic and efficient strategy, as a smaller number of individuals would need to be vaccinated for a similar level of benefit, at least to the reduction of transmission between groups.

5.5.5 Yaws transmission at Lokoué Bai

Yaws, a chronic bacterial infection causing skin and bone lesions is known to transmit through skin contact with lesions and via flies that come into contact with wounds (Levréro et al., 2007). However, the yaws infection status of individual gorillas was not clearly predicted by their group size, as would be expected if this disease was easily transmitted between individuals by social contact (Freeland, 1976, 1979; Loehle, 1995). A similar conclusion was reached by Levréro et al. (2007) who identified that the prevalence of lesions within a group from this disease was not predicted by that group's size, suggesting that yaws may not be effectively transmitted by social contact. Exposure by social contact is therefore likely to only be responsible for a small part of whether or not an individual becomes infected, with either transmission by other vectors, or the inherent susceptibility of an individual, responsible for a far larger component.

This limited transmission of yaws at Lokoué by social exposure is further supported by the inability of network centrality metrics to effectively predict yaws infection status. An alternative explanation could be that the networks estimated here do not effectively estimate contact rates and therefore transmission. However, the lack of a clear increase in yaws prevalence with group size suggests that even if the networks perfectly estimated contact rates either at the bai or across the gorilla's ranges, yaws would still be unlikely to follow a transmission pathway consistent with this network, as social exposure does not predict transmission of this disease well. Therefore a better understanding of the transmission mechanisms, and individual susceptibility and immunity of this disease in gorillas is necessary.

5.6 Conclusion

These results suggest that forest clearings may act as important transmission hubs, as not only do they represent hotspots of social interaction, but the structure of contacts taking place at these social hotspots is likely to follow a heavy-tailed, potentially super-spreader-like distribution. Social affiliations and group size effects did not appear to be driving the pattern of contact. Instead, spatial dynamics appeared to be the main driver behind this effect as centrality in the social networks at Lokoué Bai was predicted by home range distance and visit rate. This suggests that gorillas with ranges nearby to forest clearings may represent key targets for any intervention strategy, as they are likely to visit the clearings more often, coming into contact with a larger number of other groups and solitary males, and therefore be more central to the network. Whilst this has only been detected at a single forest clearing, the distance-discounting hypothesis suggests that a similar pattern may well be present across other forest clearings or feeding hotspots, with potential relevance to other species that rely on these resources, such as forest elephants.

Despite yaws infection not following a transmission route predicted by the network structure identified, networks constructed from forest clearing data may still be highly informative to the transmission of diseases for which exposure via social contact is of greater importance to transmission dynamics. Furthermore, disease is not the only factor that can be transmitted by social contact, and forest clearings may also be important hubs for the transmission of novel ideas, behaviours and culture such as the tool-use observed at Mbeli bai (Breuer, Ndoundou-Hockemba and Fishlock, 2005). Future research integrating individual and inter-group encounter rates at varying contact levels (in addition to space-use overlap within a day), through a network approach would be highly informative for modelling the spread of diseases, dependent on their modes of transmission.

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5.8 Appendices

Appendix 5.1: Betweenness centrality distributions

Figure A5.1.1. The distribution of betweenness centrality values for the raw co-visit network. Model fit using maximum likelihood bootstrapping demonstrated that a power law distribution could not be ruled out (KS goodness of fit = 0.151, $p=0.155$), however that was also the case for an exponential distribution (KS goodness of fit = 0.096, $p=0.107$).

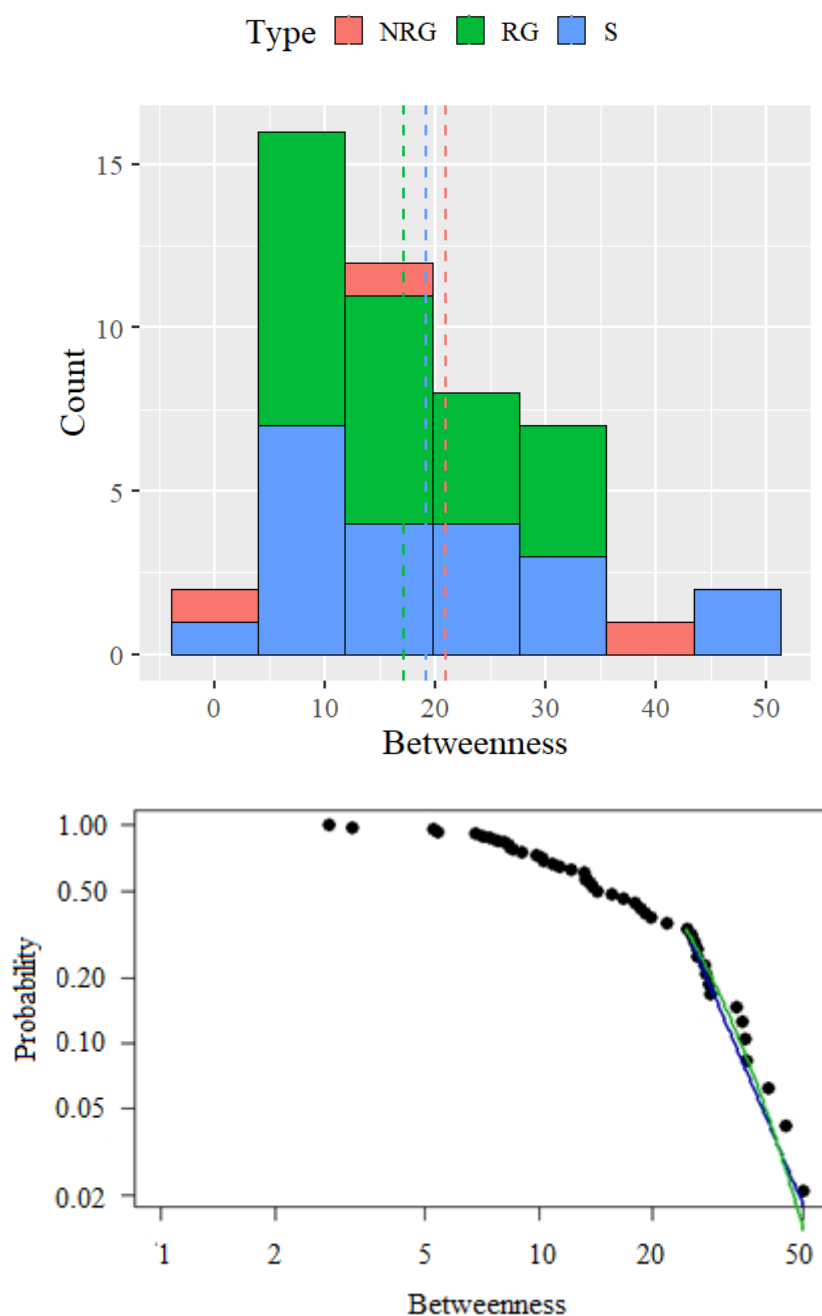
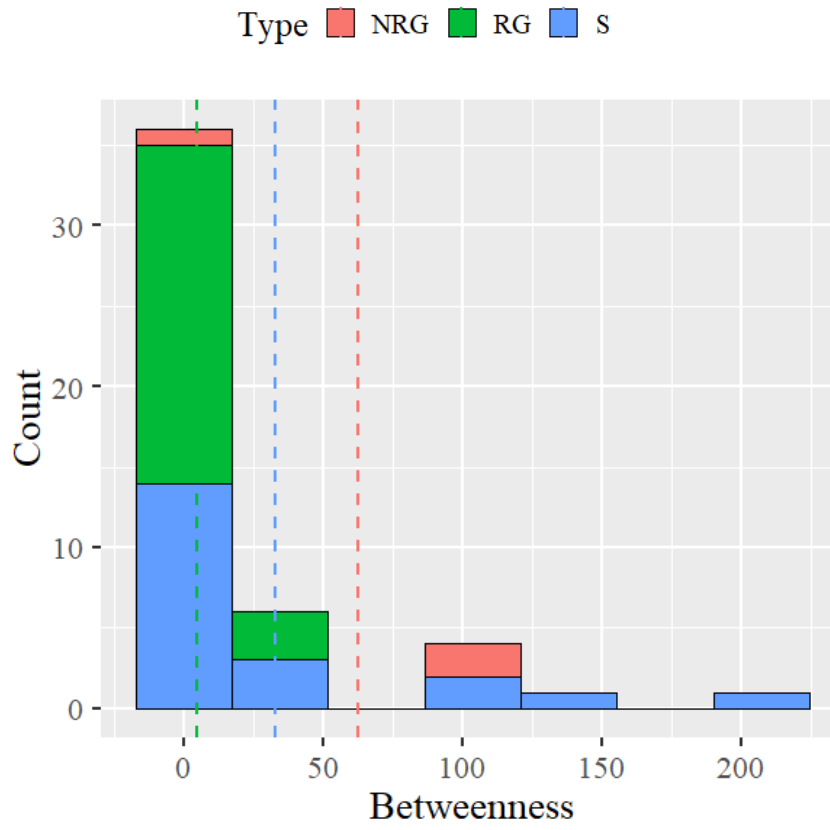


Figure A5.1.2. The distribution of betweenness centrality values for the SR association network. Model fit could not be attempted due to the large number of zero values.



Chapter 6: The Inter-Group Ranging Dynamics of Western Lowland Gorillas

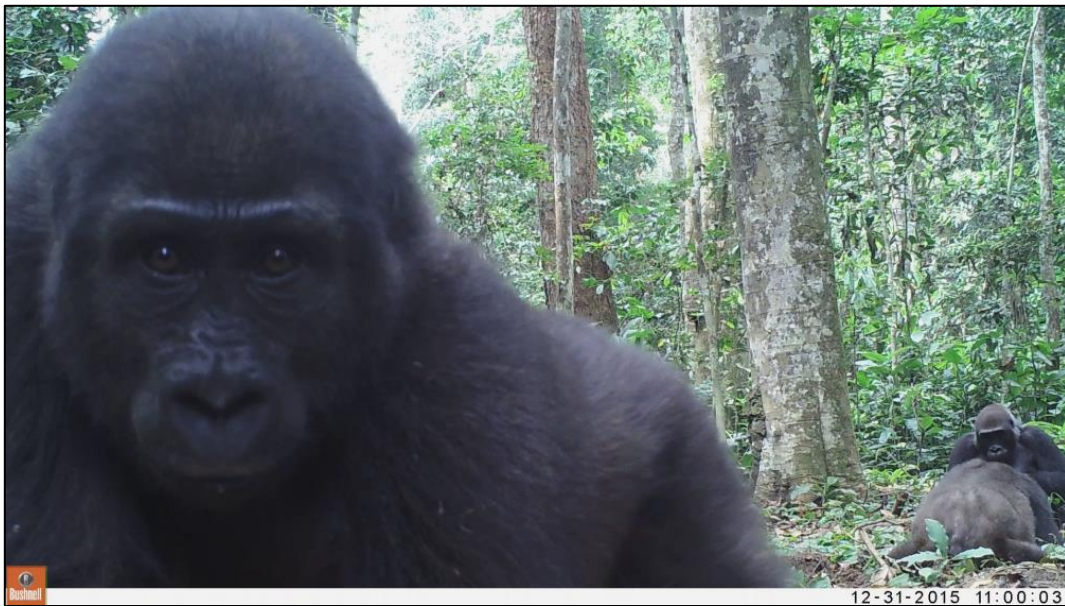


Photo: Ngaga Research Station, SPAC Foundation Congo

6.1 Abstract

Territoriality has historically been viewed in a binary manner, particularly within the great apes, with chimpanzees (*Pan*) and humans (*Homo*) deemed territorial and other great apes not. Gorilla groups have large overlapping ranges in which they regularly come into contact with one another, with multiple groups feeding on the same resources. Due to the relative lack of aggression observed in many inter-group encounters, and their extensive home range overlap, gorillas are widely assumed to be non-territorial. The difficulties of habituating and simultaneously monitoring multiple western gorillas in their dense rainforest habitat has limited previous studies on this species to small numbers of habituated groups or monitoring of a single location. This has prevented a broader understanding of the inter-group dynamics

of western lowland gorillas across their ranges and specifically any investigation of territorial behaviour. A novel approach using a large-scale camera trap study was used to overcome these problems, enabling 24 western lowland gorilla groups to be monitored across a 60 km² region. I used presence-absence data of groups and solitary males at naturally occurring root feeding sites to build models of the movement patterns of groups in this gorilla population. The results demonstrated the short term avoidance of other groups, which did not appear to vary significantly between neighbour and non-neighbour groups, but varied considerably with distance from a group's home range. Visit rates reduced with proximity to another group's home range centre suggesting some understanding of the "ownership" of specific geographic regions. This avoidance of other group's home range centres was greater when the other group was larger and more dominant than themselves. The probability of a group visiting a root site on the same day as a neighbouring group decreased with proximity to the neighbouring group's home range centre. This is consistent with a stronger defensive response from groups when closer to the centre of their ranges. The biases in movement patterns demonstrated here provide the first quantitative support for territoriality in gorillas. Gorillas appear to recognize regions of priority or even exclusive use by resident groups. This model of inter-group dynamics has considerable similarities to common patterns across human history, with core areas of resident activity dominance and large overlap zones of mutual tolerance. Thus, gorillas may provide a valuable model system for understanding the pattern of interactions occurring in early human populations. Furthermore, the non-binary, graded territoriality that these findings suggest, demonstrates the importance of investigating territoriality as a complex continuum, rather than a binary category. In gorillas, considerable location-based variation in inter-group dynamics is possible despite the presence of other behaviours that would rule out territoriality under many definitions.

6.2 Introduction

Investigating inter-group dynamics first requires an understanding of the movement patterns of individual groups. Here I will discuss approaches to modelling the home ranges of gorilla groups and their movement patterns within them, before addressing how the presence of conspecifics may alter these movement patterns. I will then further discuss how competition for resources can influence patterns of aggression and the circumstances under which territoriality may occur.

6.2.1 Home ranges

A home range is defined as the area used by an individual in its normal, day-to-day activities including food gathering, mating and caring for young (Burt, 1943). This common pattern of space use leads to individuals regularly experiencing the same regions and stimuli, enabling them to build a cognitive map of the resources in their habitat and how to best move between them (Boitani and Fuller, 2000). However, not all species demonstrate high home range fidelity, and it is thought that home ranges are observed only when the benefits of maintaining a home exceed the costs (such as resource depletion or predictable location for predation) (Boitani and Fuller, 2000). The definition of a home range excludes occasional exploratory movement; however the flexibility of this definition has led to considerable variation in home range calculation methods. Home ranges also vary over time, with the possibility of new regions being incorporated and the use of previously important areas decreasing. They are the result of a dynamic process, made up of numerous small-scale movement decisions.

To describe an animal's home range, data on the location of observations is used to build a predictive model of the relative frequency with which an animal uses different areas. The oldest and most simplistic method of home range estimation is the Minimum Convex Polygon (MCP), in which a home range is estimated by producing a convex polygon that contains all (or a chosen percentage of) the locations at which an animal has been observed (Börger, Dalziel and Fryxell, 2008). This method makes no assumptions about the animal's movement patterns but predicts only the outer limits of the home range without providing any

information on the relative use of different regions within the home range. It also requires a considerable sample size in order to produce a realistic home range. Kernel Density Estimates are widely recommended as an improvement on MCP, and produce a probability density function across the range estimate using all locations at which the animal has been observed. This method is however, highly reliant on the choice of smoothing parameter (also called bandwidth) which controls the extent to which the presence of an animal at a certain location will affect the probability density at increasing distances from that location, with estimates of home range size increasing with smoothing parameter size (Millspaugh et al., 2012).

An alternative method of modelling ranging behaviour is through the use of movement modelling, simulating individual movement decisions (e.g. through random walks, correlated random walks or biased random walks) to build animal space use distributions (Börger, Dalziel and Fryxell, 2008). One of the simplest movement models to generate realistic home range behaviour is the focal-point attraction model, developed by Holgate and Okubo, in which movements have a biased directionality towards a single home range centre (Moorcroft and Lewis, 2006). However, this model always generates circular home ranges that may not be realistic for all species. Further models have been developed to generate more variable elliptical home ranges or home ranges with multiple centres.

Western Lowland Gorilla (WLG) groups have ranges of between 11 and 18 square kilometres (Bermejo, 2004; Cipoletta, 2003; Doran-Sheehy et al., 2004; Cipoletta, 2004). However Cipoletta (2004) found that only 20% of this was used on a monthly basis, with mean monthly ranges of 3 km². Within these large ranges, far smaller core areas can be identified, in which groups spend 75% of their time. These core areas have been calculated as 20%, 31% and 32% of a group's overall range (Bermejo, 2004; Cipoletta, 2004; Doran-Sheehy et al., 2004) and are usually located in the centre of the home range. This suggests that simpler home range models with a single centre and rapid decline in habitat use with distance from that centre may fit WLG ranging behaviour well.

6.2.2 Foraging and competition

The extensive range overlap of neighbouring gorilla groups presents an interesting problem as to how the resources within these shared ranges are used. Optimal foraging theory states

that animals which maximise net energy intake per unit time spent foraging will be favoured by natural selection (MacArthur and Pianka, 1966; Perry and Pianka, 1997). Therefore the likelihood of an animal foraging in a given area will depend on the quality and abundance of the resources present there and its distance from their current location. However, the sporadic or irregular phenology of many gorilla food resources (Yamagiwa, Basabose and Kaleme, 2008), combined with the differing feeding patterns of multiple neighbouring groups, makes the task of predicting food location and abundance highly complex. Fruit makes up a substantial proportion of the WLG diet, representing 71% of food species consumed at the Mondika research site and 51% of feeding observations at Bai Hokou (Rogers et al., 2004). Indeed western gorillas have been described as “fruit pursuers” due to their preference for often very specific and quite rare fruits for which they may travel considerable distances (Williamson, 1988; Doran et al., 2002). When these foraging costs are taken into account it suggests a considerable selection pressure in gorillas for developing the cognitive skills necessary to predict when these resources may be available, using the periodicity of fruiting cycles as well as, potentially, the monitoring or estimation of the movement patterns of neighbouring groups.

Groups may adjust their foraging strategies in response to each other by avoiding resource sites where another group has recently visited or is currently present, thereby reducing feeding competition, especially in cases where the other group is more dominant and likely to prevent them accessing the resource. However, short term avoidance such as this could also be due to the avoidance of mating competition. Responses to the presence of other groups are also known to vary between neighbours (those with adjacent territories or overlapping ranges) and “strangers” (or non-neighbours) in many species, with either stronger defensive responses to neighbours (the “nasty neighbour” effect) or stronger defensive responses to strangers (the “dear enemy” effect) (Christensen and Radford, 2018).

Alternatively, rather than a signal of resource depletion or a potential threat, the presence of another group feeding in a certain location could be used to indicate the presence of a resource (such as ripe fruit) in an unpredictable environment, through social foraging. Gorillas could use the auditory signals (such as feeding calls) of other groups as a form of social information or local enhancement, reducing uncertainty about resource location and potentially quality (Poysa, 1992; Valone and Templeton, 2002). In these cases active association rather than avoidance may be beneficial, as visiting a somewhat depleted but

reliably present food source may be more beneficial than having to search for irregular food sources with little information to predict whether they will be currently edible (Danchin et al., 2004). If this social foraging is present in gorillas a further question arises: does the information shared represent inadvertent cues from noisy neighbours, or the purposeful communication of information between cooperating groups? The detection of stable social units in gorilla society made up of multiple (often related) groups (Chapter 3) and further genetic evidence of strong bonds between groups (Forcina et al., 2019), suggest that such a collaborative foraging strategy could provide considerable reciprocal benefits to neighbouring groups. Indeed it is possible that by enabling an increase in foraging efficiency when feeding on highly dispersed and often unpredictable resources, collaborative foraging could have been a key driver in the evolution of multi-level social structure in gorillas.

6.2.3 Territoriality and scramble competition

Territories are defined as regions of an animal's home range that are actively defended against intruders to enable exclusive use by the individual or social unit (Bartlett and Light, 2017). However, there is considerable debate over this definition with alternative broader definitions including areas of priority use (Boitani and Fuller, 2000; Maher and Lott, 1995). It has been increasingly suggested that defining territoriality as a binary trait cannot explain the full diversity of territorial behaviours observed (Boitani and Fuller, 2000; Seiler et al., 2018; Asensio, José-Domínguez and Dunn, 2018). Territoriality may be better described by a continuum from extreme territoriality such as that observed in chimpanzee groups, where lethal intergroup aggression may be used to defend boundaries (Mitani, Watts and Amsler, 2010), to species such as the black bear where territoriality can vary, geographically or temporally (Boitani and Fuller, 2000), through to species which do not appear to show any range defence at all.

Gorillas are widely assumed to be non-territorial due to the large size of their home ranges, the extensive range overlap observed between neighbouring groups, and the relative lack of aggression observed during some inter-group encounters (Bermejo, 2004). However, mountain gorilla groups have been demonstrated to reduce their home ranges in response to increased population density, an avoidance behaviour typically observed in territorial species (Seiler et al., 2018). The presence of range overlap in gorilla species may rule out

territoriality under its narrowest definition, but does not under broader definitions where regions of exclusive use or shared areas with a clear hierarchy of priority can represent territoriality. Bermejo (2004) found that the core area of one WLG group was never entered by the surrounding groups. However, long term data from mountain gorillas indicates that overlap of core areas does occur in these populations but that this overlap is reduced in comparison to other areas of the home range (Watts, 1998). This suggests the possible avoidance of some key areas of other gorilla group's ranges, particularly in WLGs, and the potential for some territorial behaviours. The presence of inter-group tolerance in WLGs as discussed in previous chapters should not rule out the presence of territoriality entirely, as levels of aggression could vary by location, with tolerant behaviours observed only in certain regions within a group's home range. Furthermore, territory ownership could be advertised by long-distance calls such as the chest beating sounds produced by silverback males, heard over multiple kilometres (Mirville et al., 2018). Such calls have been shown to correlate with territoriality and mate attraction in many primate species rather than mate defence as had previously been hypothesized (Wich and Nunn, 2002).

Alternatively, avoidance of key regions of other groups' ranges could be explained by optimal foraging, where the best strategy could be to avoid regions that are popular with other groups in order to maximise the likelihood of finding available resources. When regions are too large to be effectively defended, preventing territoriality, competition for resources occurs through scramble competition. Under scramble competition other groups or individuals may use up resources before another individual or group comes across them, and those that find the resources first are able to benefit the most from them (Janson and van Schaik, 1988; Teichroeb and Sicotte, 2018). Under this form of competition, core regions of other groups' ranges may be visited more rarely, as the low likelihood of finding key resources before they are consumed by the resident group makes the travel costs of reaching those locations prohibitive. Reducing the costs of scramble competition and improving foraging efficiency could therefore be driving the delineation of gorilla group home ranges.

6.3 Methods

6.3.1 Camera trapping

Camera traps were deployed across the 60 km² study area at locations where evidence of root feeding behaviour by gorillas was observed (Figure 6.1), primarily surrounding *Maranthes glabra* trees. Traps were visited every two weeks to collect the footage and install new batteries. Bushnell Trophy Cam and Reconyx camera traps were used, with one camera at each location, set to record 30 seconds of video footage with each activation. Footage was recorded over 5403 camera trap days, calculated as the sum of the total number of days that cameras were deployed and functioning at each location (Appendix 6.1), from date of installation (or check) to last functional day (last day footage was successfully recorded).

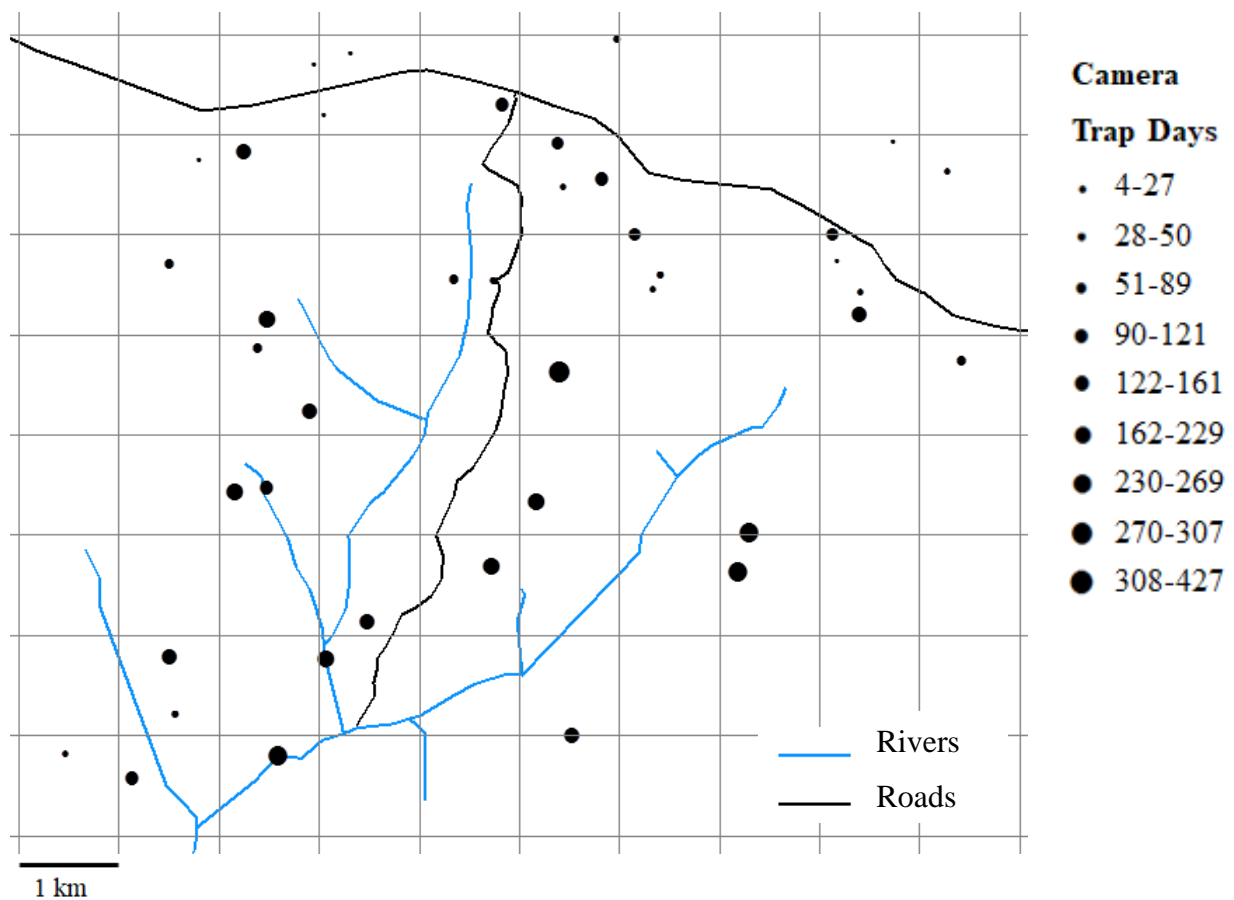


Figure 6.1. The distribution of camera traps across Ngaga Research Site, with number of camera trap days at each location indicated by the size of black dot and a 1 km² grid overlaid. Black lines indicate roads and blue lines indicate rivers.

6.3.2 Gorilla identification and range estimation

Gorillas were detected and identified at 35 locations, with the group or individual identified in 76.9% of visits (Table 6.1). All identifications were carried out by Magdalena Bermejo using qualitative features of individuals recorded in the camera trap footage. Multiple camera trap activations were classed as a single visit when <1 hr had passed between consecutive activations by the same group or solitary male. Home range centroid and minimum convex polygon range estimation was attempted for groups that visited 10 or more times in 3 or more locations (Table 6.2). The sizes of focal groups were estimated as the total number of unique individuals identified within the group over the study period.

Table 6.1. The total number of distinct groups and solitary males identified in the camera trap footage, and the number of discrete gorilla visits by each category type.

	Number of	Visits by
Known groups	24	386
Known Solitaries	6	51
Unknown groups	-	90
Unknown solitaries	-	41
Total		568

Table 6.2. The total number of discrete visits by each focal group, and the number of locations those visits took place at.

	Group	Visits	Locations
1	GR	104	7
2	JP*	65	7
3	NN*	32	6
4	US	22	6
5	ND	20	3
6	VL	16	3
7	BC	12	3
8	PL*	11	5

*groups undergoing habituation

6.3.3 Gorilla movement models

Whilst the home range estimation models discussed in the introduction can provide excellent estimates of space use, they require large datasets of fine scale movement data from telemetry or trail-follows of individuals or groups. Given our limited sample of visits at specific root feeding sites (Table 6.2) generated through camera trapping, these methods would be unlikely to give realistic visit rate probability distributions. Therefore I used elements of the home range models and optimal foraging theory to predict a group's presence at a site, given the site's distance from the group's home range centre (centroid). Group centroids were estimated from visit data using an MCMC algorithm that searched for the most likely location of the centre of a group's range under the assumption that the frequency with which a site was visited would decline as a function of distance from the centroid. Research on gorilla ranging patterns suggests that the majority of their time is spent in a single core range roughly 20-30% of the size of the total range used. Therefore, models using convex curves, where visit rate declined slowly close to the centroid but declined faster as distance from the centroid increased, were compared with simpler linear distance discounting models (Figure 6.2a).

Bayesian MCMC algorithms which predicted the likelihood of a focal group visiting a camera trap location on a given day were developed and run in Python. Model selection was done by AIC comparison using ΔAIC and Akaike weight (Wagenmakers and Farrell, 2004). After identifying the best fitting relationship between visit likelihood and distance from a focal group's centroid, two further variables were incorporated to control for qualities of the root sites themselves. 'Current Quality' was estimated using the mean number of visits to the root site per day by any other gorilla group or solitary male, over the 7 days either side of the day in question. Only days on which the camera trap was active were included within these means. 'Current Quality' was incorporated to control for any seasonal or phenological influences on visit probability at that location e.g. the fruiting of a nearby tree. 'Overall Quality' was estimated as the mean number of visits to the root site by any group or solitary male across all days on which a camera trap was functioning at that location. This was incorporated to control for the differing quality of each root site as a resource for gorillas. Centroids estimated in the Bayesian model including these controls were plotted along with minimum convex polygon range estimates using arcGIS. Posterior distributions from MCMC

analysis were plotted in R using ggplot2. Posterior values were scaled by the comparative size of their variables (for non-binary variables) to allow clearer comparison and plotting.

6.3.4 Modelling inter-group dynamics

The influence of other gorilla groups and solitaries movement patterns on visit likelihood was then investigated by incorporating this data in models including the distance-discounting relationship and controls. Visits by any other group and any other solitary on a given day were incorporated in the models to predict the likelihood of a given focal group visiting that site on the same day. When running models to investigate whether the presence of groups or solitaries on the previous day influenced visit patterns, a smaller subset of the data (5258 camera trap days) were used. This included only days when roots had also been monitored the day before. When investigating whether avoidance or association varied based on the frequency of contact between groups, a directional pair-wise neighbour parameter was calculated to enable an estimate of the effect of neighbours versus non-neighbours on visit patterns. The pair-wise neighbour parameter was calculated as described in equation 6.1. For each group, all other groups were then assigned to either neighbour or non-neighbour status depending on whether their pair-wise neighbour parameter was above a given percentile (specified as 80% initially in priors but estimated within the MCMC algorithm).

$$(6.1) \sum \frac{\textit{Visit rate of group B at site}}{\textit{Distance of site from group A's centroid}}$$

To investigate whether avoidance of other groups varied based on geographic location, in addition to the current location of other groups, the distance to the closest centroid of another group from the root site in question was investigated. A smaller sample of visits using only the 8 focal groups (for whom centroids could be estimated) was used to investigate whether groups avoided visiting a root site on the same day as another group, based on the proximity to that other group's home range centre. To investigate whether location-influenced avoidance of other gorilla groups was better explained by territoriality or scramble competition, two further variables were calculated. Firstly, the relative size of a group compared to the group with the closest home range centre to the root site in question (termed

the resident group), and secondly the combined size of both groups. All combinations of these variables and the distance of the root site from the resident group's home range centre, were tested to identify the model that best fitted the observed data. Model selection for inter-group dynamics models was done by AIC comparison using ΔAIC and Akaike weight (Wagenmakers and Farrell, 2004), and through plotting the distributions of posterior values.

6.4 Results

6.4.1 Root site use

Considerable overlap in root site use by groups was observed, with up to 5 different gorilla groups identified feeding at the same root site (Appendix 6.1), demonstrating that these resources would often be shared by multiple groups. However, since the number of groups identified would be expected to increase with the number of camera trap days, direct comparison between root sites would not be informative. Figure 6.2. shows the mean and standard deviation of the cumulative number of unique gorilla groups identified at 50 camera trap day intervals for the 8 root sites that were monitored for more than 250 days each. After controlling for the number of camera trap days, there is still considerable variation in the number of groups using a site, and no clear plateau in the number of groups identified. The overlap in root site use and home ranges within this population is further demonstrated by the minimum convex polygon home range estimates connecting the root sites at which each of the eight focal groups were observed (Figure 6.3).

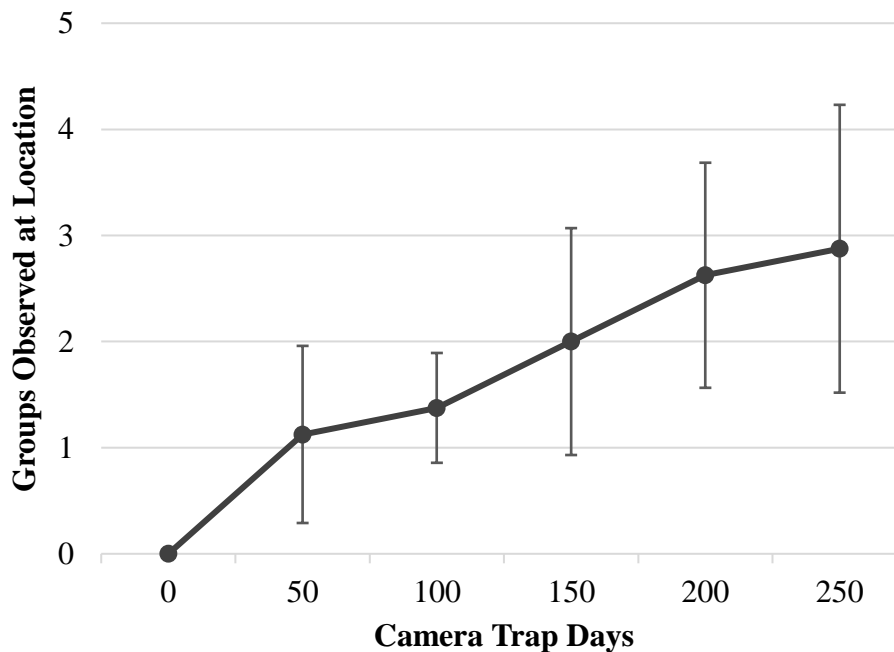


Figure 6.2. Mean cumulative number of different groups observed at a given root site with increasing length of camera trap sampling period. Error bars indicate 1 standard deviation from mean in both directions.

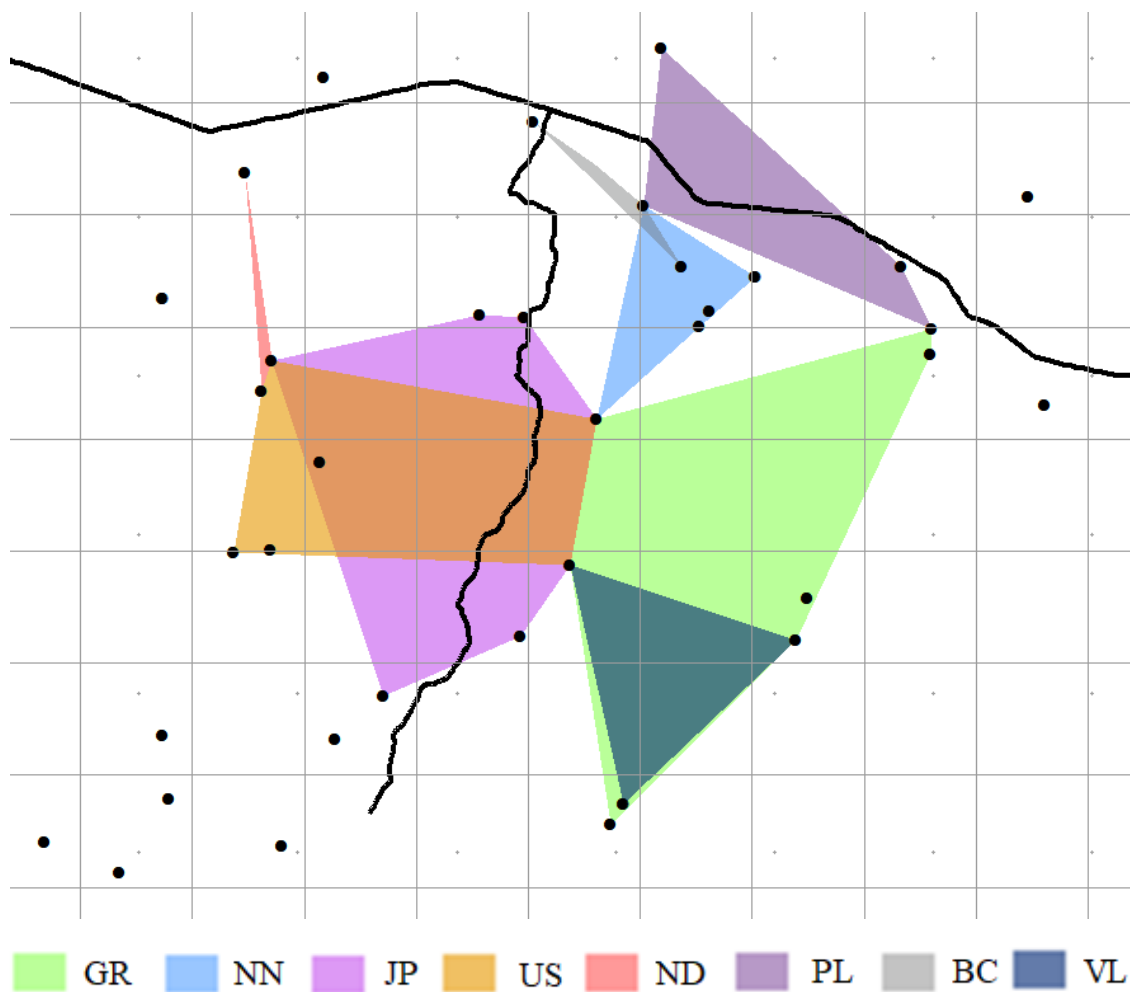


Figure 6.3. Minimum convex polygon ranges for the eight focal groups, from presence/absence at camera trap locations (black dots), with 1km² grid overlaid. Roads indicated by black lines.

6.4.2 Distance discounting

The following three models of distance discounting relationships were investigated:

Linear Model A1: $effect \sim \beta - (\alpha \times distance)$

Gaussian Model A2: $effect \sim \beta + e^{-(distance^2)/\alpha}$

Polynomial Model A3: $effect \sim \beta + (\alpha \times distance) + -(\gamma \times distance^2)$

All three models were run on visit data from focal groups 1-4 for whom the most visit data was available, with fixed values of alpha and beta for all groups. The lowest AIC score was

produced using the linear distance discounting rule (Table 6.3), which was substantially better supported than the Gaussian model ($\Delta\text{AIC} = 23.95$), and marginally better supported than the polynomial model ($\Delta\text{AIC} = 1.69$). As can be observed from the distance effect plots from prior compared to posterior values (Figure 6.4), the polynomial equation producing these low AIC values was almost identical to the linear relationship, and no longer convex as specified in the priors.

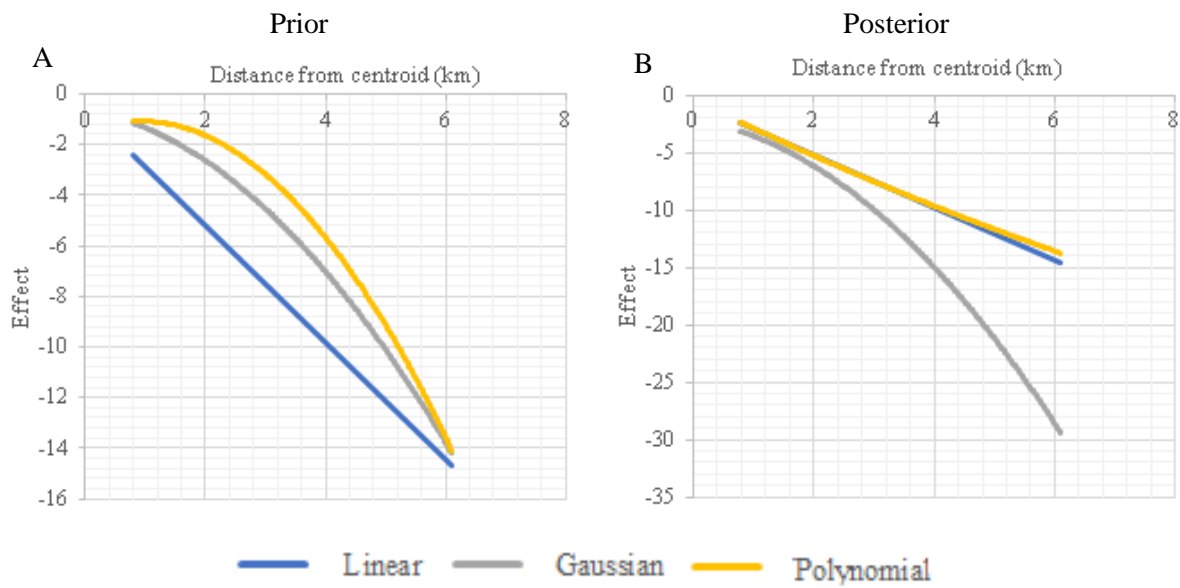


Figure 6.4. The predicted presence of a gorilla group with distance from their home range centroid under three alternative distance discounting models, a) using prior parameter estimates and b) using posterior parameter estimates, when run on visit data from the 4 groups with highest data coverage.

Table 6.3. Prior and posterior variable values for the three alternative distance discounting relationship hypotheses tested, and their relative support from AIC values. Best model fit (lowest AIC) indicated in bold.

Model	Alpha		Beta		Gamma		AIC
	Prior	Posterior	Prior	Posterior	Prior	Posterior	
Linear (A1)	25.65	25.36	-0.58	-0.61	-	-	1746.87
Gaussian (A2)	0.02	0.01	-51	-103.77	-	-	1770.82
Polynomial (A3)	10	28.58	-1.5	-0.35	-60	7.52	1748.56

All three models were then run on the same 4 groups, with a different intercept value (β) allowed for each group, such that a common distance discounting rule was used across groups, but groups could vary in the general frequency with which they visited root sites overall (Appendix 2a). The linear model again produced the lowest AIC score (1681.20) which was a better fit than all models with constrained β values, including the previously highest linear model ($\Delta\text{AIC} = 65.67$), and both Gaussian ($\Delta\text{AIC} = 4.81$) and polynomial ($\Delta\text{AIC} = 158.99$) models with varying β values.

Allowing α but not β to vary and allowing both β and α to vary between groups in the linear model both produced a poorer fit than allowing only β to vary (Appendix 2a) (α but not β vary: $\Delta\text{AIC} = 15.83$, both β and α vary: $\Delta\text{AIC} = 5.40$), suggesting that these groups are applying a common distance discounting rule in their ranging behaviour, but the frequency with which groups choose to feed at root sites overall varies (Figure 6.5).

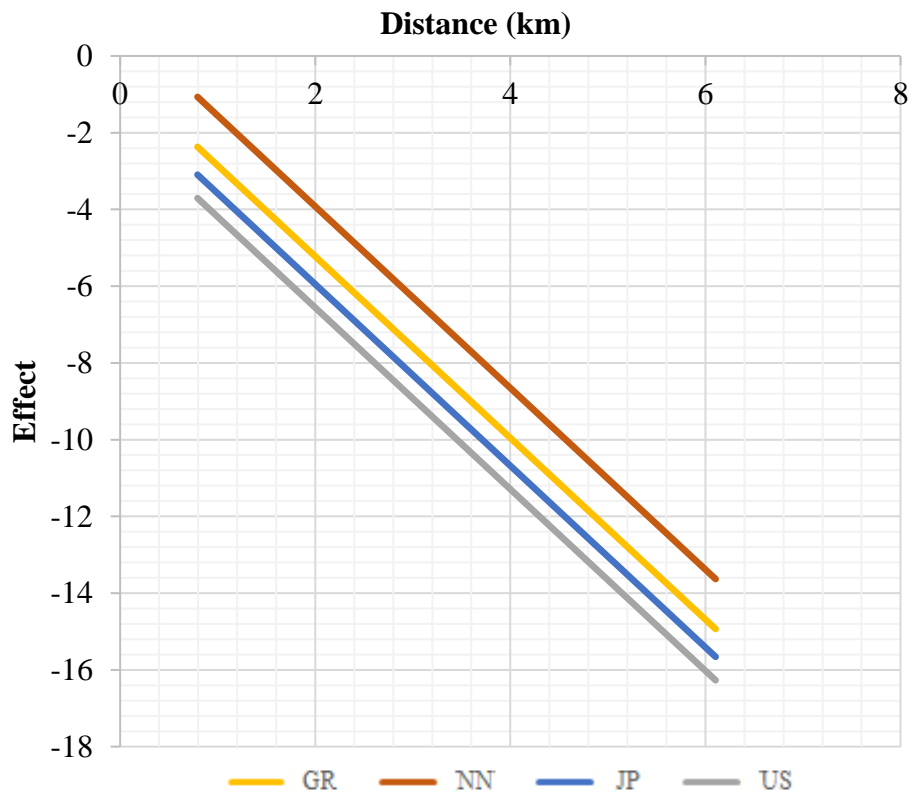


Figure 6.5. The predicted presence of the four gorilla groups with highest coverage (GR: yellow, NN: red, JP: blue, US: grey) with distance from their home range centroid under the best fitting model: common linear distance discounting across groups with group-specific intercept values.

Model selection was then run with focal groups 1-8 included in the analysis (Appendix 2b). The linear distance discounting rule again produced the best fitting model, however this time, constraining β but allowing α to vary produced the best model fit (AIC=2272.75), as shown in Figure 6.6. This model (Linear A1: $effect \sim \beta - (\alpha_{1-8} \times distance)$) was subsequently used as the basic model of distance discounting as it provided the best fit for the largest number of groups.

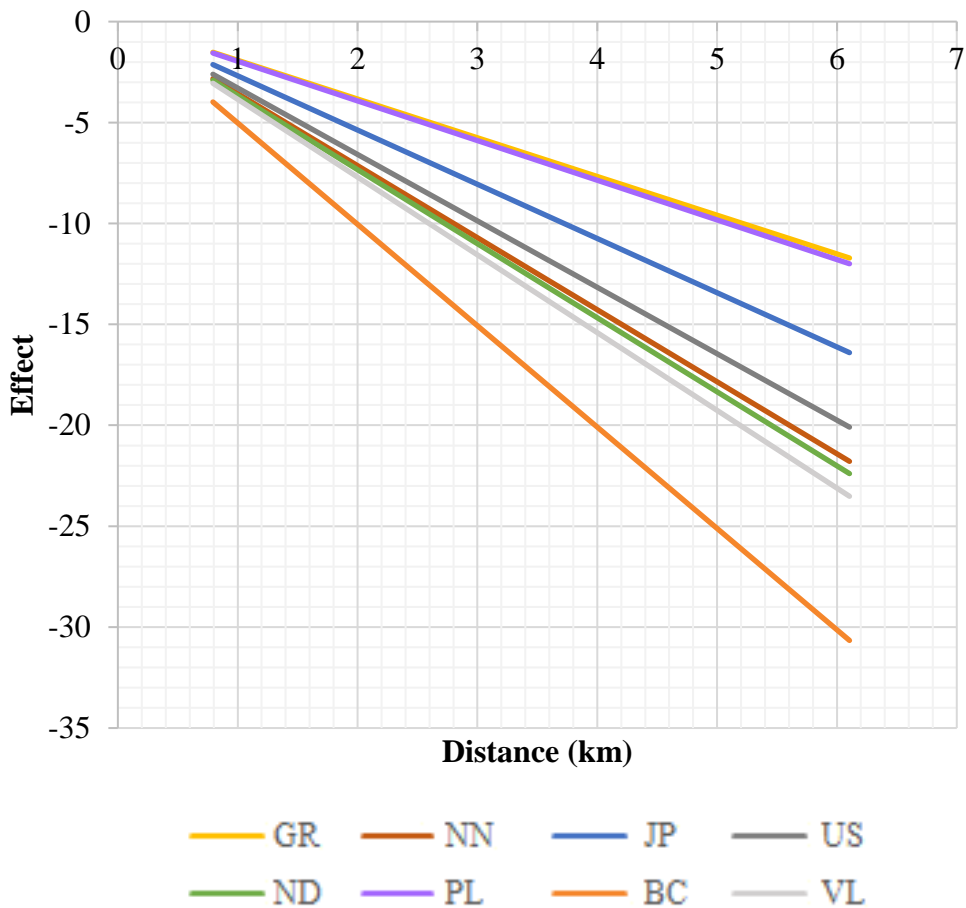


Figure 6.6. The predicted presence of all eight gorilla groups (GR: yellow, NN: red, JP: blue, US: dark grey, ND: green, PL: purple, BC: orange, VL: light grey) with distance from their home range centroid under the best fitting model: common linear distance discounting across groups with group-specific gradients.

6.4.3 Controls and home range estimates

Building on the underlying distance discounting model of gorilla visits to root sites, two further variables to control for the current and overall quality of roots were investigated. These additional variables were run in the following models both with group-specific distance discounting rates and a constrained universal distance discounting rate:

$$\text{Model B: } \textit{effect} \sim \beta - (\alpha \times \textit{distance}) + \gamma\text{O}$$

$$\text{Model C: } \textit{effect} \sim \beta - (\alpha \times \textit{distance}) + \delta\text{C}$$

$$\text{Model D: } \textit{effect} \sim \beta - (\alpha \times \textit{distance}) + \gamma\text{R} + \delta\text{C}$$

Where: O = Overall Quality (root popularity across study period)

C = Current Quality (root popularity 7 days either side of the day in question)

Models with group specific rates (α values) produced a better fit for all three variable combinations verifying that group specific rates still produced the best models once controls were included (Appendix 2c). Further model discussion includes only models with group-specific α values. Including the root-specific Overall Quality variable that controlled for the popularity of a root site across the study period, improved model fit, compared to Model A1 (Model B: $\Delta\text{AIC} = 15.29$). Including the root-specific Current Quality variable that controlled for the popularity of the root site over the 7 days either side of the day in question, to account for phenology at the root site (or other resources such as ripe fruits in the surrounding area that could be drawing gorillas to the area), substantially improved model fit, compared to Model A1 (Model C: $\Delta\text{AIC} = 187.67$). Model D, with both control variables included, provided the best fit ($\text{AIC}=2078.19$), which was a considerably better fit than Model A1 ($\Delta\text{AIC} = 194.56$) and the previously best model, Model C ($\Delta\text{AIC} = -6.89$). Model D including distance from home range, Overall Quality and Current Quality was then used as the baseline against which to test hypotheses relating to inter-group dynamics. This model produced the home range centre estimates (mean posterior output values) shown in Figure 6.7.

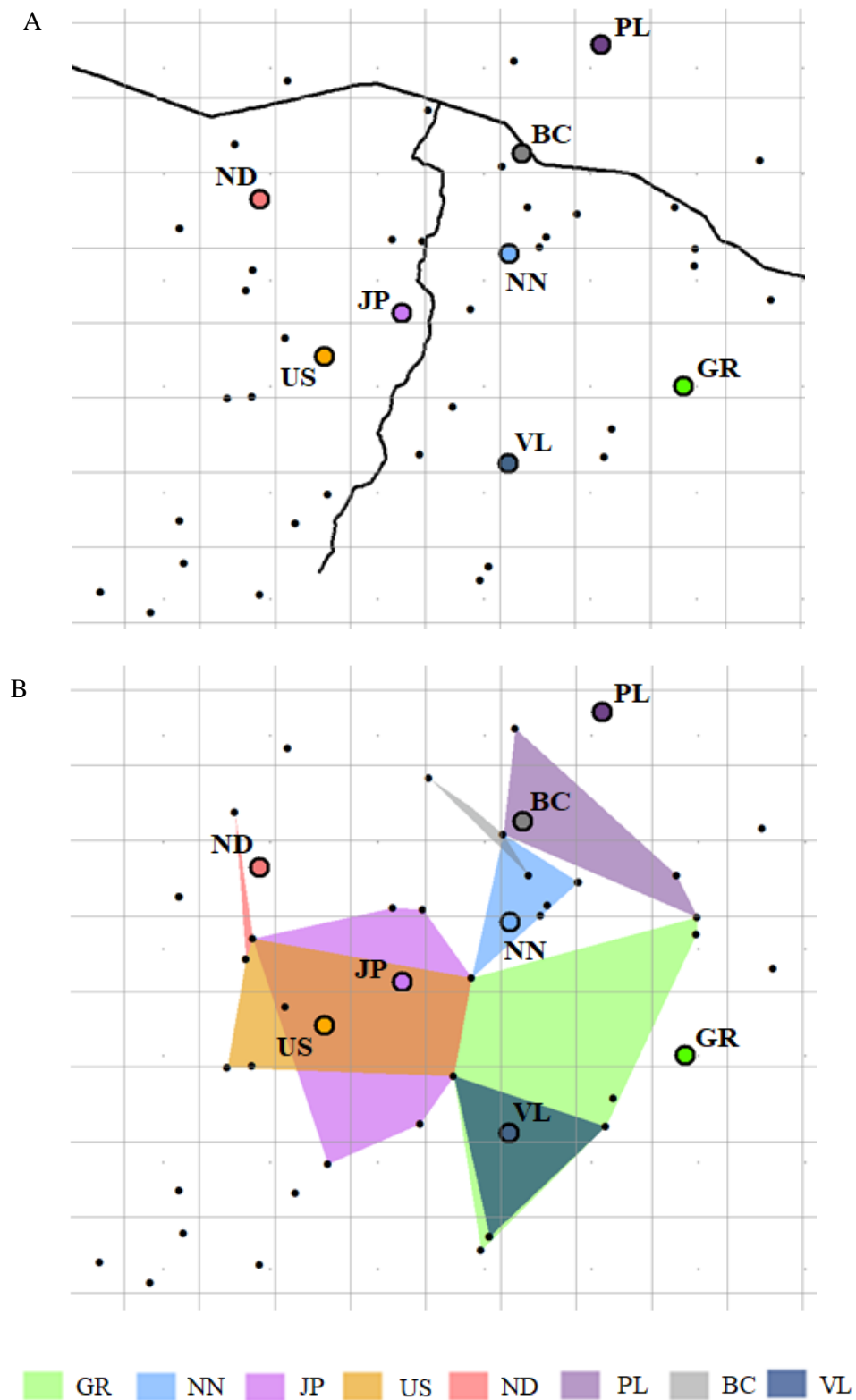


Figure 6.7. Estimated range centroids for the eight focal groups from Model D indicated by large coloured dots with 1 km² grid overlaid, camera trap locations indicated by small black dots a) with road indicated by black line and b) with minimum convex polygon ranges.

6.4.4 Avoidance or association

To investigate the extent to which groups avoided or associated with other groups or solitaires, the following models building on model D were investigated:

$$\text{Model E} \sim \text{Model D} + \varepsilon\text{S}$$

$$\text{Model F} \sim \text{Model D} + \zeta\text{G}$$

$$\text{Model G} \sim \text{Model D} + \zeta\text{G} + \varepsilon\text{S}$$

Where: S = Visits by solitary gorillas on the same day

G = Visits by other gorilla groups on the same day

The inclusion of the presence of solitary gorillas on the same day in the model did not improve model fit, indicating that avoidance of solitary gorillas was not a good predictor of group presence (AIC=2080.98). In contrast, including visits by other gorilla groups on the same day did improve model fit (AIC= 2042.33, $\Delta\text{AIC}= 35.86$), with a negative coefficient of -2.87 indicating that gorillas avoided other groups (Table 6.4). This model was a better fit than Model G in which both group presence and solitary presence were included ($\Delta\text{AIC}= 0.91$), as the posterior distribution for solitary presence, S, overlapped with zero considerably (Figure 6.8).

Table 6.4. Posterior variable values (mean with 95% confidence intervals in brackets) from Models E-G and their AIC scores demonstrate that the best fitting model includes avoidance of other groups but not solitary males. Best model fit (lowest AIC) indicated in bold.

Model	Solitary presence (ε)	Group presence (ζ)	AIC	Akaike weight
Model E	-0.51 (-1.47, 0.32)	-	2080.98	4.05E-09
Model F	-	-2.87 (-4.02,-1.81)	2042.33	0.612
Model G	-0.70 (-1.60, 0.12)	-2.90 (-3.98,-1.83)	2043.24	0.388

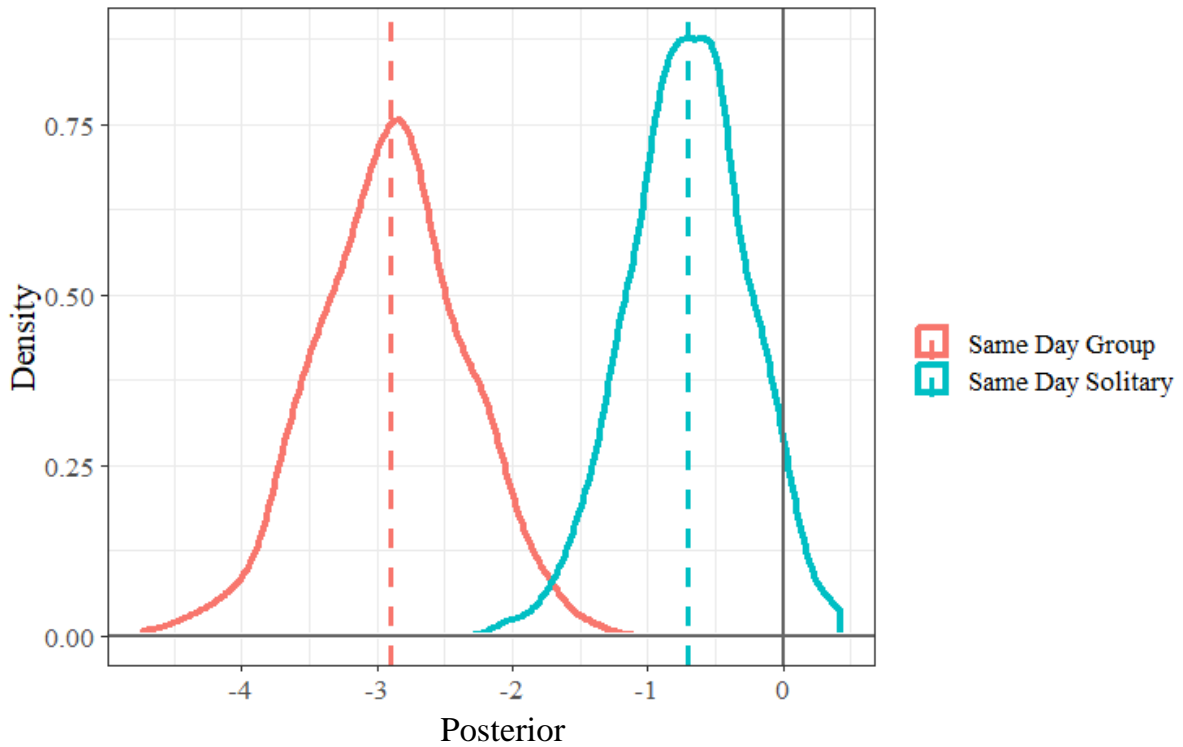


Figure 6.8. Posterior distributions for the presence of groups (red) and solitaries (blue) on whether a group visited a site on a given day from Model G.

To investigate whether the presence of groups or solitaries on the previous day influenced visit patterns, a smaller data subset was used which included only days when roots were also monitored the day before. The following models were then tested to determine which combination of variables provided the best fit to the data:

- Model F (as above)
- Model H \sim Model D + ηG_1
- Model I \sim Model D + ζG + ηG_1
- Model J \sim Model D + ϵS_1
- Model K \sim Model D + ζG + ϵS_1
- Model L \sim Model D + ζG + ηG_1 + ϵS_1
- Model M \sim Model D + ζG + ηG_1 + θS + ϵS_1

Where: G_{-1} = Visits by other gorilla groups the day before
 S_{-1} = Visits by solitary males the day before
 S and G as above

Unlike same day group presence, presence of a group the day before did not reduce the likelihood of observing another group at that location (Table 6.5). 95% CIs of group presence on the previous day overlapped with zero (Figure 6.9A) and the model including this variable did not produce a better fit. Solitary presence the day before overlapped with zero across all models.

Table 6.5. Posterior variable values (mean with 95% confidence intervals in brackets) from Models F and H-M ordered by Akaike weight, using only visit data when the site had also been monitored the day before. None of these additional variables improved model fit in comparison to model F. Best model fit (lowest AIC) indicated in bold.

	Group same day (ζ)	Group day before (η)	Solitary same day (θ)	Solitary day before (ε)	AIC	Akaike weight
Model F	-1.39 (-2.39, -0.64)	-	-	-	1992.87	0.505
Model K	-1.42 (-2.41, -0.58)	-	-	-0.72 (-1.61, 0.06)	1994.71	0.201
Model M	-1.43 (-2.39,-0.61)	0.16 (-0.37,0.64)	-0.79 (-1.78, 0.06)	-0.59 (-1.44,0.21)	1996.01	0.105
Model I	-1.43 (-2.38, -0.64)	0.21 (-0.30, 0.66)	-	-	1996.16	0.098
Model L	-1.43 (-2.33, -0.64)	0.18 (-0.30, 0.67)	-	-0.68 (-1.70, 0.10)	1996.31	0.090
Model J	-	-	-	-0.60 (-1.45, 0.21)	2007.34	3.64e ⁻⁴
Model H	-	-2.9e ⁻⁴ (-0.41, 0.58)	-	-	2045.29	2.09e ⁻¹²

To investigate whether controlling for Current Quality of root sites (presence of other gorillas during 7 days either side) could be obscuring any potential predictive value of the presence of another group the day before, Model M was also run removing the Current Quality control. All variables became slightly better supported when the control was removed (Figure 6.9), with 95% confidence intervals of group visit the day before no longer overlapping 0 (mean: 0.056, 95% CI: 0.06-1.03). The lack of a well supported previous day visit effect in the controlled model (Figure 9b) implies that the positive effect in the uncontrolled model

(Figure 9b) may not reflect attraction to other gorillas but, rather, short term peaks in the attractiveness of particular root sites.

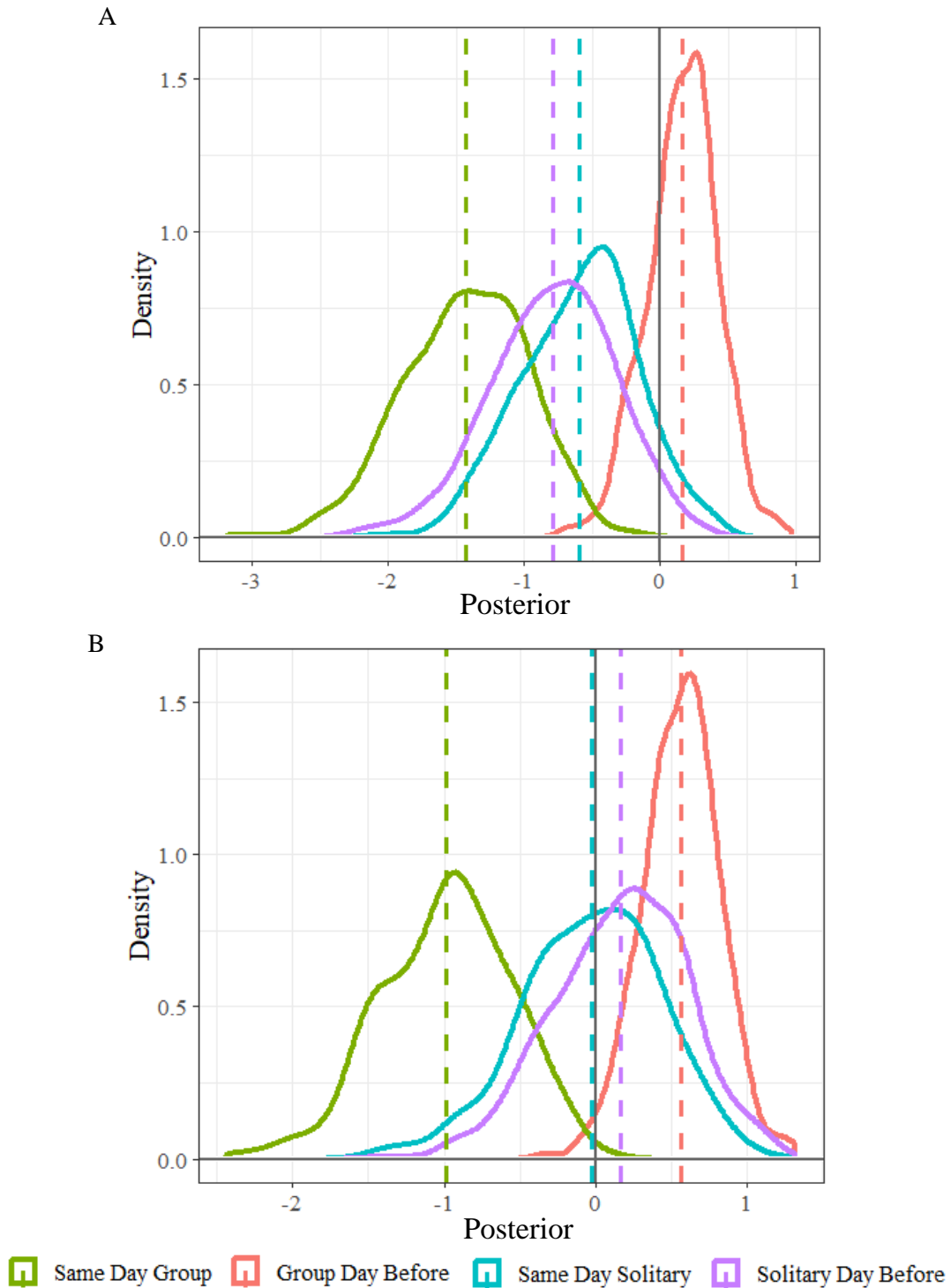


Figure 6.9. Posterior distributions for the presence of groups on the same day (green), groups on the day before (red), solitary males on the same day (blue) and solitary males on the day before (purple) on whether another group visited a site on a given day, a) when Current Quality was included as a control (AIC=1996.01) and b) when it was not (AIC=2198.02).

6.4.5 Neighbour effects

To test whether groups showed less same day avoidance of neighbours compared to non-neighbours, avoidance of known groups on the same day was investigated with the following models:

$$\text{Model N} \sim \text{Model D} + \epsilon\text{KG}$$

$$\text{Model O} \sim \text{Model D} + \zeta\text{NP} + \eta\text{NNP}$$

Where: KG = Visits by known groups
 NP = Visits by neighbouring groups that day
 NNP = Visits by non-neighbouring groups that day

Unidentifiable groups had to be removed from the predictive model as it could not be determined whether they represented neighbouring or non-neighbouring groups. Similar levels of avoidance were observed for both neighbouring ($\zeta = -2.03$ [-3.78, -0.73]) and non-neighbouring groups ($\eta = -2.50$ [-4.77, -0.98]) as shown in Figure 6.10. Including these additional parameters did not improve model fit (Model N: AIC=2061.91, Model O: AIC=2066.23, $\Delta\text{AIC} = -4.32$), demonstrating that the avoidance difference was not well supported enough for separate neighbour/non-neighbour avoidance variables to be justified.

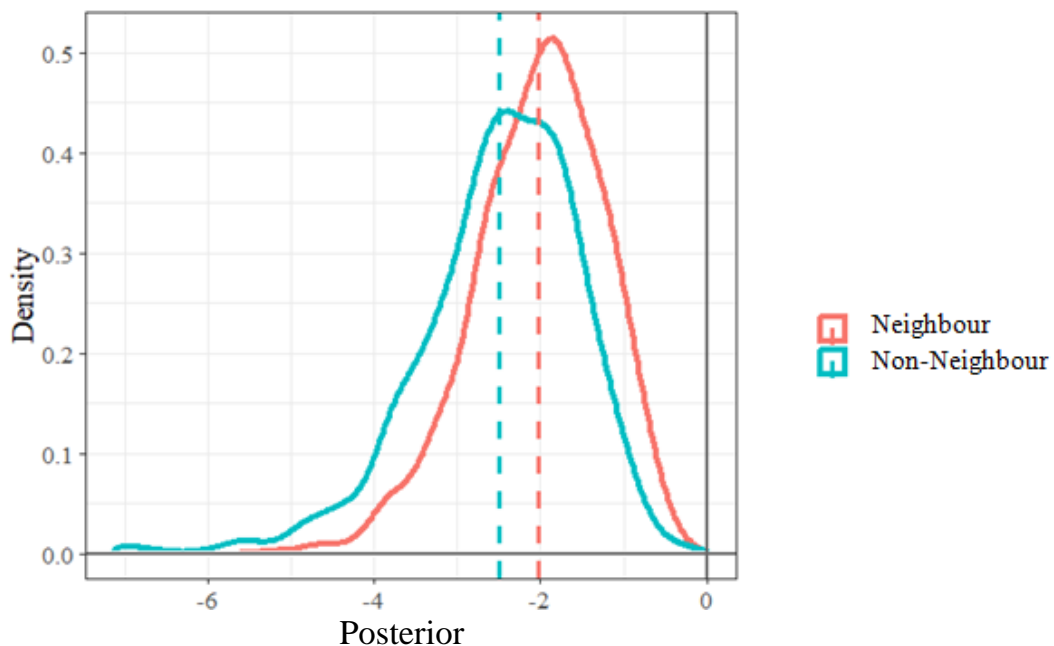


Figure 6.10. Posterior distributions for the presence of neighbouring (red) and non-neighbouring groups (blue) on the same day in Model O (AIC=2066.23).

The same approach was used to investigate avoidance and association based on visits the day before (again using the smaller data subset) with the following models:

$$\text{Model P} \sim \text{Model D} + \varepsilon\text{KG}_1 + \theta\text{G}$$

$$\text{Model Q} \sim \text{Model D} + \zeta\text{NP}_1 + \eta\text{NNP}_1 + \theta\text{G}$$

Where: KG_1 = Visits by known groups the day before
 G = Visits by other gorilla groups on the same day
 NP_1 = Visits by neighbouring groups the day before
 NNP_1 = Visits by non-neighbouring groups the day before

In model Q posterior distributions for both neighbour and non-neighbour presence overlapped with zero with mean values close to zero ($\zeta = -0.146$ [-0.97, 0.61], $\eta=0.115$ [-0.87, 0.95]), demonstrating that there was no avoidance or association of either neighbours or non-neighbours that visited the previous day, over that controlled for already in Model D. Inclusion of neighbour/non-neighbour variables did not improve model fit (Model P: AIC=1996.49, Model Q: AIC=2001.15, $\Delta\text{AIC} = -4.66$).

6.4.6 Territoriality

To investigate whether avoidance of other groups varied based on geographic location, in addition to the current location of other groups, Model F (including distance discounting, both controls and the same day presence of other groups) was used as a baseline model against which to test models relating to territory avoidance.

The following models were tested using the entire dataset:

$$\text{Model F: } effect \sim \beta - (\alpha \times distance) + \gamma\text{R} + \delta\text{D} + \zeta\text{G}$$

$$\text{Model R} \sim \text{Model F} + \eta\text{NC}$$

And the following models were tested using only the visits of focal groups (individuals with estimated home range centres), to determine how avoidance varied with distance from another groups home range centre:

Model F

Model S \sim Model F + ϵ (TC \times G)

Model T \sim Model F + η NC + ϵ (TC \times G)

Where: NC = distance from nearest home range centroid of another group
 G = Visits by another gorilla group on the same day
 TC = distance from that specific other group's home range centre

The probability of a group visiting a root site decreased with proximity to another group's home range centroid (Table 6.6 and Figure 6.11). This suggests that range delineation may be maintained through either active avoidance of other groups' territories or avoidance of areas that other groups are known to regularly use. Furthermore, the depressive effect of a same day group visit (same day avoidance of another group) strengthened with proximity to that group's home range centre (Table 6.7, Figure 6.12). This demonstrates that groups avoid the current location of another group to a greater extent when they are close to that group's home range centre, as well as showing a general avoidance of the home range centres of other groups. This suggests a territorial basis to the avoidance pattern, as avoidance of mating competition or contest competition at resource sites would be expected to remain constant regardless of where in each group's home range the competition was occurring.

Table 6.6. Posterior variable values (mean with 95% confidence intervals in brackets) from Models F and R and their AIC scores, tested using the entire dataset. Best model fit (lowest AIC) indicated in bold.

	Group presence on day (ζ)	Distance from centroid of another group (η)	AIC
Model F	-2.87 (-4.02, -1.81)	-	2042.33
Model R	-2.82 (-4.08, -1.76)	3.64 (1.31, 6.23)	2036.08

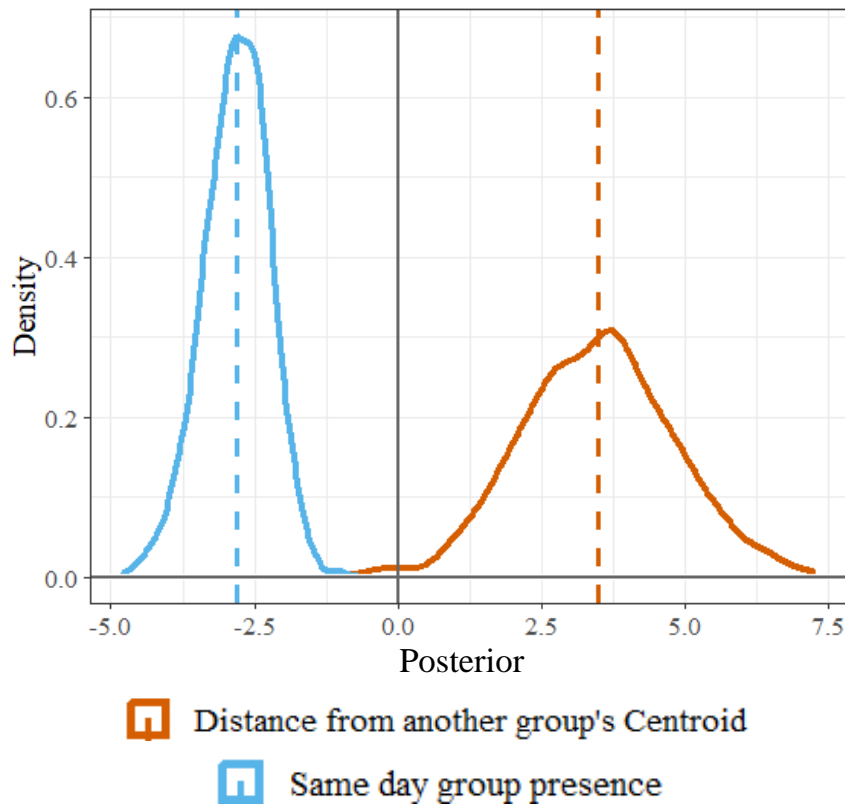


Figure 6.11. Model R posterior distributions for the presence of other groups (blue) and the distance from the closest group’s home range centre (red) on whether a group visited a given site on a given day, demonstrates that groups are more likely to visit a site, the further away it is from another group’s home range centre

Table 6.7. Posterior variable values (mean with 95% confidence intervals in brackets) from Models F, S and T and their AIC scores when using only presence of the 8 focal groups (rather than all groups) as a predictor. Best model fit (lowest AIC) indicated in bold. Models ordered by Akaike weight

	Group presence on day (ζ)	Distance from centroid of another group (η)	Avoidance with distance from other group’s centroid (ϵ)	AIC	Akaike weight
Model T	-8.14 (-17.20, -3.17)	4.82 (1.33, 8.94)	1.94 (0.86, 4.01)	2237.65	0.967
Model S	-8.50 (-16.93, -3.16)	-	1.95 (0.78, 3.65)	2244.38	0.033
Model F	-0.83 (-1.98, 0.05)	-	-	2260.25	1.20e ⁻⁵

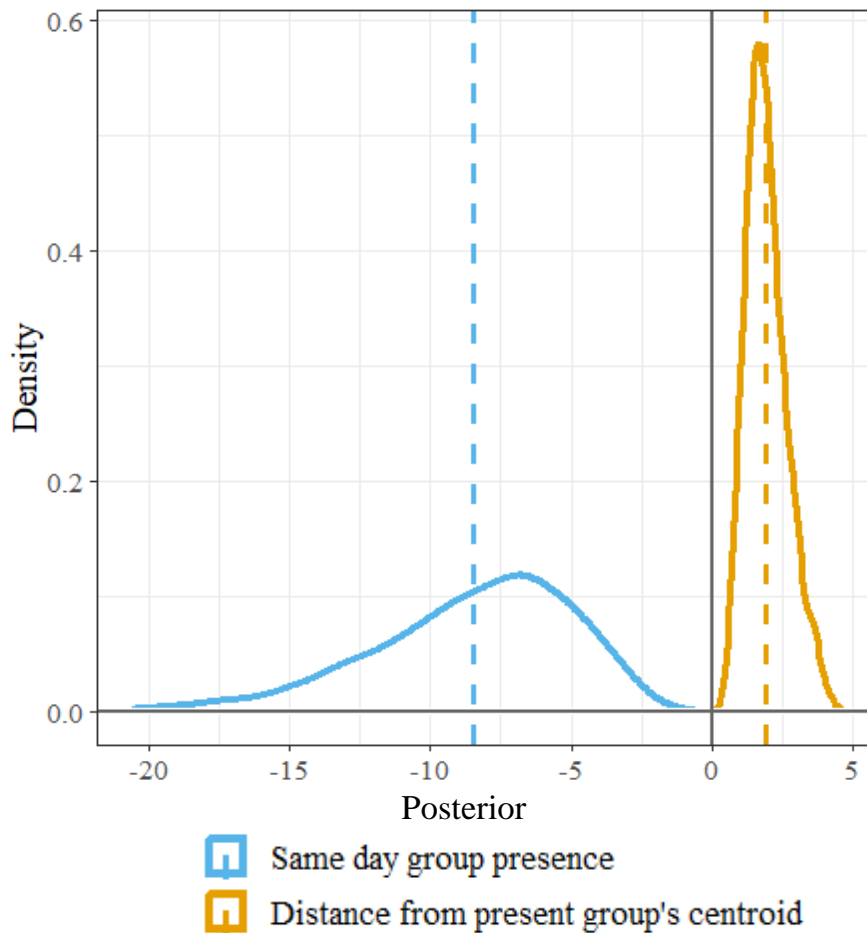


Figure 6.12. Model S posterior distributions for the effects on visit probability of another group's presence (blue) and the distance from that other group's home range centre (yellow).

To investigate whether this location-influenced avoidance of other gorilla groups and avoidance of geographic regions was better explained by territoriality or scramble competition, two further models were assessed. First, a model in which avoidance occurred based on the other group's relative size (Model U) was investigated. This model was built to investigate the hypothesis that larger groups would be more strongly avoided, under the rationale that territory defence capability should be correlated with mate defence capability and group size (Cheney, 1987). Second, a scramble competition model (Model V) used the combined size of both groups to predict group presence. Scramble competition could feasibly explain groups avoiding the home range centres of neighbouring groups, simply due to a lower likelihood of finding resources if another group regularly feeds there. If this were the case, a group's presence would be well predicted by the combined size of both their group, and the group with the closest home range centre (the resident group). This is because a

larger group would consume more resources close to their home range centre, leaving fewer resources for another group. That other group may then be unlikely to find adequate resources in that region themselves, especially if they themselves were a large group.

All combinations of variables (NC, RS and CS), in addition to those present in Model F, were tested in the following models to identify the model that best explained the observed visit patterns:

$$\text{Model R} \sim \text{Model F} + \eta\text{NC}$$

$$\text{Model U} \sim \text{Model F} + \eta\text{NC} + \varepsilon\text{RS}$$

$$\text{Model V} \sim \text{Model F} + \eta\text{NC} + \theta\text{CS}$$

$$\text{Model W} \sim \text{Model F} + \eta\text{NC} + \varepsilon\text{RS} + \theta\text{CS}$$

$$\text{Model X} \sim \text{Model F} + \varepsilon\text{RS}$$

$$\text{Model Y} \sim \text{Model F} + \theta\text{CS}$$

$$\text{Model Z} \sim \text{Model F} + \varepsilon\text{RS} + \theta\text{CS}$$

Where: NC = distance from nearest home range centroid of another group
RS= relative size
CS = combined size

The territoriality model (Model U: AIC= 2024.49) produced the best fit (Figure 6.13a and Table 6.7), and fitted the observed visit patterns considerably better than the scramble competition model (Model V: AIC= 2031.23, $\Delta\text{AIC} = 6.74$) (Figure 6.13b). This demonstrates that gorilla groups avoided the home ranges of relatively larger groups to a greater extent than relatively smaller groups, potentially due to territorial or range defence by more dominant males or groups. Both Model T and Model U provided a better fit than those without any group size value (Model R: AIC=2036.68). However, when both RS and CS were included in the model (Model W), combined group size overlapped considerably with 0 (Figure 6.13c), demonstrating that the variation explained by combined group size was better explained by relative group size once both were included. This suggests that territoriality alone is a better explanation for movement patterns, rather than territoriality in combination with scramble competition.

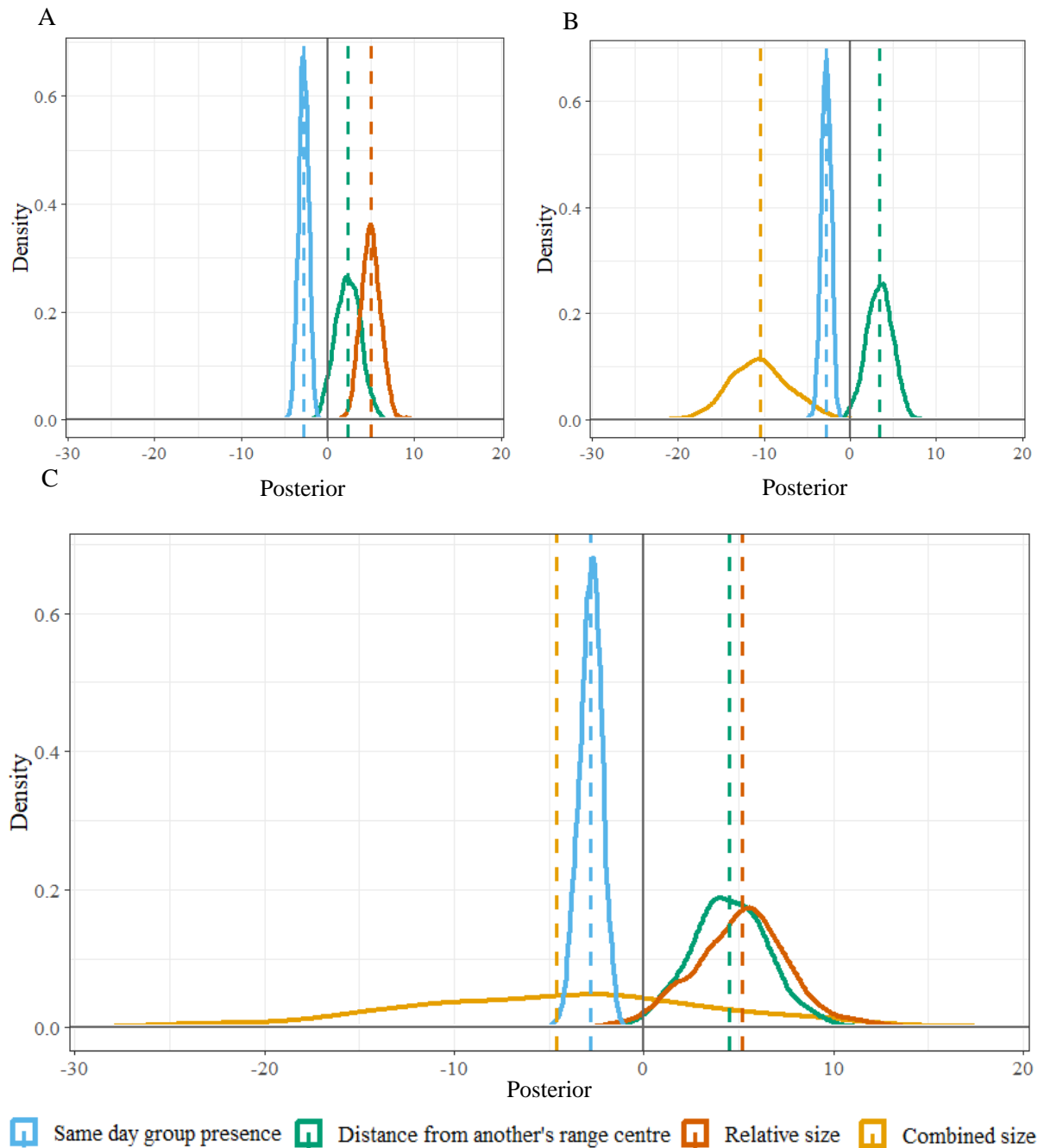


Figure 6.13. Posterior distributions for a) Model U (AIC= 2024.49), b) Model V (AIC=2031.23) and C) model W (AIC = 2027.78), with the presence of other groups shown in blue, the distance from another group’s home range centre in green, the relative group size in red and combined group size in yellow, predicting whether a group visited a given site on a given day.

Table 7. Posterior variable values (mean with 95% confidence intervals in brackets) from Models R, and T - Z, and their AIC scores. Best model fit (lowest AIC) indicated in bold. Models ordered by Akaike weight

	Group presence on day (ζ)	Distance from centroid of another group (η)	Relative size (territoriality)	Combined size (scramble competition)	AIC	Akaike weight
Model U	-2.80 (-3.95, -1.73)	3.22 (-0.49, 7.02)	6.66 (3.85, 9.65)	-	2024.49	0.696
Model W	-2.83 (-4.01, -1.70)	4.53 (0.48, 8.78)	5.15 (0.15, 10.50)	-4.63 (-23.85, 12.06)	2027.78	0.134
Model X	-2.89 (-4.21, -1.85)	-	6.16 (3.36, 9.00)	-	2028.35	0.101
Model Z	-2.90 (-4.00, -1.89)	-	6.16 (2.57, 9.83)	-1.28 (-19.15, 13.71)	2030.12	0.042
Model V	-2.79 (-3.91, -1.80)	4.72 (0.61, 8.59)	-	-18.11 (-29.81, -5.61)	2031.25	0.024
Model R	-2.82 (-4.00, -1.78)	4.80 (1.39, 8.54)	-	-	2036.68	0.002
Model Y	-2.92 (-4.10, -0.10)	-	-	-15.82 (-27.80, -2.78)	2037.07	0.001

6.5 Discussion

6.5.1 Gorilla territoriality

The results in this chapter provide several lines of evidence supporting the presence of gorilla territoriality. Gorilla groups visited sites less often the closer they were to another group's home range centroid, and therefore appear to be factoring in the location of their conspecifics' ranges in the movement decisions they make. This suggests some understanding of the "ownership" of specific geographic regions, usually associated with territoriality. Avoidance of other groups also increased with proximity to that other group's home range centre, suggesting a potential increase in the costs of inter-group interaction, consistent with a stronger defensive response from groups when closer to the centre of their ranges. Mating competition or contest competition over food could not explain this pattern as this would be expected to remain constant regardless of where in each group's home range the competition was occurring. Scramble competition for resources could be a potential explanation for the decreased likelihood of visiting an area close to another group's home range centre, due to a lower likelihood of finding resources when another group regularly feeds there. However, comparison of the scramble competition model with a model in which the relative size (and therefore defensive capabilities) of the other group was taken into account demonstrated that movement patterns were better explained by range defence, consistent with the presence of territoriality in gorillas.

The presence of territoriality in primates is correlated with a group's ability to patrol its home range daily (Mitani and Rodman, 1979). However, the fact that gorilla home range size far exceeds the average daily path length of 1.7-2 km observed in habituated groups (Bermejo, 2004; Cipolletta, 2003; Doran-Sheehy et al., 2004; Cipolletta, 2004) suggests that entire gorilla group home ranges are not defensible. The considerable range overlap of groups already demonstrates that territoriality under the definition of exclusive use of defended space (Bartlett and Light, 2017) cannot be present across the entirety of a group's home range. What my results suggest is that gorillas demonstrate biases in their movement patterns consistent with the presence of some broader elements of territoriality. They suggest the presence of regions of priority or even exclusive use by a group, close to their home range centre (Boitani and Fuller, 2000; Maher and Lott, 1995), which could be defended by physical aggression (as these smaller regions could be more feasibly patrolled), using

olfactory cues or advertised by long-distance auditory inter-group communication such as chest-beating (Wich and Nunn, 2002).

These findings further emphasise the importance of approaching territoriality with a less rigid, non-binary view. Whilst systems have historically been categorised as “territorial” or “non-territorial”, there appears to be a considerable grey area between these two categories, into which gorillas fall. Western gorilla groups appear to have some level of “ownership” over regions close to their home range centre, leading to the avoidance of those regions by other groups, but are able to overlap and even peacefully co-mingle in other regions of their ranges. Furthermore, whilst the extreme territorial-based violence observed in chimpanzees suggests that territorial defence could provide an evolutionary basis for present day warfare, with warfare being a shared evolutionary trait between chimpanzees and humans (Wilson and Wrangham, 2003), this warfare likely represents a minority of inter-group interactions in human history (Fuentes, 2004; Wrangham and Glowacki, 2012; Fry, 2007). In humans, the more common pattern of inter-group interactions may in fact be closer to that observed in gorillas in which core areas of resident activity dominance and large overlap zones of mutual tolerance are observed (Fuentes, 2004; Dyson-Hudson and Smith, 1978). This suggests that the inter-group dynamics of gorillas may provide a valuable model system for understanding the patterns of interaction occurring in early human populations, showing simultaneous territoriality and inter-group affiliations and cooperation.

6.5.2 Resource sharing and avoidance

Up to five different identifiable gorilla groups were observed feeding at a single root site within the study period, demonstrating that overlap of gorilla group ranges results in multiple groups sharing resources within those ranges. A linear decline in the likelihood of visiting a site with increased distance from the home range centre best predicted group presence at a root site, showing that gorilla groups appear to follow linear distance discounting rules in their foraging patterns. The best discounting model using the four groups with the highest number of visits suggested that a common distance discounting rule may be present across these groups. However, this was no longer the case when the larger sample of 8 groups was investigated, which showed far more variation in the gradient of the decline in visit rate with

distance. This may be due to the lower accuracy of estimates with lower sample size of visits per group or a steeper decline in visit frequency with distance in groups that visit root sites less often, as groups that are less interested in feeding on roots may be less willing to travel further for them.

The avoidance of other groups on the same day but not other solitaries suggests that resource competition rather than mating competition could be driving this avoidance pattern, as solitary males would consume fewer resources than a family group but still represent a potential competitor attempting to attract females away from the group. However, with solitary male visits only representing 16.2% of the total visits recorded (92 out of 568), this lack of solitary male avoidance may just be due to a failure to detect it with the lower sample. Furthermore, Mirville et al (2018), found that solitary male mountain gorillas were more likely to initiate interactions with groups, compared to groups with solitaries or groups with other groups. As our avoidance estimate is non-directional, it is possible that whilst gorilla groups are avoiding both other groups and other solitaries, solitaries may be actively associating with groups, as they have little to lose from mating competition (no females) and everything to gain.

Whilst a group was more likely to visit a root site if another group had visited the day before, this was no longer the case once the visits of other groups during the week either side of the day in question was included as a control. This does not support the hypothesis that groups use the location of other groups to identify feeding opportunities at root sites through social foraging. Rather it suggests instead, that common environmental factors such as the phenology of the root sites themselves or surrounding resources may be driving gorilla groups to visit in close succession. This would be expected to take place over a greater time period rather than as a response to the calls of another group, which might be expected to take place over a matter of hours or days. However, these root sites do not appear to be highly seasonal, with feeding consistently observed throughout the year. In contrast, fruiting trees are highly seasonal, with the presence of ripe fruit being far less predictable. This would therefore represent a better resource on which to test hypotheses relating to inter-group social foraging, as the difficulty in predicting the presence of this resource could lead to social information on resource quality being of far greater value.

Investigating the effect of the presence of neighbours versus non-neighbours on the likelihood of a group visiting a site demonstrated no clear difference in response. This

therefore provided no support for the presence of either the “dear enemy” or “nasty neighbour” effect (Christensen and Radford, 2018) in gorillas, suggesting that groups may not respond differently depending on whether they were “neighbours” or “strangers”. This is consistent with the observation in mountain gorillas that kinship and social exposure rather than range overlap were predictive of interaction patterns (Mirville et al., 2018). However, neighbour versus non-neighbour status had to be estimated very roughly due to the small amount of data available for groups that were not considered focal groups. There may not have been adequate data on a large enough number of groups to detect any difference in effect. Furthermore, the 8 focal groups that made up the majority of the dataset all had home ranges in quite close proximity to one another, meaning the lack of data on more distant groups may have further prevented the detection of a difference in response. Whilst the degree of range overlap, and therefore the frequency with which groups come into contact, may still influence the nature of inter-group relations, it appears likely that factors such as kinship and presence in the same natal group are of considerable importance. Further investigation with a larger sample of groups, ideally of known kinship and natal group, is required to better understand neighbouring group relationships in WLGs.

6.6 Conclusion

These results provide the first model of how western gorilla group movement patterns influence one another across their ranges, and a foundation for novel hypotheses on the cognitive rules applied by gorilla groups in their movement and foraging decisions. This analysis provides the first quantitative evidence for territoriality in a gorilla species. Gorilla groups appear to actively avoid one another, both through avoidance of other groups at resource hotspots, and avoidance of areas regularly used by other groups. The reduction in visit frequency with proximity to another group's home range centre suggests some understanding of the "ownership" of certain regions, with groups avoiding larger, more dominant groups' home range centres to a greater extent. This, along with the avoidance of other groups' current location increasing with proximity to their home range centre, is highly suggestive of the presence of territorial defence in western gorillas. This contrasts greatly with previous classifications of gorilla species as non-territorial.

However, our data do not provide any direct evidence of territorial defence through aggressive interactions. Further research is required to determine how inter-group interactions vary with distance from their home range centres, to identify the mechanisms by which the territorial avoidance patterns detected here may occur. As all western gorilla groups studied here had a single silverback male, further research could also investigate whether male alliances in mountain gorillas could cooperate to defend these communal territories. Under the narrowest definitions of territoriality gorillas cannot be classified as territorial. But, then, neither can humans. Our results suggest that, like humans, gorilla groups occupy regions of priority or even exclusive use. This brings into question gorillas' historical classification as a non-territorial genus, and highlights the considerable problems with approaching territoriality from a rigid, binary viewpoint. The clear similarities between gorilla and human social organisation in both their flexible territoriality and inter-group social bonding demonstrates the value of western gorillas as a model system for understanding human social evolution. This is particularly the case in relation to understanding the simultaneous capacity for both exceptional forms of cooperation and extreme forms of territorial-based aggression and warfare in humans.

6.7 References

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6.8 Appendices

Appendix 6.1: Sampling and detection by root site

Site	Camera Trap Days	Gorilla Visits	Unique identifiable Groups
R019	427	68	5
R169	308	41	2
R198	307	67	1
R172	284	43	3
R030	269	17	2
R008	259	14	4
R007	257	52	5
R178	255	20	4
R033	242	32	4
R146	231	20	2
R106	226	27	3
R017	212	14	1
R065	212	26	2
R100	206	17	1
R035	183	11	3
M01	161	1	0
R092	151	2	1
R703	149	17	3
R104	135	9	2
R018	122	11	4
R152	99	5	2
R111	90	5	1
R023	84	3	1
R020	76	7	2
R372	71	2	2
R323	70	3	1
R465	52	8	1
R224	45	5	1
R394	45	6	1
R040	41	2	2
GMB03	38	3	1
R063	27	4	2
R251	26	1	0
R630	21	3	1
R101	18	0	0
R107	4	2	0
Total	5403	568	24

Appendix 6.2a. Model Comparison by AIC using the 4 groups of highest visit number (GR, JP, NN and US). Best model fit (lowest AIC) indicated in bold.

Model	Group-specific α	Group-specific β	AIC
A1 Linear	No	No	1746.87
A2 Gaussian	No	No	1770.82
A3 Polynomial	No	No	1748.56
A1 Linear	No	Yes	1681.20
A2 Gaussian	No	Yes	1686.01
A3 Polynomial	No	Yes	1840.19
A1 Linear	Yes	No	1697.03
A1 Linear	Yes	Yes	1686.60

Appendix 6.2b. Model Comparison by AIC using the 8 groups of highest visit number (GR, JP, NN, US, ND, VL, BC and PL). Best model fit (lowest AIC) indicated in bold.

Model	Group-specific α	Group-specific β	AIC
A1 Linear	No	No	2349.90
A2 Gaussian	No	No	3431.356
A3 Polynomial	No	No	2475.792
A1 Linear	No	Yes	2494.93*
A3 Polynomial	No	Yes	2449.14
A1 Linear	Yes	No	2272.75
A1 Linear	Yes	Yes	2422.074*

*could not converge

Appendix 6.2c. Linear model comparison by AIC using the 8 groups of highest visit number (GR, JP, NN, US, ND, VL, BC and PL) with controls added. Best model fit (lowest AIC) indicated in bold.

Model	Group-specific α	Group-specific β	AIC
A1 Linear	No	No	2349.90
A1 Linear	Yes	No	2272.75
B Linear	No	No	2323.95
B Linear	Yes	No	2257.46
C Linear	No	No	2149.39
C Linear	Yes	No	2085.08
D Linear	No	No	2146.52
D Linear	Yes	No	2078.19

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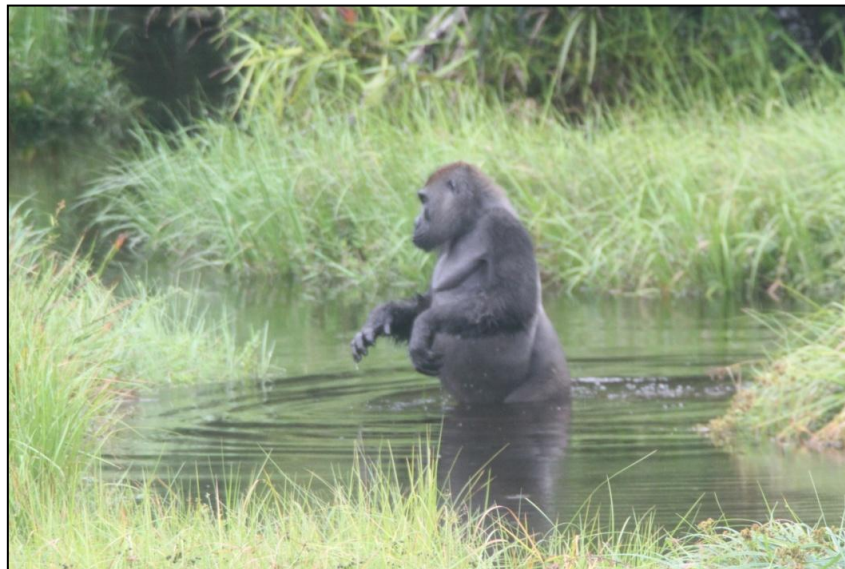


Photo by Robin Morrison at Mbeli Bai Study, WCS Congo

7.1 Abstract

The study of western gorilla social behaviour has primarily focused on family groups, with research on inter-group interactions usually limited to the interactions of a small number of habituated groups or those taking place in a single location. However, gorilla groups are known to have extensively overlapping home ranges, show affiliative inter-group interactions and often aggregate at resource hotspots. There is also genetic evidence of kin-biased behaviour between dispersed kin. This is all suggestive of a complex society in which inter-group interactions follow an underlying multi-level social structure where affiliations are influenced by kinship, social exposure, ranging patterns, territoriality or foraging decisions. Using observational data from two forest clearings in the Republic of Congo, I quantified community structure by network modularity analysis and hierarchical clustering, demonstrating the presence of a previously unquantified kin-based multi-level social structure in western lowland gorilla. The social structure detected at these forest clearings was

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consistent with a super-spreader structure, indicating that clearings may act as important transmission hubs for disease, novel ideas, behaviour or culture. This suggests that intervention strategies targeting gorillas with home ranges near to forest clearings, particularly solitary males, might be highly effective for limiting the transmission of certain diseases. Modelling the movement patterns of a gorilla population across their ranges using camera trap data demonstrated that western gorillas show biases in their movement patterns consistent with the presence of broader elements of territoriality, with regions of priority or even exclusive use, close to their home range centres. My findings strongly emphasise the importance of gorillas as a model system for human social evolution, due to both the common underlying multi-level social structure and the considerable similarities in territorial dynamics with those observed across human history. Gorillas may be a key study species for understanding the dichotomy of how humans have evolved to be simultaneously highly cooperative and also show extreme forms of aggression and warfare between groups. In contrast to previous assumptions that interactions between gorilla groups are primarily random or due to aggressive mate competition, I find that these interactions appear to be based around a complex social structure influenced by kinship, range defence and dominance.

7.2 Gorilla social structure

Due to the considerable difficulties of habituating and monitoring western lowland gorilla (WLG) groups in their dense forest habitat, little is known about the patterns of interactions taking place between them. However, using modern network-based analytical methods on historic forest clearing data, and the most extensive gorilla camera trapping project to date, my PhD investigated biases in gorilla movement patterns to better understand the social dynamics taking place at the meta-group level in WLGs.

Using datasets of gorilla visit patterns from forest clearings I was able to quantify the multi-level social structures of two gorilla populations from biases in group and solitary visit patterns. By confirming the presence of this structure in two distinct populations through network analysis of spatio-temporal overlap, my findings suggest that this multi-level social structure may be present species (or even genus) – wide. However, further research is necessary to confirm that this structure is not unique to forest clearings, and whether it represents meaningful social affiliations across gorilla's normal home ranges, even within populations that do not visit forest clearings. Further investigation of social structure in mountain gorillas is also necessary to determine whether the first above-group level of social affiliation detected in WLGs (between roughly 2.1 silverbacks), may represent a social unit equivalent to that of multi-male mountain gorilla groups. The kin basis to the multi-level social structure detected is broadly consistent with the kin-biased behaviours observed in both WLG and mountain gorillas, however as only male genetic data was available, this thesis cannot provide a complete picture of the importance of kinship to inter-group relations. Genetic data on females will be crucial to develop a fuller understanding of how kinship affects the strength of bonds between dispersed gorilla groups and solitary males.

The scaling pattern observed between gorilla social levels, consistent with those in other multi-level mammalian social systems provides further evidence that the gorilla multi-level social structure detected at forest clearings may represent a genuine component of the gorilla social system, rather than a phenomenon of the forest clearing. Analysis of demographic data suggests that this scaling pattern could have a basis in reproductive rates, with strong social bonds between male siblings (both half and full), but whether this could lead to the consistent scaling observed across a variety of mammalian species needs to be further investigated. The identification of multiple social tiers, following a common scaling pattern strongly supports a

multi-level approach to understanding gorilla society over traditional approaches focusing on individual reproductive groups. It suggests that such an approach in future may enable the detection of further social tiers and increased social complexity in some of our closest evolutionary relatives. The high levels of territoriality observed in *Pan troglodytes* (Watts & Mitani 2001; Mitani et al. 2010) suggest that higher level associations are unlikely to be common in this species, however the range overlap and peaceful between-group encounters observed in *Pan paniscus* (Idani 1990; Furuichi 2011) combined with the findings of this thesis, suggest that a multi-level social system in this species warrants further investigation.

Analyses of movement patterns from camera trap data provided the first model of how WLG group movement patterns influence one another across their ranges, showing that groups actively avoid each other at root sites. My findings could not demonstrate the use social foraging cues from neighbouring groups. However, they were limited to the specific root resources monitored in this camera trapping project and a small sample of focal groups. The investigation of transient and less predictable resources such as fruiting trees might identify greatly differing dynamics, particularly with regard to the potential for social foraging. Groups did not show differences in avoidance between neighbours and non-neighbours which is consistent with findings in mountain gorillas that inter-group relations may be more strongly influenced by kinship and social bonds from natal groups rather than familiarity from range overlap (Mirville et al. 2018). However, again the sample size of groups studied may be preventing the detection of any differences, and investigation of a larger number of groups across a greater range is required to confirm this result.

The detection of a reduction in visit frequency with proximity to another group's home range centre strongly suggests some understanding of the "ownership" of certain geographic regions by specific gorilla groups. Furthermore the avoidance of larger, more dominant group's home range centres to a greater extent, suggests that this "ownership" or territoriality may be sustained through aggressive defence, with larger groups (with greater defensive capacity) providing a greater threat, and therefore being more strongly avoided. However my analyses do not provide any direct evidence of territorial defence through aggressive interactions or acoustic communication, which could potentially be investigated using the long term mountain gorilla inter-group interaction data. Although, due to the considerable ecological differences between WLG and mountain gorilla habitat and feeding patterns it should not be assumed that a similar avoidance pattern would necessarily be observed in

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mountain gorillas. Whilst WLGs cannot be classified as territorial under the narrowest definitions of territoriality, my results suggest the presence of regions of priority or even exclusive use by a group, consistent with broader definitions of territoriality (Boitani & Fuller 2000; Maher & Lott 1995), bringing into question gorilla's historical classification as a non-territorial genus.

7.3 Disease implications

Disease has been one of the major contributors to the rapid decline of gorilla populations over the past few decades (Ryan & Walsh 2011). In order to better understand the transmission of diseases through gorilla populations, an understanding of the interaction patterns of gorillas within these populations is required, particularly the patterns of contact between gorilla groups and solitaries. Since these are extremely difficult to observe directly, movement biases such as those investigated in this thesis, may provide some of the best information on what these contact patterns are likely to look like. Camera trapping data demonstrated that gorilla groups showed active avoidance of one another at root sites over the short term (one day), but were otherwise more likely to visit a site with increasing visit frequency of other gorillas over the week either side. Whilst this was hypothesized to relate to the phenology of resources in the area, rather than active social association, this nonetheless suggests that diseases that do not require direct physical contact to transmit, and can remain active in the environment for more than 1 day, may be transmitted more rapidly than expected under models assuming random movement. This effect would be expected to be even stronger for resources such as fruiting trees that are only in-season for brief periods of time, in comparison with root sites that appear to be used fairly regularly.

Forest clearing sites represent such abundant resources that feeding competition at these sites is thought to be relatively non-existent (Metsio Sienne et al. 2014; Magliocca & Gautier-Hion 2002). Instead, interactions between groups actually occur to a greater extent than expected under random movement models, suggesting active social affiliation (Levréro 2005). As such, they therefore represent potential hotspots for disease transmission due to increased contact rates when feeding competition is relaxed. Analysis of visit rates and networks of spatio-temporal overlap at the Lokoué Bai forest clearing suggested that these clearings may act as important transmission hubs, as not only do they represent hotspots of social interaction, but the structure of contacts taking place at these social hotspots are likely to follow a heavy-tailed, potentially super-spreader-like distribution. The presence of long-term affiliations between specific groups and solitaries identified in Chapter 2 suggests that past data on social interactions could be used to predict how a given outbreak may spread through a population, with the potential to provide significant reductions in disease transmission. Gorillas with ranges nearby to forest clearings appear to represent key targets in intervention

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strategies as they are likely to visit clearings more often, coming into contact with a larger number of groups and solitary males. However, further research integrating individual and inter-group encounter rates at varying contact levels through a network approach would be highly informative for modelling the spread of diseases dependent on their modes of transmission.

7.4 Gorillas as a model system for human social evolution

A major component of humanities complex social structure, and arguably the core of our society, is the extent of higher level social tiers, such as nations, uniting huge numbers of weakly related or entirely unrelated individuals in cooperation. This is possible despite the considerable levels of territoriality, inter-group aggression and even warfare, observed across human history. Chimpanzee (*Pan troglodytes*) populations appear to show similar territorial-based extreme aggression, leading to the hypothesis that human warfare has an evolutionary basis in territoriality, but chimpanzees do not appear to show stable affiliations between groups or an underlying multi-level society. The research in this thesis demonstrates that western gorillas appear to show stable affiliations and a multi-level structure, as well as underlying elements of territoriality. Their more flexible form of territoriality (relative to *Pan troglodytes*) appears to enable long-term affiliative bonds between groups, whilst still maintaining ownership of particular areas, as often observed in human societies. This suggests that gorillas may be a key model system for understanding the dichotomy of how humans have evolved to be simultaneously highly cooperative and also show extreme forms of aggression and warfare between groups (Wrangham & Glowacki 2012).

Extensive comparison between humans and the chimpanzee/bonobo sister clade has been used to suggest that the evolution of complex between-group social interactions and multi-level social structure occurred after the chimpanzee-human split. This has also been used to suggest that the common ancestor of humans and chimpanzees had a MM-MF social structure from which smaller family groups formed, with higher social tiers developing subsequently. However, by demonstrating the presence of kin-based social modules made up of multiple group and solitary core units in gorillas, clear parallels to tribal and clan based human social structure can be observed. Not only do western gorillas appear to share a multi-level social system, but they also show strongly bonded single-male family groups similar to those observed across human history. This suggests that a more parsimonious explanation of human social evolution is that single-male family groups and a multi-level social structure were already present in the common ancestor of gorillas, chimpanzees and humans, with MM-MF social groups acquired in the chimpanzee lineage after its divergence. Multi-level social structure could be present within the *Pan* lineage, particularly within *Pan paniscus*, however in *Pan troglodytes* at least, the potential for extra-group social affiliations appears to

be prevented by strong territoriality. The manner in which the kin-based, multi-tiered social structure in gorillas follows a common scaling structure also suggests that some common mechanism may be driving the patterns of social unit sizes across mammalian multi-level social structures, including that in humans. These results imply that fundamental elements of human social complexity may have far deeper evolutionary roots than previously assumed, and that the social brain enhancements observed within the hominin lineage were not necessary to enable this multi-level social structure. Peering more deeply into our evolutionary past will therefore be crucial to determining when key transitions in social evolution took place, and ultimately the true extent of human social uniqueness.

Human territoriality is a hotly debated topic tying in with long-standing discussion on the evolution and nature of human aggression and warfare (Wrangham & Glowacki 2012). However, it is widely accepted that some form of territoriality is observed across the broad variety of human societies, and is a fundamental component underlying many of the interactions taking place within them (Sack 1986; Malmberg 1980), despite the diversity in patterns of spatial organisation observed (Dyson-Hudson et al. 1978). Human territoriality rarely follows the pattern of exclusive defended home ranges, as observed in chimpanzees (at least within societies sharing languages or dialects and cultural practices), with large areas of mutual overlap, tolerance and even cooperation observed (Wrangham & Glowacki 2012). This shows considerable similarities to the underlying elements of territoriality in gorilla ranging dynamics demonstrated in this thesis. Whilst it was not possible to demonstrate direct evidence for inter-group cooperation in gorillas, the stable affiliations detected between groups suggest that there may be considerable advantages to these social affiliations, of which cooperation in foraging, defence of females or even defence of territories, could be potential drivers. If territoriality were also present in mountain gorillas it could provide a system in which to investigate whether male alliances in multi-male mountain gorilla groups could cooperate to defend these communal territories. Future research on the potential for cooperation between gorilla groups should therefore be a priority, as understanding how potential cooperative behaviours are influenced by location and territoriality may provide considerable insight into the social evolution of both gorillas and humans.

7.5 References

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