Assessing sociality: catarrhine microsatellites and the dynamics of glucocorticoids with social relationships in wild male Assamese macaques (*Macaca assamensis*)

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Table of Contents

Summary

In order to navigate within-group competition and maximise fitness, strategies have evolved in group-living animals, including social dominance ranks and affiliative relationships. Both of these play a crucial role in shaping an individual's long-term fitness. The association between dominance rank and fitness benefits has been long established in males, with higher ranked individuals showing improved fitness outcomes compared to their subordinates, such as through improved access to mating opportunities. Similarly, recent work has highlighted that strong, equitable, and stable affiliative relationships or social bonds can confer fitness benefits, including increased longevity or a pathway to improved rank position.

The extent to which the fitness outcomes of dominance ranks and affiliative relationships are also associated with more immediate costs can be investigated by quantifying the underlying hormonal responses. Dynamics in sociality can induce costs through affecting glucocorticoids (GCs), a key mediator of homeostasis, and an indicator of the physiological response to challenges and within-group competition. Glucocorticoids are a group of steroid hormones that form part of the vertebrate stress response system and a high GC response can be indicative of either an appropriate, adaptive response to a challenge or of a cost; with chronic stress causing homeostatic overload and somatic damage. To understand the cost-benefit balance of sociality, both the short and long-term consequences of within-group competition and social relationships need to be considered, which is what I aimed to do for primates in this thesis, focusing on catarrhines species and male Assamese macaques (*Macaca assamensis*).

In order to assess the long-term fitness consequences of sociality, the genetic variation of a population needs to be accurately quantified. Microsatellites, short repetitive DNA sequences found in non-coding regions of the genome, are a common marker for doing so in wild species due to their cross-species amplifiability, high heterozygosity, and compatibility with low-quality, non-invasive DNA samples. However, issues such as undetected allele variation, null alleles, or allelic dropout remain. Microsatellite data is also often not comparable between labs due to the use different loci or genotyping methods, hindering cross-species comparisons and collaborative work. I addressed these methodological issues and describe a refined panel of 42 microsatellites for catarrhine primates; developed from an extensive literature review of published catarrhine microsatellites, in combination with a genotype-by-sequencing (GBS) pipeline. The microsatellite loci were optimised using available published catarrhine genomes and validated on both blood and faecal samples. Given its universal applicability to catarrhine species, the panel can facilitate comparative and integrative studies between species and studies. In addition, as it can more accurately assess genetic variation, the panel is an excellent tool for assigning parentage and determine kin relationships, which are key factors in the fitness outcomes of social relationships.

To investigate the short-term costs of sociality and competition, I studied the correlated glucocorticoid responses to dynamics in dominance rank and affiliation in wild male Assamese macaques, using over 4,100 faecal samples from 62 adult males, spanning 15 years at Phu Khieo Wildlife Sanctuary, Thailand. Our previous work on this population suggested that increased competition in the mating season induced elevated glucocorticoids and that unusually for male primates, lower rank position correlated with higher glucocorticoids, matching the cost of subordination hypothesis. It was suggested that the burden of competition lay with the subordinates as they received most of the aggression, whereas high status males had sufficient agonistic support and rank stability to avoid an elevated physiological response. Using a markedly larger dataset and dynamic cardinal metrics that avoided aggregating social data and instead linked specific GC samples to dynamics in social relationships, I re-examined these results. Contrary to our previous work, dominance rank showed a positive relationship with glucocorticoids, as high status correlated to elevated glucocorticoids. Replicating our previous finding, glucocorticoids were upregulated at the start of the mating season, which may have had a preparative function before the onset of the increased competition.

In addition, I tested for the social buffering hypothesis, which posits that the presence of a bonded social partner can have an attenuating effect on glucocorticoid production. We found evidence of the social buffering effect, adding a third primate species for whom adult male social buffering has been reported. As the strength of a male’s top affiliative relationship increased, the correlated GC response lowered; showing that dynamics in affiliation can correlate to changes in the physiological response for the first time in a wild primate. Investing in strong bonds could have ameliorated the physiological demands of competition and provided a mechanism for bond maintenance in male Assamese macaques.

Assamese macaques are therefore no longer an “exception that proves the rule” in male primates and show that, even in a species with low-contest competition, dominant males incur a greater physiological cost of social competition, likely due to the energetic demands of rank maintenance. These physiological costs are likely to be adaptive in the long run as they provide access to mating opportunity through higher status, but over an extended period of time, the negative costs of GCs can also compound. Therefore, the attenuation of the GC response by social bonds could be key mediator of the true costs of sociality.

Chapter 1: General Introduction

1.1 Living in a social group

Living in a social group has evolved independently in multiple lineages of mammals as it offers numerous fitness benefits to all group members such as protection from predation and access to better food resources (Krause and Ruxton, 2002). Protection from predation risk is thought to be the primary driver for the evolution of social groups in non-human primates (hereafter primates) whereas the benefits of cooperative hunting and infant rearing are likely behind the rise of groups in carnivores (Macdonald, 1983; van Schaik, 1983). Group living can only evolve if the benefits it provides outweigh the negatives (Alexander, 1974) but group membership can also result in costs such as a greater infection risk (Altizer et al., 2003) and an increase in competition with group members for food or access to mating (Ellis, 1995; Majolo et al., 2008). In order to navigate within-group competition and maximise fitness, strategies evolved including social relationships between group members. In addition to affecting fitness outcomes, social relationships can induce more immediate costs and benefits, such as by changing the underlying physiological responses (Thompson, 2019).

In this thesis, I am interested in the cost-benefit balance of group-living and sociality, over both the short and long-term. I approach these questions from two different angles. In Chapter 2, I present a tool for an improved understanding of the long-term, genetic consequences of sociality in catarrhine primates (Old world monkeys and apes), such as by measuring inclusive fitness. In Chapter 3, I study the dynamics of sociality and competition over a shorter timeframe, investigating the glucocorticoid response of male Assamese macaques (*Macaca assamensis*). In the current chapter I will first describe social relationships and fitness, before discussing how to assess fitness in wild populations, with a focus on microsatellites and their advantages and issues. Next, I overview the relationship between glucocorticoids and sociality, highlighting the role of within-group competition and the need for dynamic measures. Finally, I present the detailed aims of my thesis.

1.1.1 Agonistic Relationships

Once individuals repeatedly interact with each other and recognise their fellow group members, the pattern of their previous interactions can predict the type and outcome of their next interaction (Hinde, 1976). Then, these repeated interactions develop into a relationship and can be formed of either affiliative or agonistic behaviours (Hinde, 1976). Agonistic relationships can be structured into a group-wide dominance hierarchy with each individual having a dominance rank that represents their social status and ability to dominate others (Kaufmann, 1983; Schjelderup-Ebbe, 1922). Dominance ranks can be found across vertebrates and some invertebrates (Ellis, 1995; Lord et al., 2021). The ability to dominate a single competitive interaction depends on a number of factors including intrinsic attributes such as body mass or fighting ability, as well as the resource being competed for and access to support in conflicts (Clutton-Brock and Huchard, 2013; Smith and Parker, 1976). However, the dominance relationship, composed of the long-term agonistic interaction history between the two competing individuals also has a major effect on the outcome of a dominance interaction (Tibbetts et al., 2022). If an individual has repeatedly lost interactions in the past then often this will produce an unprovoked submission in order to avoid a direct conflict (Reddon et al., 2021). The dominance hierarchy therefore structures behaviour at the group level and allows for within-group competition to be resolved without severe consequences (from injury for example) for both competing individuals (Holekamp and Strauss, 2016).

In both sexes, the intensity of within-group competition underlies the formation and structure of the dominance hierarchy, as well as the type of agonistic behaviours used in agonistic interactions (Kappeler et al., 2022). For males, within-group competition is primarily with other males over mating access to fertile females and can be referred to as the contest potential, which is reflective of a single male’s ability to monopolise access to fertile females in his group (Cowlishaw and Dunbar, 1991; Emlen and Oring, 1977). If receptive females are solitary or few in number they can be defended by a single male, who monopolises access and excludes rivals (Clutton-Brock, 1997). However, if female fertility is concentrated into a short time span (high reproductive synchrony), there are too many females to be defended, and too many rivals to exclude (as is the case in many group-living species); a single male might not be capable of monopolising economically all the sexually receptive females in his group or territory (Emlen and Oring, 1977; Ostner et al., 2008c). As a result, mating opportunity and reproduction are skewed by dominance rank position, with higher ranked males having priority of access to fertile females (Altmann, 1962). If a highly ranked male can still monopolise access to a large proportion of the females by himself, there is a high contest potential as dominance status can confer a significant benefit in terms of controlling reproductive opportunity. Therefore, males in high contest potential species form dominance hierarchies based on high-risk high-reward within-group competition, focused on directly and intensely competing with each other for dominance status (Clutton-Brock and Huchard, 2013). In these species, dominance status is linked to fighting ability and males often evolve traits that enable this competition such as musculature, weaponry, or ornaments that act as honest signals of fighting ability (Emlen, 2008; Lüpold et al., 2019; Setchell et al., 2006).

The contest potential is also driven by the number of co-residing males, who are not only rivals but also potential partners. As the number of males increase, the presence of a suitable partner (e.g. of a similar age) becomes more likely which may allow for the use of alternative, less risky methods of rank competition (Noë, 1994). Equally, as the number of competitors increases, the ability of a single male to monopolise females decreases so combined with more potential partners for alternative dominance tactics, the intensity of competition decreases (Van Schaik et al., 2004). Behaviours such as coalitions, a relatively rare behaviour but one found in many in male primates (Bissonnette et al., 2014), or queuing for dominance status (East and Hofer, 2001) become more prevalent. In lower contest species, higher ranked males still enjoy a greater access to females but reproductive opportunities are spread more evenly across the dominance hierarchy (Altmann and Alberts, 2003). The reduced reward of a high rank and the presence of coalitionary alliances therefore makes intense, direct competition (without a partner) highly costly, with the risks such as injury outweighing the benefits (van Noordwijk and van Schaik, 2004). Male dominance ranks are thus highly dependent on maximising the rewards (i.e. increased reproductive success) while minimising the costs of group-living.

1.1.2 Affiliative relationships

Similar to agonistic relationships, in order for affiliative relationships to be formed, there needs to be an associated adaptive benefit (Kummer, 1978). Engaging in an affiliative relationship with a partner can be viewed as a way to maximise the resulting benefits from the relationship or minimise the losses that would otherwise be suffered (Cords, 1997). Affiliative relationships affect behaviour at the dyadic or individual level more than the group and can be deconstructed into different dimensions and types of affiliative relationships which provide different functional benefits (Ellis et al., 2019; Schülke et al., 2022). For example, how socially integrated an individual is, i.e. how many affiliative relationships they have, regardless of the type or quality of the relationship could influence access to information or disease (Romano et al., 2022). In this thesis, I focus on direct connectedness or social bonding, a dimension of affiliation where individuals preferentially interact with only a few partners to build up those relationships, forming social bonds (Ostner and Schülke, 2018). Social bonds are defined as strong, equitable, and stable affiliative relationships (Silk et al., 2006) and as they require more engagement or social investment, the expected benefit of the relationship is likely to be larger (Cords, 1997). Both agonistic relationships and social bonds (a term that will be used interchangeably with strong affiliative relationships) can influence the immediate costs or benefits of sociality and competition within groups and subsequently have fitness consequences for males.

1.1.3 Fitness benefits of social relationships for group living males

Fitness is a complicated concept to assess but can be described as the ability of an organism to survive and reproduce in the environment that it lives in (Orr, 2009; Sæther and Engen, 2015). An individual's fitness is more than simply producing offspring and surviving, it is dependent on ensuring the transmission of genetic material to the next generation (Kimbrough, 1980). An individual has a greater fitness if they can produce more viable offspring over their lifetime and spread their genes further in the population than their competitors (Koch and Narum, 2021). Social relationships can therefore provide fitness benefits if they allow an individual to improve their capacity to reproduce or to live longer relative to conspecifics, both of which contribute to the overall lifetime reproductive success of an organism (Arnold and Wade, 1984).

The relationship between male dominance rank and fitness benefits has been well established (Heer, 2013; Huang et al., 2011; Røed et al., 2002; von Rueden et al., 2011). Higher ranked individuals typically achieve greater fitness outcomes, in part because they avoid the negative costs faced by lower ranked individuals, and this pattern can occur through a variety of mechanisms such as having greater access to food, avoidance of predators, or foraging efficiency (Bulger and Hamilton, 1987; Hirsch, 2007; Krause, 1994). If female parental care significantly outweighs male care and the operational sex ration is biased towards males, then an increased opportunity for mating is key for male fitness (Clutton-Brock and Huchard, 2013; Ellis, 1995). Male dominance rank is positively correlated to mating frequency and access to females (Dewsbury, 1982; Majolo et al., 2012) though the strength of the relationship to fitness varies with the contest potential and numerous other factors including female mating preferences (Pereira and Weiss, 1991) and the age structure of the population (Willisch et al., 2012). For example, a negative correlation between the number of males or the number of synchronously receptive females and paternity concentration with rank has been found in cross-species comparisons of primates (Gogarten and Koenig, 2013; Ostner et al., 2008c) and within specific species (Boesch et al., 2006; Setchell et al., 2005). These benefits of high dominance ranks do not come without costs. A high rank can confer negative fitness outcomes too, such as an increased risk of parasitism (Habig et al., 2018), accelerated aging (Anderson et al., 2021) or higher rates of wounding (MacCormick et al., 2012) which could reduce an individuals' lifespan. Despite this, a high rank in sum confers significant net fitness benefits to males. An example of this is in male yellow baboons (*Papio cynocephalus*), for whom a high rank results in an increased risk of mortality but provides much greater access to mating opportunities (Alberts et al., 2003; Campos et al., 2020).

As with dominance rank, affiliative relationships provide fitness benefits for individuals by changing their access to mating or increasing their lifespan. The link between affiliative relationships and a reduced mortality is well established in humans (Holt-Lunstad et al., 2010) and an increasing number of animals (Snyder-Mackler et al., 2020). For example, in the same study of yellow baboons where a high dominance status correlated to a greater mortality risk, males who formed social bonds with adult females had an increased survival probability (Campos et al., 2020). Subordinate male olive baboons (*Papio anubis*), by contrast, develop social bonds with females that may increase their probability of reproductive success (Smuts, 1985) as did prairie volves (*Microtus ochrogaster*) who formed only a select few affiliative ties to either sex (Sabol et al., 2020). One way for same-sex social bonds between males to affects fitness is via trust and reliability in mutual aiding, joint resource defence or sharing (Carter et al., 2020; Wiszniewski et al., 2012) and crucially in coalition formation for rank competition (Young et al., 2014b). The link between social bonds, coalitionary support, and future dominance rank (and therefore an improved fitness outcome) has been established in bottlenose dolphins (*Tursiops aduncus*), horses (*Equus caballus*) and numerous primates (Bray et al., 2021; Feh, 1999; Gerber et al., 2022; Neumann et al., 2022; Schülke et al., 2010). However, an individual's lifetime reproductive success i.e. the number of offspring an individual has over their lifespan, while often used as a measure of individual fitness in wild populations (Koch and Narum, 2021), is only part of the story.

1.1.3 What really is fitness? Indirect effects

Inclusive fitness theory, first proposed in Hamilton's seminal work in the 1960s, posits that each individual's overall fitness is dependent not only on their own reproductive success, but also on the reproductive success of their relatives with whom they share genetic material (Hamilton, 1964). Since then, the definition of fitness is: the relative contribution of an individual's genes to the next generation's gene pool. An individual's fitness can therefore be deconstructed into direct fitness, the component of fitness due to their own reproduction (such as lifetime reproductive success) and indirect fitness, which is the fitness gained from aiding related individuals in their reproduction (West et al., 2007). Indirect fitness benefits are thought to be a key mechanism in the evolution of both cooperation and group-living as individuals are often found to preferentially interact and help their close kin or relatives (Griffin and West, 2002). Kin biases can affect association and affiliation patterns (Bercovitch and Berry, 2013; Silk, 2009), including social bonds for whom kin are often preferred partners (De Moor et al., 2020a; Schuttler et al., 2014). Indirect fitness benefits can also influence dominance ranks if related individuals provide coalitionary support to their relatives (Smith, 2014; Widdig et al., 2006) and can affect key behavioural decisions such as dispersal strategies (Wikberg et al., 2014). Therefore, in order to understand the fitness consequences of sociality, the indirect fitness benefits influencing selection need to be accounted for, in addition to direct Darwinian fitness (Silk, 2007). To assess indirect fitness, the genetic composition, diversity, and variation in a population must be quantified, specifically the distribution of kin relationships (Städele and Vigilant, 2016). Equally, for many wild populations, even determining direct fitness effects such as how many offspring an individual produces can be difficult. Parentage assignment is complicated by births not being directly observed, aspects of the mating systems (e.g. reproductive synchrony and polygamy) presenting multiple possible parents, or a lack of behavioural clues such as parental care, which is the case for males of many species (Archer et al., 2022; Cords and Gometz, 2022; Sorin, 2004). Genetic methods of assigning parentage and assessing the relatedness or genetic variation within group-living species are therefore a key tool for understanding the evolution and fitness consequences of sociality and competition.

1.2 Genetic methods

A wide variety of techniques have been developed to assess the genetic diversity of wild populations. Genetic analysis of wild populations faces the issue of frequently working with low-quality non-invasive DNA samples such as faeces, hair, or feathers, particularly if the species in question is endangered or protected (Carroll et al., 2018; Taberlet et al., 1999). While sequencing the whole genome of each individual would be the most accurate and informative method, it is labour and time intensive, in addition to expensive and often unfeasible from low-quality samples (Ekblom and Wolf, 2014). To combat this, short marker sequences have been developed that can be amplified reliably from low-quality samples while providing highly informative genetic information (Schlötterer, 2004). The most prevalent of these markers are microsatellites or short tandem repeats (STRs) and single nucleotide polymorphisms (SNPs), each with their own benefits and pitfalls (Flanagan and Jones, 2019). SNPs, single base-pair differences between the genomes of two individuals, are an increasingly popular tool as they are found throughout the genome, have a lower error rate and are less expensive per marker than microsatellites (Weinman et al., 2015). However, SNPs require more markers to achieve the same statistical power as microsatellites, which can be of particular importance in smaller studies and lack cross-species amplifiability (Städele and Vigilant, 2016). Comparisons of each marker and their suitability for a wide variety of research questions have been discussed at length elsewhere (Flanagan and Jones, 2019; Guichoux et al., 2011; Hauser et al., 2021; Zimmerman et al., 2020) but microsatellites remain the method of choice for many researchers (Hodel et al., 2016; Hohenlohe et al., 2021).

1.2.1 Microsatellites as a genetic marker

Microsatellites are short DNA sequences, typically 100 – 400 base-pairs long which are comprised of short, tandem repeat motifs of 1 – 7 base-pairs, thought to be generated through replication slippage (Kelkar et al., 2010) and to escape repair mechanisms because they lie in non-coding regions (Bhargava and Fuentes, 2010). Microsatellites are therefore considered to be neutral markers, free from selection pressure (Ellegren, 2004). As a consequence of their elevated mutation rates (10^{-3} or 10^{-4} per locus per generation, compared to approximately 10^{-9} nucleotides per generation for nucleotide substitutions across eukaryote genomes), individuals exhibit variation in the number of repeated sequences, resulting in highly polymorphic markers (Li et al., 2002). Microsatellite markers are combined into panels with multiple markers to cover the breadth of the genome and accurately capture genetic diversity (Wang et al., 2021). The high levels of polymorphism per locus combined with codominance and Mendelian inheritance mean that approximately six times as many SNPs may be needed to elucidate parentage or sibships (Städele and Vigilant, 2016). Microsatellites also have high heterozygosity, allowing for the construction of pedigrees and dyadic relatedness even in species with a low genetic diversity (McLennan et al., 2018). The polymorphic nature and high power of microsatellites has therefore made them a popular tool in studies of kinship but they also have a wide range of further research applications (Guichoux et al., 2011; Vieira et al., 2016). One area is in conservation where microsatellites are used in managing captive populations in zoos (Fox et al., 2018) and in-situ efforts such as assessing inbreeding depressions, quantifying movements between fragmented populations and biodiversity monitoring (Galla et al., 2022; Hindrikson et al., 2017; Kerry et al., 2022; Wang et al., 2017). In addition, microsatellites are a key part of wildlife forensics to monitor the trade in illegally trafficked species and animal parts (Iyengar, 2014; Oklander et al., 2020) and for understanding the hybridization of species (Charpentier et al., 2012).

However, microsatellites are not without their issues (Putman and Carbone, 2014). Microsatellite genotyping was typically achieved by calculating the repeat number of STRs at loci via fragment length analysis (Ellegren, 2004). This led to only approximate lengths of microsatellites, with ambiguous results resolved by manual correction. Size homoplasies, where the alleles at the same loci are the same length but have a different flanking sequence, were unable to be detected (Vieira et al., 2016). In addition, polymerase chain reaction (PCR, used to amplify the target DNA from the sample) produced artifacts such as stutter peaks or off-target amplification that were difficult to detect with software and account for, resulting in a high level of researcher expertise being needed to correctly determine genotypes (Guichoux et al., 2011). Combined with the limited number of loci that could be analysed simultaneously, traditional microsatellite genotyping was a labour intensive and expensive process that generated inconsistent results between labs or different researchers (Pasqualotto et al., 2007).

Microsatellites also have high rates of null alleles and allelic dropout (Putman and Carbone, 2014) due to one of their properties that is also a strength. Microsatellite markers developed in one species can be amplified in phylogenetically related species (Barbará et al., 2007) allowing for research into recent evolutionary events or hybridisations (Van Wyk et al., 2018). In addition, the development of de novo primers or identifying microsatellite loci on the genome of a target species was expensive, often prohibitively so (Flanagan and Jones, 2019), thus the cross-species ability of microsatellites was a major bonus for many researchers. Microsatellites are identified and amplified by using primers, short lengths of DNA that bind to the flanking regions of the microsatellite and direct DNA amplification during PCRs (Selkoe and Toonen, 2006). Primers that work in one species were tested on a closely related species and if they were still able to bind and produce polymorphic alleles with Mendelian inheritance, used in the closely related species too (Roeder et al., 2009). For example, microsatellite loci designed for humans have been applied successfully in many catarrhine primates (Arandjelovic et al., 2009; Coote and Bruford, 1996) and cross-species amplification has been shown in bats, sharks, and wildebeest to name a few (Grobler et al., 2005; Maduna et al., 2017; Méndez-Rodríguez et al., 2018). However, if microsatellites are not highly conserved between species, null alleles occur when mutations in the flanking regions of the microsatellite prevent the primer from binding and the allele does not amplify (Selkoe and Toonen, 2006). Allelic dropout, by contrast, occurs if the target allele is too long due to mutations (more STRs added to the allele) and is no longer able to be amplified, which is a particular issue for low-quality DNA samples (Pompanon et al., 2005). Both of these result in the misclassification of individuals as homozygous instead of heterozygous, which can induce significant errors in parentage analysis (Dakin and Avise, 2004) and underestimate the genetic variation of a population (Šarhanová et al., 2018).

The final issue with the cross-species amplification of microsatellites is that research into the same species (or closely related species) was often carried out using different panels of microsatellites, hindering collaboration and comparison between researchers (Reiner et al., 2019). To understand the fitness consequences of sociality, it is important to be able to accurately assess kinship and to compare genetic patterns across populations. Microsatellites are a vital tool but their technical limitations present researchers with many well-known issues (Putman and Carbone, 2014). Recently, the development of new techniques such as genotype-by-sequencing (GBS) are being used to address these limitations.

1.2.2 Microsatellites in the modern era

GBS can ameliorate many of the issues associated with microsatellites. Instead of determining microsatellite genotypes by traditional fragment length analysis, the PCR products are sequenced, providing an accurate allele length and the DNA sequence itself instead of just the length of the amplicon (De Barba et al., 2017; Metzker, 2010). This allows for the detection of size homoplasies and assigning genotypes directly from the PCR amplicon, reducing genotyping error significantly (Zhan et al., 2017). In addition, as the data produced is DNA sequence information, it is independent of the sequencing platform and laboratory protocol allowing for easier comparisons between studies and labs. Efforts to apply GBS methods to microsatellite research have increased rapidly in recent years, with examples including European hedgehogs (*Erinaceaus spp.*) (Curto et al., 2019); flying squirrels (*Glaucomys oregonensis*) (Yuan et al., 2022); East African nile tilapia (*Oreochromis niloticus*) (Tibihika et al., 2019); and Arctic charr (*Salvelinus alpinus*) (Layton et al., 2020). This has been complemented by the development of bioinformatic software to aid with automating downstream analysis (Barbian et al., 2018; Huo et al., 2021; Roy et al., 2021).

Unfortunately, GBS does not address the problems of allelic dropout and null alleles, particularly in cross-species studies (Donaldson et al., 2020; Salado et al., 2021). Redesigning primers, changing their sequence to minimise mismatches with the target genome and to shorten the PCR product is the most efficient way to improve rates of dropout and null alleles (Fox et al., 2019). Designing and developing new primers used to be expensive (Abdelkrim et al., 2009) but the availability of reference genomes online and next-generation sequencing has reduced the cost significantly (Hodel et al., 2016). While online genetic data is not always available, particularly for rare or endangered species, using the wealth of genomic information online to adapt primers in silico is an underutilised method. Recent diverse examples range from the Blue-fronted Amazon (*Amazona aestiva*, Fernandes et al., 2019), bananas (*Musa spp.* Biswas et al., 2020) and big cats (Hyun et al., 2021) has shown that microsatellites can be improved by this, particularly if combined with GBS (Bradbury et al., 2018; Pimentel et al., 2018).

Given their advantages, microsatellite markers remain a popular tool for researchers studying primates (Arandjelovic and Vigilant, 2018). The vast majority of microsatellites used catarrhine primate research are based off human-derived markers, which have been applied effectively to investigate questions ranging from kinship to conservation (Charpentier et al., 2012; Dal Pesco et al., 2021; De Moor et al., 2020b; Kolleck et al., 2013). Human-derived microsatellites are typically not modified if they successfully amplified and were polymorphic in a given species (although see Inoue et al., 2016; Bradley et al., 2000; Engelhardt et al., 2017) but markers that did not work were dropped. As a result, there is a broad range of microsatellite panels currently in use for primates, each with slightly different properties and markers, making collaborative work and reproducible results difficult. For example, in studies of Guinea baboons (*Papio papio*) two panels of microsatellites have been used, one with 14 microsatellite loci on a population in Guinea-Bissau and one with 25 loci on a Senegalese population (Ferreira da Silva et al., 2014; Kopp et al., 2015). Although 13 loci were shared between the studies, differences in the genotyping procedure made it difficult to combine them and a sub-set had to subsequently be reanalysed with both procedures in order to achieve consistency between the datasets (Ferreira da Silva et al., 2018). Equally, cross-species or even cross-population comparisons are hindered when different panels are used, as was the case for two different chimpanzee (*Pan troglodytes*) populations (Newton-Fisher et al., 2010; Wroblewski et al., 2009) and in the *Macaca* genus where 31% of primers (12/39) selected from closely related species did not amplify in samples of crested macaques (*Macaca nigra*) (Engelhardt et al., 2017) and of those that did, one subsequently failed in my study species, the Assamese macaque (De Moor et al., 2020a).

While new microsatellite markers are being developed de novo (Chang et al., 2019; Liu et al., 2018), there is a need in primate research for microsatellite panels that have minimised the errors traditionally associated with them, while taking advantage of next-generation techniques such as GBS to improve the accuracy and quantity of data. As science becomes broader and even more collaborative, refined microsatellite markers combined with GBS, such as the one I present in Chapter 2 of this thesis, can be a key tool to further our understanding of the long-term fitness consequences of primate sociality and competition.

1.3 Short-term responses to sociality

The fitness effects of sociality have an impact over an extended period, shaping long-term outcomes such as an individual's lifetime reproductive success and group structure through generations. A classic example is in cercopithecine primates where female rank position is achieved and maintained through matrilineal kin alliances (Wrangham, 1980), so the indirect fitness benefits of supporting kin can determine group structure (Silk, 2007). However, individuals form, maintain, or change dominance ranks or affiliative relationships not because of long-term fitness outcomes but due to the immediate costs and benefits associated with them. Both agonistic and affiliative social relationships shape an individual's risk of predation (Hegner, 1985; Josephs et al., 2016), access to food (Carrascal et al., 1998; King et al., 2011) or thermoregulatory ability (Cunningham et al., 2017; McFarland and Majolo, 2013), which have long and short-term impacts. Other short-term impacts include access to the removal of ectoparasites through affiliative relationships (Dunbar, 1991; Zamma, 2002) and dominance ranks can determine the likelihood of injury (Pavez-Fox et al., 2022).

Similarly, navigating the challenges of competition with other group members is a daily occurrence (Borgeaud et al., 2016; Silk, 2007) and can induce short-term impacts for an individual by affecting their underlying hormonal response (Thompson, 2019). In vertebrates, a group of steroid hormones called glucocorticoids (GCs) are a key part of the stress response (Charmandari et al., 2004) and correlate to the dynamics of sociality and its associated challenges. As part of the vertebrate stress response, they therefore provide a pathway by which short-term physiological impacts of sociality can be generated.

1.3.1 Glucocorticoids and the vertebrate stress response

The stress response, in one form or another, has evolved in all organisms to cope with all types of challenges (Taborsky et al., 2021). In vertebrates, the hypothalamic-pituitary-adrenal (HPA) axis forms a major part of the stress response along with the sympathetic nervous system, and once activated promotes the release of glucocorticoids from the adrenal cortex (Smith and Vale, 2006). GCs are upregulated and released within minutes of a stressor, then gradually decrease to a baseline level in the course of a few hours via negative feedback (Selye, 1956). GCs are found in all vertebrate stress responses, with cortisol the primary form in most mammals (Ralph and Tilbrook, 2016). GCs have an allostatic function, allowing the body to respond to challenges or changes in their environment while simultaneously maintaining or returning to homeostasis (Romero et al., 2009), which is defined as "the maintenance of the internal environment within life-sustaining limits via physiological mechanisms" (McEwen, 2005). GCs are primarily metabolic hormones and during periods of increased energetic demand, such as in the face of a stressor, promote the mobilisation of stored energy to provide an organism with energy (in the form of blood glucose) to respond to a challenge (Creel et al., 2013). GCs simultaneously limit processes that have a less immediate benefit including those involved in somatic maintenance, energy storage, or growth (Charmandari et al., 2004; MacDougall-Shackleton et al., 2019). Equally, if the challenge is predictable, GCs can have a range of preparative actions including stimulating food intake, the building of fat reserves, and augmenting catecholamine production to respond to anticipated stressors (Landys et al., 2006; Sapolsky et al., 2000). A GC response can also aid with future stressors by helping to memorise the current challenging circumstance and response (Schwabe et al., 2012).

Given their broad function and central role in the stress response, GCs are a key mediator of the adaptive physiological response to many challenges above and beyond those caused by sociality. For example, GCs can help to regulate a reduced availability of food or overall energy intake (Laver et al., 2020; Touitou et al., 2021), respond to infections (Behie and Pavelka, 2013), and have been shown to correlate to temperature stress, particularly cold stress (de Bruijn and Romero, 2018) and predation risk (Clinchy et al., 2013). The link between GCs and energetic state has made them a popular tool for conservation studies where they are used as a proxy of population health (Newediuk and Bath, 2023) and are correlated to anthropogenic factors (Mentesana and Hau, 2022). The popularity of GCs is also driven by their ability to be quantified from non-invasive samples such as hair, urine, or faeces which enables their use in a wide range of wild populations, including those of conservation concern (Palme, 2019).

As they allow for the individual to effectively cope with (or prepare for) the challenge facing them, acute GC responses are thought to be adaptive in wild populations (MacLeod et al., 2023). However, if a stressor is significantly more intense, frequent, or unpredictable than normal, it can induce elevated GC levels that are either extreme or are sustained for an extended period of time (Sapolsky, 2021). In these circumstances an individual can be in a state of chronic stress or homeostatic overload, where the normally beneficial GC response starts to cause damage (Romero et al., 2009). This has been reported in captive settings, where elevated GCs are linked to negative health consequences (Hostinar et al., 2014). Chronic GCs can accelerate senescence through telomere attrition and increase the rate of oxidative damage (Angelier et al., 2018; Haussmann and Marchetto, 2010). Changes to DNA repair mechanisms as well as a greater risk of parasitic infection have also been correlated to chronic GCs (Flint et al., 2007; Gervasi et al., 2016). Recent evidence has suggested that the accumulation of harmful effects from chronic GCs, such as repeated wear and tear from neglecting somatic maintenance, can reduce survival in long-lived species (Schoenle et al., 2021).

With the possible exception of those in degraded or anthropogenically changed habitats (e.g. Boonstra et al., 2020), no wild populations as a whole appear to be under chronic stress (Dantzer et al., 2016; Dickens and Romero, 2013). However, as challenges are not equally distributed within a group or an individual’s lifetime, certain individuals may be under chronic stress for extended periods of time (Shively et al., 2023; Taborsky et al., 2022). As glucocorticoids are crucial for mounting an appropriate, adaptive response to stressors in a challenging environment (Romero & Beattie, 2022), the impacts of GCs on an individual are highly context dependent (Breuner et al., 2008). GC concentrations are regulated by negative feedback mechanisms (Vitousek et al., 2019), and the capacity to optimise GC exposure through elevating and down-regulating GCs is key for addressing environmental challenges (Lattin and Kelly, 2020). An elevated GC response could therefore either be adaptive or evidence of a potentially harmful homeostatic overload and so GC values cannot be used as direct proxies for fitness (Beehner and Bergman, 2017). The multi-functional nature of GCs means that they are not just “stress” hormones either (MacDougall-Shackleton et al., 2019) but they do provide a validated and well-studied method of tracking the responses to the stressors an organism faces (Beehner and Bergman, 2017).

For group-living animals, the challenges of sociality and within-group competition are both frequent and intense (Silk, 2007). In Wistar rats (*Rattus norvegicus domestica*), social defeat or victory in a variety of experimental setups induced stronger GC responses than many other physical stressors (Koolhaas et al., 2011) and social status has been consistently correlated with

GC responses across all vertebrate classes (Baker et al., 2013). GCs can therefore provide an insight into the competitive regime driving sociality and the associated short-term impacts.

1.3.2 Dominance ranks and Glucocorticoids: Cost of dominance or subordination?

The association between dominance status and glucocorticoids has been studied across a wide variety of species (Korzan and Summers, 2021), with early laboratory work on mice suggesting that subordinate or lower ranked individuals showed higher GC levels (Louch and Higginbotham, 1967). Since then extensive research, much of which comes from wild populations such as the pioneering work in olive baboons by Sapolsky and colleagues (Sapolsky and Ray, 1989), has shown that it is not dominance status per se that influences the GC response. Instead, in addition to factors such as the mating system (Creel, 2022), the underlying competitive regime that establishes the hierarchy drives the associated relationship with GCs. In vertebrates, this has crystalised into two hypotheses: the cost of dominance hypothesis and the cost of subordination hypothesis (Abbott et al., 2003; Goymann and Wingfield, 2004).

The cost of dominance hypothesis posits that if the acquisition and maintenance of a higher dominance rank is energetically expensive, then GC levels are predicted to have a positive relationship with dominance rank, with higher GC values expected in higher ranked individuals (Goymann and Wingfield, 2004). By contrast, the opposite relationship is predicted by the cost of subordination hypothesis, which posits that if dominance ranks are inexpensive to attain and maintain, GCs will have a negative relationship with dominance status and lower ranked individuals demonstrate higher GC levels (Abbott et al., 2003). Under this hypothesis, higher GCs correlate with subordinate positions due to limited access to food resources, or lack of control and social support in social interactions (Abbott et al., 2003; Sapolsky, 2005).

Which hypothesis the observed relationship between GC and rank matches is frequently related to the intensity of the rank competition (see contest potential in section 1.1.1), with more intense, direct competition imposing a greater energetic demand from the behaviours involved in rank competition. For example, aggression can be a saliently costly behaviour (Emery Thompson, 2017) and in species where dominance status is maintained through aggressive interactions, higher ranked individuals show elevated GC levels as has been suggested for some cooperatively breeding carnivores (Creel, 2022). In male rock hyraxes (*Procavia capensis*) an energetically costly "singing" behaviour is used in establishing the hierarchy and more dominant, singing males had higher GC production (Koren et al., 2008). On top of agonistic behaviours directly linked to rank competition, species with a higher contest potential can evolve expensive armaments (Emlen, 2008) or musculature (Setchell et al., 2006). Higher ranked individuals may also engage in a greater rate of reproductive effort (Pavitt et al., 2015) or other energetically demanding behaviours such as mate guarding, group defence, and anti-predator defence (Emery Thompson and Georgiev, 2014; Kitchen and Beehner, 2007; van Schaik et al., 2022). Alternatively, having a higher rank position could induce physiological stress as a consequence of the “behavioural state”, such as a readiness to fight or the threat of being challenged (Feng et al., 2016; Sands and Creel, 2004).

If rank competition is inexpensive, psychological stress can also be a key mechanism for the cost of subordination hypothesis, where lower ranked individuals are predicted to have higher GCs due to the stress of reduced access to food as well as less support in or control over social interactions (Sapolsky, 2005). In humans, people in leadership positions are shown to have lower levels of cortisol, linked to the control a leadership position confers to a person (Sherman and Mehta, 2020). Consistent with this, the more powerful and controlling a leader is, the lower their correlated hormonal response (Knight and Mehta, 2017; Sherman et al., 2012). A meta-analysis of group-living fish also reported that subordinate individuals tended to have to higher cortisol than dominants, thought to be driven by psychological stress (Bessa et al., 2021). Dominant individuals often use random acts of aggression directed down the hierarchy to intimidate subordinates (Silk, 2002). This lack of control and predictability over aggressive interactions is stressful and combined with less access to social support, results in an elevated GC response in subordinates, linked to the rates of aggression they receive (Abbott et al., 2003; Silk, 2002). There is strong evidence of this mechanism for the cost of subordination (Shively et al., 2023); including in meerkats (*Suricata suricatta*) where subordinate females had elevated GC secretions that were dependent on the rates of aggression directed to them by dominant females, if they lacked the support of close kin in their group (Dantzer et al., 2017).

The effect of differing competitive mechanisms driving dominance ranks is seen in primates and particularly for Cercopithecines, where there is a broad split (with some exceptions) in the correlation between dominance rank and GCs for adult males and females (Cavigelli and Caruso, 2015). Male primates typically compete aggressively for rank resulting in frequent changes to their agonistic relationships and ranks over time (Foerster et al., 2016). However, for many female primates, rank position is achieved and maintained through their matrilineal kin alliances (Wrangham, 1980), resulting in agonistic relationships that are relatively stable and low cost to maintain. Female primates can therefore show a negative correlation between rank and GCs whereas males of the same species have a cost of dominance, such as in chacma baboons (*Papio ursinus*). Higher ranked males had greater average GC production, likely driven by intense contest competition for ranks (Kalbitzer et al., 2015), with the opposite effect found in the female hierarchy (Seyfarth et al., 2012; Wittig et al., 2008).

In a review of GC patterns in primates, 12 out of 15 studies that report a direct correlation between dominance rank and male GC levels found evidence to support the cost of dominance hypothesis (Beehner & Bergman, 2017). Recent examples from Verreaux's sifakas (*Propithecus verreauxi*) (Rudolph et al., 2020); chimpanzees (*Pan troglodytes schweinfurthii*) (Muller et al., 2021) and rhesus macaques (*Macaca mulatta*) (Milich et al., 2018) have added further evidence of a positive correlation between high dominance status and GCs. However, the distinction between the two hypotheses may not always be clear cut. In yellow baboons, the alpha male had the highest GC levels due to engaging in frequent aggressive behaviours to maintain his rank which follows the cost of dominance hypothesis (Gesquiere et al., 2011). Outside of the alpha male, lower ranked males had greater GC secretion, which was suggested to be due to being targeted by higher rates of aggression, following the predictions of the cost of subordination (Gesquiere et al., 2011). The same pattern was reported in rhesus macaques (Milich et al., 2018) so alpha males can therefore have elevated rates of competition to maintain their position and unique GC responses. By contrast, egalitarian species with a low within-group competition for ranks, such as Tonkean macaques (*Macaca tonkeana*) may show no correlation between rank and physiological responses (Thierry et al., 2023). However, in general it is unusual for male primates to match the predictions of the cost of subordination hypothesis.

Of the three reported cases of a lower dominance rank correlating to higher glucocorticoids in male primates (Beehner and Bergman, 2017); one referred to the immediate effects of single aggressive interaction (chimpanzees, Wittig et al., 2015) and another was a pilot study in long-tailed macaques (*Macaca fasicularis*) where male ranks were not calculated but categorised into broad groups that confounded with age (van Schaik et al., 1991). Neither of these arguably demonstrated a true “cost of subordination” whereas the final example from my study species, Assamese macaques, does provide evidence for the hypothesis. Adult male Assamese macaque rank position was negatively correlated with concentrations of GCs during the mating season, suggested to be due to subordinates lacking social support and being targeted by more aggressive behaviours (Ostner et al., 2008a). An individual’s access to support is determined by both their dominance rank and affiliative relationships (Schino, 2007). Male Assamese macaques form and maintain social bonds with males of a similar rank (Kalbitz et al., 2016), who are subsequently allies in coalitionary aggressions for rank acquisition and maintenance (Schülke et al., 2010). The vast majority of coalitions were directed down the hierarchy at lower ranked individuals (Ostner et al., 2008a; Young et al., 2014c) suggesting that dominant males are more easily and frequently able to recruit support from their partners to help maintain their rank, driving the observed cost of subordination. Assamese macaques appear to be an exception to the pattern of GC responses and dominance ranks in male primates although there are some caveats to this conclusion (see

Section 1.4 on Assamese macaques). Through mediating access to social support, strong affiliative relationships can therefore mediate GC production in relation to dominance rank for group-living animals but can also have independent effects on an individual's physiological response to stressors.

1.3.5 Social Bonds and Glucocorticoids: Social Buffering

Numerous affiliative behaviours have been shown to correlate to GCs (Raulo and Dantzer, 2018) and a key pathway by which social bonds affect the hormonal response (and the associated costs and benefits thereof) is providing a reliable companion for social support (MacLeod et al., 2023). Social support (in a non-dominance hierarchy context) is a phenomenon where an individual benefits from the presence of a companion, either physically or emotionally (Cohen and Wills, 1985). A mechanism by which these benefits can occur is suggested by the *social buffering hypothesis*, which predicts that the presence of a close, bonded social partner attenuates the activation of the HPA axis and therefore reduces GC levels (Hennessy et al., 2009). For example, romantic partners can provide a buffering effect for men during stressful events like public speaking (Kirschbaum et al., 1995).

The social buffering hypothesis was derived from human (Gunnar and Hostinar, 2015) and laboratory studies (Davitz and Mason, 1955) where experiments initially focused on the ability of parent-offspring relationships or pair-bonds to buffer the HPA axis (Levine 2000; Masis-Calvo et al., 2018) but has since expanded to included social bonds between all group members (DeVries et al., 2003). Individuals with stronger affiliative relationships have greater predictability and stability in their dyadic social interactions and are therefore predicted to have a lower GC production overall (Cohen and Wills, 1985; MacLeod et al., 2023; Kikusi et al., 2006). The stronger the social bond to their partner, the greater the attenuation on physiological correlates is predicted to be (Kiyokawa and Hennessy, 2018). In addition to providing less stressful interactions, the presence of a bonded social partner or even just stimuli (auditory or visual) that evokes the partner can provide an attenuation on the GC response, along with active behaviours such as physical touch to reinforce the buffering effect (Lim and Hong, 2023; Wu, 2021).

Evidence for the social buffering effect of social bonds comes from a broad range of both domestic animals (Rault, 2012) and wild group-living species such as in fish (Gilmour and Bard, 2022), birds (Szipl et al., 2019), and mammals (Kusch et al., 2023; Woodruff et al., 2013). As might be expected given their gregariousness, primates were some of the first laboratory species studied for a social buffering effect (Coe et al., 1978) and remain among the most commonly studied wild taxa (Beehner and Bergman, 2017). Studies are predominantly on female primates, who are typically the philopatric sex and can access a network of bonded matrilineal kin for support (Clutton-Brock and Lukas, 2012; De Moor et al., 2020a). Evidence for an attenuated GC response from social bonds was reported in female chacma baboons who experienced an increase in GCs following the loss of a bonded partner (Engh et al., 2006) and later studies in the same population reported that females with fewer but stronger bonds had a buffered GC response (Crockford et al., 2008; Wittig et al., 2008). Similarly in Barbary macaques (*Macaca sylvanus*) and rhesus macaques, more dominant females showed reduced GC levels if they focused their affiliative behaviours on a few select bonded partners (Brent et al., 2011; Sonnweber et al., 2015). As the (usually) dispersing sex, bonds between male primates are often not as long lasting (Schoof and Jack, 2014; Schülke et al., 2023) and social buffering of the stress response may be less effective as result. Consistent with this, there is a paucity of evidence for social buffering in males, which has so far only been reported in two species, Barbary macaques and male-philopatric chimpanzees (Wittig et al., 2016; Young et al., 2014a). An attenuated GC response through social buffering could be a key mechanism by which the daily stressors of living and competing in a social group, such as those imposed by the energetic costs of dominance rank competition, could be ameliorated.

1.3.6 Social Stress and Glucocorticoids: The Seasonal Effect in Males

The costs of sociality are not consistent throughout an individual's life span, with highly stressful events such as migrating into a new group or integrating into the adult hierarchy correlating to GC upregulation (Akinyi et al., 2017; Marty et al., 2017). The frequency and intensity of group-wide social challenges also fluctuate and show strong temporal dynamics (Higham et al., 2013). For males in seasonally breeding species, the increase in social challenges corresponds to the mating season as females become sexually receptive and males compete to gain mating access (Clutton-Brock and Huchard, 2013). In order to maintain homeostasis, GCs are upregulated and elevated during the mating season compared to the non-mating season (Romero et al., 2017). This has been consistently reported across vertebrates (Baker et al., 2013) including primates (Charpentier et al., 2018a; Lynch et al., 2002; Ostner et al., 2008a; Rudolph et al., 2020).

There are two non-exclusive hypotheses that suggest a mechanism for how the additional demands of social competition generate elevated GCs. The *energy mobilisation hypothesis* predicts that during the mating season males have, on average, higher GCs than in the non-reproductive season due to the energetic costs of more competition (Romero, 2002). Competitive behaviours such as aggression (Gesquiere et al., 2011), mate guarding (Higham et al., 2011), and injuries (Cords and Arguelles, 2023) are more frequent during the mating season. Males also engage in an increased mating effort in general (Pavitt et al., 2015) and in many species use courtship behaviours to attract females (Woolley et al., 2004). All of these could impose an energetic cost on males and therefore the energy mobilisation hypothesis more specifically predicts that GCs will be upregulated when energetic behaviours are at their peak (Romero, 2002). For example, rates of mate guarding and aggression peak early in the mating season in some primates (Girard-Buttoz et al., 2014; Ostner et al., 2011) and GC peaks early in the mating season have been reported from rhesus macaques and Japanese macaques (*Macaca fuscata*) (Barrett et al., 2002; Milich et al., 2018).

Alternatively, the *preparative hypothesis* suggests that the upregulation in GC during the mating season could be due to a preparative phase, priming males for the upcoming period of intense competition (Sapolsky et al., 2000). The elevated GCs would act as a form of physiological preparation for the upcoming costs of competition (Sapolsky et al., 2000) and are therefore predicted to peak before rates of competitive or mating behaviours, such as in Eastern hellbender salamanders (*Cryptobranchus alleganiensis alleganiensis*) (Galligan et al., 2021). Evidence of preparative GC upregulation is more common in female primates (Fürtbauer et al., 2014) although there is some evidence in males. For example, long-tailed macaques showed maximal GC levels 1 to 2 months before the onset of the mating season (Girard-Buttoz et al., 2009).

Male primates living in social groups face a litany of challenges due to within-group competition and sociality. The demands of dominance rank and the seasonal stress of elevated competition over mating could be consequential for their long-term fitness; in addition to imposing physiological demands on homeostatic regulation, which the social buffering effect from strong affiliative relationships could modulate. In Chapter 3 of this thesis, I assess the correlated glucocorticoid response to sociality in a population of wild male Assamese macaques at Phu Khieo Wildlife Sanctuary (PWKS), Thailand.

1.4 Assamese macaques, sociality and GCs

Assamese macaques are cercopithecine primates, native to South and South-East Asia (Thierry, 2007). They are primarily arboreal and live in multi-male, multi-female groups with female philopatry and male dispersal prior to sexual maturity (Ostner et al., 2013; Schülke et al., 2011). Juvenile and subadult males emigrate from their natal group between three to seven years old and migrate repeatedly throughout their life (Anzà et al., 2022). The agonistic relationships of both sexes are structured into linear dominance hierarchies, with all adult males outranking adult females (Macdonald et al., 2013; Ostner et al., 2008a). Females form same-sex and male-female social bonds that provide an increased feeding tolerance or efficiency (Haunhorst et al., 2017, 2016; Macdonald et al., 2013). The male-female bonds also confer an increased mating opportunity for the males (Haunhorst et al., 2017; Ostner and Schülke, 2014). Assamese macaques are seasonal breeders with a distinct mating from October to February followed by a non-mating or birthing season from March to September (Heesen et al., 2013). Female fertility is concealed and receptivity is synchronised (Fürtbauer et al., 2011, 2010), making the monopolisation of females by high-ranked males difficult, which is reflected in a low alpha male paternity concentration (29%) (Sukmak et al., 2014).

The relatively low contest potential shapes the competitive behaviours used by the males in structuring the dominance hierarchy. Male Assamese macaques form and maintain strong affiliative bonds with males of a similar rank (Kalbitz et al., 2017, 2016) and compatible personality (Ebenau et al., 2019), independent of the presence of kin (De Moor et al., 2020b). Bonded males support each other in coalitionary aggressions that lead to rank acquisition and maintenance, which in turn predicts a greater reproductive success for both bonded partners over an extended time period (Schülke et al., 2010). Males still compete aggressively for dominance ranks, with individual aggressive tendencies partly explained by genetic variation (Gutleb et al., 2018). Males engaged in higher rates of aggression during the mating season for access to females which correlated to a spike in testosterone levels (Ostner et al., 2011, 2008a). In addition, male Assamese macaques use mate guarding behaviours, with high status males performing more, following a priority of access model (Ostner et al., 2011).

Following the cost of dominance hypothesis, the increased energetic demands of these behaviours would predict a positive relationship between dominance rank and GCs (Emery Thompson, 2017; Goymann and Wingfield, 2004), although there appears to be no energetic consequences from mate guarding (Schülke et al., 2014). However, during the mating season, adult male Assamese macaque rank position was negatively correlated with concentrations of GCs (Ostner et al., 2008a). The authors suggest this correlation was driven by lower ranked males being the target of more dyadic aggressive behaviours and crucially, lacking the social support that higher ranked males had (Ostner et al., 2008a). If ranks are inexpensive to maintain, a lack of social support is one of the primary mechanisms of the cost of subordination hypothesis (Abbott et al., 2003).

The vast majority of recorded coalitions were directed down the hierarchy at lower ranked individuals (Ostner et al., 2008a; Young et al., 2014b) indicating that dominant males were able to more easily and frequently recruit support from their bonded partners to help maintain their rank. Coupled with a relaxed within-group competitive regime, as shown by an alpha male paternity of only 29% (Sukmak et al., 2014), dominant Assamese macaques were suggested to be the exception to the cost of dominance hypothesis in male primates and have frequently been cited as such (Beehner and Bergman, 2017; Cavigelli and Caruso, 2015). However, this conclusion rests on a relatively short study with only six males and needs to be confirmed with a larger dataset to be more definitive.

Male Assamese macaques show seasonal fluctuations in social challenges, combined with strong social bonds and a highly unusual reported relationship between rank and glucocorticoids. The population in PWKS has been studied since 2005 (Schülke et al., 2011) and as such there is substantial longitudinal data on many individuals, groups, and their dynamic social interactions; making them an ideal candidate population to answer questions on the hormonal consequences of sociality.

1.5 Dynamic methods of sociality

There is a growing body of evidence to support that glucocorticoids can elucidate the short-term impacts of sociality and competition within vertebrates and in particular primates. An individual's sociality is not static, instead it is constantly changing either as a result of their own actions or those of their group members. Glucocorticoids are dynamic too, mediating homeostatic responses and phenotypic flexibility. Therefore, the dynamics of sociality and the associated costs of the stressors this generates should correlate to dynamic hormonal responses, in tandem with the temporal dynamics of GCs. However, dominance and affiliative metrics typically summarise and conjugate these changes into composite measures over a specific timeframe to represent relationships (Silk et al., 2013; Strauss and Shizuka, 2022), missing the social dynamics that occur (Mielke et al., 2017; Neumann et al., 2011).

The development of cardinal metrics has taken steps to quantify dynamic social changes; such as Elo ratings for dominance ranks or the dynamic dyadic sociality index (DDSI) for affiliative relationships that track sociality over time (Albers and De Vries, 2001; Mielke et al., 2017). These metrics take into account the history of social interactions within a group and between dyads, allowing for updates to rank position or affiliative relationships after each interaction (Goffe et al., 2018) and can help researchers to address hypotheses with greater precision. For example, Elo ratings, like other cardinal metrics, do not assume an equal distance between ranks but instead the difference between two individuals indicates the probability of the higher ranked individual winning the interaction (Levy et al., 2020b). Elo ratings are therefore suggested to be a better reflection of the competitive structure of a hierarchy and could more accurately depict the costs that individuals face, such as a narrowing of competitive ability or rank difference without a rank reversal (Foerster et al., 2016). These can impact on the associated physiological correlates but might not otherwise be detected. Similarly, the changes to social bonding and the subsequent dynamics of the social buffering effect, without major events such as swapping a preferred partner could also be assessed. This is of particular relevance for male primates as they aggressively compete for ranks and form non-kin social relationships that can impact on their competitive ability too. Cardinal metrics therefore present a method to highlight the fine-grain dynamics that produce costs and benefits of sociality for male primates, rather than aggregated scores that may hide temporal variation.

As with genetic methods in primatology, there is a need to improve and evolve how sociality is assessed to not only capture the dynamics of sociality but to standardise concepts, in order to facilitate cross-species and population research (Schülke et al., 2022). Both affiliative relationships and dominance ranks have been under reappraisal in recent years (Dehnen et al., 2022; Ellis et al., 2019; Ostner and Schülke, 2018; Strauss and Holekamp, 2019) and a major part of this has been to refine the multi-faceted nature of sociality and how to integrate information from dyadic interactions into individual level social metrics (Ellis et al., 2019). Comparisons of dominance rank methods and how to elucidate the competitive regime underpinning it have been focused on (Davidian et al., 2021) but at present, few steps have been made for social buffering in wild populations.

In research into the social buffering hypothesis, a wide variety of social metrics have been used to assess how social bonds affect GC values. For example, the combined strength value of an individual's top 3 relationships was used to examine social buffering in male Barbary macaques (Young et al., 2014a). By contrast, to test for the buffering of GCs in chimpanzees in the presence of a bonded partner, relationships were classified with a binary variable as either social bonds or not (Wittig et al., 2016) and a recent study of Black-tailed prairie dogs (*Cynomys ludovicianus*) used social integration as the metric for research (Kusch et al., 2023). Not only does this variety hinder cross-species comparisons but these metrics are integrated and combined over a defined time period, missing the dynamic nature of sociality. A recent examination of 16 different sociality metrics used to quantify affiliation in primate research and identified an independent social bonding dimension (Schülke et al., 2022). Broadly speaking, the social bonding dimension is the primary aspect of affiliative sociality that has been linked to an attenuated GC response with stronger bonds predicted to have a greater effect (Wu, 2021). In order to assess the interplay between changes in sociality and the social buffering effect, there is a need to have a dynamic measure that accurately captures the social bonding dimension. To do this I followed the methods of Schülke et al., 2022 and correlated 14 metrics that represent social bonding in my study species, Assamese macaques, and quantified a dynamic metric (ΔTopAff) that can be used to assess social buffering (see Chapter 3, further discussion in Chapter 4 and Appendix: Figures A1 – A10).

1.6 This thesis

In this thesis, I aim to address consequences of sociality from two directions. Agonistic and affiliative relationships play a crucial role in shaping an individual's long-term fitness but determining an individual's fitness can be complicated in wild animals with large social groups. In order to do so, the transmission of genetic material from one generation to the next needs to be tracked to assign parentage and to determine kin relationships (Städele and Vigilant, 2016). Microsatellites are a common marker for doing so in wild species due to their cross-species amplifiability and high heterozygosity but issues such as undetected allele variation, null alleles, or allelic dropout remain (Flanagan and Jones, 2019; Putman and Carbone, 2014). In Chapter 2, I aim to address these methodological issues and describe a refined panel of microsatellites, developed from an extensive literature review of published catarrhine microsatellites. The panel was optimised using available published catarrhine genomes and validated on both blood and faecal samples. Combined with genotype-by-sequencing, I aim to provide a tool to accurately and cost-effectively quantify the genetic variation within catarrhine primates, which can be of particular use for addressing the long-term fitness consequences of sociality.

Sociality also has more immediate impacts, such as through affecting the underlying physiological response (Thompson, 2019). Glucocorticoids are a group of steroid hormones that form part of the vertebrate stress response system and a high GC response can be indicative of either an appropriate, adaptive, response to a challenge or of a cost; with chronic stress causing homeostatic overload and somatic damage (MacDougall-Shackleton et al., 2019). Dynamics in social relationships are driven by the competitive regime that structure social groups and by examining hormonal responses, the more immediate costs, benefits, or consequences of competition and sociality can be elucidated. In Chapter 3, I examined correlated glucocorticoid responses to social dynamics in wild male Assamese macaques to further understand how sociality and competition can impact individuals in the short-term. By combining longitudinal, behavioural, and hormone data with dynamic cardinal metrics, I test the cost of subordination, social buffering, and energy mobilisation/preparative hypotheses in wild male Assamese macaques. I aim, firstly, to replicate analyses of Ostner et al., 2008, by providing evidence for the *cost of subordination* hypothesis across multiple years and groups, using a dynamic measure of dominance and competitive ability. Secondly, I investigate the social buffering hypothesis by assessing how the dynamics in strong relationships correlate to GC responses. Finally, I investigate the seasonal dynamics of GCs, testing the predictions of the energy mobilisation and preparative hypotheses.

Chapter 2: A refined panel of 42 microsatellite loci to universally genotype catarrhine primates

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ORIGINAL RESEARCH

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A refined panel of 42 microsatellite loci to universally genotype catarrhine primates

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Abstract

1. Microsatellite genotyping is an important genetic method for a number of research questions in biology. Given that the traditional fragment length analysis using polyacrylamide gel or capillary electrophoresis has several drawbacks, microsatellite genotyping-by-sequencing (GBS) has arisen as a promising alternative. Although GBS mitigates many of the problems of fragment length analysis, issues with allelic dropout and null alleles often remain due to mismatches in primer binding sites and unnecessarily long PCR products. This is also true for GBS in catarrhine primates where cross-species amplification of loci (often human derived) is common.
2. We therefore redesigned primers for 45 microsatellite loci based on 17 available catarrhine reference genomes. Next, we tested them in singleplex and different multiplex settings in a panel of species representing all major lineages of Catarrhini and further validated them in wild Guinea baboons (*Papio papio*) using fecal samples.
3. The final panel of 42 microsatellite loci can efficiently be amplified with primers distributed into three amplification pools.
4. With our microsatellite panel, we provide a tool to universally genotype catarrhine primates via GBS from different sample sources in a cost- and time-efficient way, with higher resolution, and comparability among laboratories and species.

KEYWORDS
apes, genotyping-by-sequencing, high-throughput sequencing, Old World monkeys, simple tandem repeats

1 | INTRODUCTION

Microsatellites have been and are still widely applied in various biological sciences including population genetics, kinship/pedigree analysis, human and wildlife forensics, linkage analysis, or disease association studies (e.g., Cunningham et al., 2001; Goodwin et al., 2011; Gulcher, 2012; Wasser et al., 2004). Population genetic information obtained by microsatellite genotyping is also

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important for monitoring wild populations in conservation contexts, for reintroduction programs or to refine captive breeding management (Arandjelovic & Vigilant, 2018; Norman et al., 2019). Microsatellites are also often the markers of choice to genetically characterize (wild) populations in order to determine degrees of population fragmentation and hybridization, dispersal patterns, mating systems, and reproductive success (e.g., Charpentier et al., 2012; de Moor et al., 2020; Ferreira da Silva et al., 2018; Kheng et al., 2017; McCarthy et al., 2020). The ongoing popularity of microsatellites is largely based on their high abundancy in animal genomes (Hamada et al., 1982; Tautz & Renz, 1984), the high levels of allelic diversity (Ellegren, 2000), and the possibility to amplify them across related species. Accordingly, microsatellites are preferred, for example over SNPs, because of their higher statistical power per locus and their cross-species amplifiability, particularly when applied to small sample size datasets as typically found in forensic and kinship studies (Barbian et al., 2018; Guichoux et al., 2011).

However, traditional microsatellite genotyping via fragment length analysis (FLA) using polyacrylamide gel or capillary electrophoresis has several disadvantages, such as fragment size homoplasy, allele calling difficulties (stutter and split peaks, off-target PCR products), laborious work and relatively high laboratory costs, as well as poor comparability of results among laboratories (De Barba et al., 2017; Guichoux et al., 2011; Pasqualotto et al., 2007). Even with attempts to improve PCR amplification and more accurate/reliable genotyping procedures (Arandjelovic et al., 2009; Buchan et al., 2005; Navidi et al., 1992; Sefc et al., 2003; Taberlet et al., 1996), many of the problems remained.

With microsatellite genotyping-by-sequencing (GBS) using high-throughput sequencing technologies most of the difficulties can be mitigated (Barbian et al., 2018; Johannesen et al., 2017; Pimentel et al., 2018; Vartia et al., 2016). For instance, with GBS the exact length of the microsatellite alleles can be determined, which is a typical problem of FLA genotyping, particularly when alleles differ by only one basepair (bp) (Barbian et al., 2018; Vartia et al., 2016). Moreover, the nucleotide sequence is revealed so that cryptic alleles (alleles with the same length but containing a nucleotide variant) can be detected, resulting in an increased number of alleles and consequently greater statistical power per locus.

Nevertheless, problems with null alleles due to relatively large PCR products and allelic dropout as a result of primers binding in unconserved regions remain with GBS (Pompanon et al., 2005). As many microsatellites can be cross-amplified in phylogenetically related species, primers designed for one species are often tested in related species and then applied if successfully amplified and informative (i.e., polymorph) (Barbara et al., 2007; De Barba et al., 2017). For example, various microsatellite loci characterized for humans can be successfully amplified in nonhuman catarrhine primates (Old World monkeys, apes) (Coote & Bruford, 1996; Ely et al., 1998; Kayser et al., 1996; Morin et al., 1998; Newman et al., 2002; Roeder et al., 2009; Smith et al., 2000) and have been used since then in numerous studies (e.g., Arandjelovic et al., 2014; Kopp et al., 2015; Minkner et al., 2018; Städele et al., 2019). Yet, attempts to reduce PCR product size or to adapt primers specifically to the study species have been rare (but see Bradley et al., 2000; Engelhardt et al., 2017; Inoue et al., 2016). Furthermore, various research groups use different panels of microsatellites preventing a direct comparison of results, particularly of measures such as genetic diversity and heterozygosity, which are important in a conservation context (Kolleck et al., 2013).

In our study, we aimed to establish a microsatellite panel to universally genotype catarrhine primates via GBS from different sample sources in a cost- and time-efficient way, with higher resolution, and comparability among laboratories and species. Therefore, we screened a total of 269 microsatellite loci, widely targeted in catarrhine primates, and designed conserved primers for 45 loci based on available catarrhine genomes. We then tested the new microsatellite panel in ten primate species representing all major lineages of Catarrhini and further validated their applicability to low-quality DNA samples using fecal samples of wild Guinea baboons (*Papio papio*).

2 | MATERIAL AND METHODS

2.1 | In silico selection of microsatellite loci

We screened 269 human microsatellite loci widely used in catarrhine population genetic studies. We extracted the human (GRCh38/hg38) sequence of each locus with 500 bp flanking regions from GenBank (https://www.ncbi.nlm.nih.gov/genbank/) and performed BLAT searches against the 16 available (status: 5 December 2018) nonhuman Catarrhini reference genomes (Table S1) using the UCSC (http://genome.ucsc.edu) or Ensembl (www.ensembl.org) genome browsers with standard settings. In addition, we checked the human sequence for repetitive elements (SINEs, LINES, etc.) in flanking regions using the RepeatMasker Web Server (http://www.repeatmasker.org/) with standard settings. We generated alignments for each locus containing the 16 nonhuman catarrhine species, the human, and the human repeat-masked sequences with Muscle 3.8.31 (Edgar, 2004) in SeaView 4 (Gouy et al., 2010) and added published primer sequences to the alignments.

Loci were selected for further analysis if they fulfilled the following criteria: (a) primer binding sites are not in repetitive elements thus increasing locus-specific amplifiability and reducing the risk of off-target PCR products particularly in multiplex PCR reactions; (b) primer binding sites are conserved among catarrhines so that loci can be universally amplified in this taxonomic group with >180 species (Mittermeier et al., 2013); (c) the microsatellite motif is relatively short (max. 150 bp) to allow small amplicon size (max. 250 bp) and increase locus amplification success from degraded DNA samples, such as fecal samples; and (d) loci are evenly (1–3 loci per chromosome) distributed throughout the genome (using the genomes of *Homo sapiens*, *Nomascus leucogenys*, *Macaca mulatta*, and *Chlorocebus sabaeus* as reference) to avoid potential linkage problems.

For loci which passed the selection criteria, we designed new primers using Primer-Blast (http://www.ncbi.nlm.nih.gov/tools/primer-blast/). To allow for multiplexing, primers were designed to have similar annealing temperatures. Locus specificity of primers was checked by BLAT search against the 17 available catarrhine genomes. As primer binding sites were not always fully conserved among the 17 catarrhines, primers of 21 loci were designed with wobble positions. To simplify library preparation for GBS, we added adapter nucleotide sequences to the 5′ end of the locus-specific primers (5′-ACACTCTTTCCCTACACGACGCTCTTCCGATCT-3′ to forward primers, 5′-GTGACTGGAGTTCAGACGTGTGCTCTTCCGATCT-3′ to reverse primers; locus-specific primers are provided in Table S2).

2.2 | Laboratory work

First, we tested in singleplex reactions for the locus specificity of selected primers and their universal applicability to catarrhine species in a panel representing all major lineages of catarrhines (Table 1). High-quality DNA from a male of each of the ten species was obtained from the Gene Bank of Primates at the German Primate Center. PCRs were performed in total volumes of 25 µl containing 1× Qiagen Multiplex PCR Master Mix (Qiagen), 0.4 µM of each primer, and 50 ng genomic DNA. Cycling conditions comprised of 15 min at 95°C, 30 cycles each with denaturation at 94°C for 30 s, annealing at 57°C for 90 s and extension at 72°C for 90 s, and a final extension step of 10 min at 72°C. All reactions were run together with no-template controls (NTCs) to check for contamination. PCR performance was checked on 2% agarose gels stained with ethidium bromide (Carl Roth GmbH). Sequencing of singleplex PCR reactions was omitted.

Next, we tested for the possibility of running multiplex PCR reactions to reduce overall laboratory work and costs. Therefore, we pooled either all 45 primer pairs in a single PCR reaction (1-pool approach) or divided them into five PCR reactions each containing nine primer pairs (5-pool approach) or three PCR reactions containing 18 and 2 × 12 primer pairs (3-pool approach; for rationale of pooling and locus exclusion see Results section). Amplifications were conducted as described for the singleplex PCRs (same PCR set-up, DNA samples, cycling conditions, NTCs), but with different primer concentrations (see Tables S3–S5 for pooling schemes and concentrations of single primers within pools). To minimize PCR errors, we ran PCR reactions in two independent replicates. PCR performance was again checked on 2% agarose gels. Replicate PCR products (including the NTCs) were pooled and then cleaned with the MinElute PCR Purification Kit (QIAGEN). DNA concentrations were measured with a Qubit 3.0 (Thermo Fisher Scientific) and 100 ng were subjected to indexing PCR. Indexing PCR was performed in total volumes of 25 µl containing 1× KAPA HiFi HotStart ReadyMix (Roche), 0.4 µM of each indexing primer and 100 ng purified PCR product. Cycling conditions comprised of 45 s at 98°C, 4 cycles each with denaturation at 98°C for 15 s, annealing at 62°C for 30 s and extension at 72°C for 30 s, and a final extension step of 1 min at 72°C. Subsequently, indexed PCR products were purified with the MinElute PCR Purification Kit (Qiagen) and ran on a Bioanalyzer 2100 (Agilent) to check for PCR performance and molarity. Libraries were diluted to a final concentration of 10 nM and then pooled and sequenced with 51 cycles forward and 251 cycles reverse on Illumina's MiSeq desktop sequencer.

To check for Mendelian inheritance and whether our new microsatellite panel is also applicable to low-quality and low-quantity DNA as typically extracted from fecal samples (Monteiro et al., 1997; Perry et al., 2010), we tested our panel in 12 fecal samples of wild Guinea baboons. The samples comprised of six males and two "families" each composed of a male, a female, and their known offspring. DNA from these 12 specimens was previously genotyped via FLA at 24 microsatellite loci (Dal Pesco, 2019). The amplification procedure and follow-up steps for the applied 3-pool approach were the same as described above, but the number of cycles in the initial amplification was increased to 40, the total DNA amount was increased to 200 ng, and each PCR was performed in triplicates (Barbian et al., 2018).

2.3 | Bioinformatic analysis

The data analysis was performed using the software package CHIIMP v.3.0.0 (Barbian et al., 2018). The raw data (FASTQ files) as well as all input files (config-file, sample-file, locus-attributes-file) are available in the online supplement resources. As our microsatellite

TABLE 1 Catarrhine species used to test the new microsatellite panel

Family	Subfamily	Tribe	Species
Hominidae	Homininae		*Pan troglodytes*
			Gorilla gorilla
	Ponginae		*Pongo abelii*
Hylobatidae			*Hylobates lar*
Cercopithecidae	Colobinae	Presbytini	*Trachypithecus obscurus*
			Pygathrix nemaeus
		Colobini	*Colobus guereza*
	Cercopithecinae	Cercopithecini	*Cercopithecus diana*
		Papionini	*Papio papio*
			Macaca mulatta

TABLE 2 Number of amplified loci and alleles, as well as the level of heterozygosity per species generated in three approaches with high quality DNA (blood) and degraded DNA from fecal samples

	High-quality DNA			Degraded DNA
	5-pool approach (45 loci)	1-pool approach (45 loci)	3-pool approach (42 loci)	3-pool approach (42 loci)
Mean number of loci amplified per sample/species (range)	40.2 (37–43)	25.9 (21–32)	37.8 (33–41)	38.8 (35–41)
Mean number of alleles amplified per sample/species (range)	60.1 (53–69)	36.9 (31–45)	55.5 (46–68)	52.2 (47–56)
Mean level of heterozygosity per sample/species (range)	49.8% (23.3%–69.4%)	43.5% (22.6%–71.4%)	47.1% (19.5%–66.7%)	34.3% (23.1%–47.4%)[a] 46.3% (31.0%–64.3%)[b]

[a] Including all 42 loci.

[b] Including only the 32 loci that were polymorphic in the study species.

panel included several di-repeat loci, which stutter more frequently than tetra-repeats, we increased the stutter count ratio to 0.70 (stutter.count.ratio_max: 0.7). We further implemented a broad range of possible allele lengths in the locus attributes by setting the length buffer to 100 bp. This ensured the inclusion of all tested species even if the allele sizes at a given locus varied between species according to the available reference genomes. The minimum number of reads per locus was set to 100 (counts.min: 100). All other parameters were set to default.

With the current version of CHIIMP, wobble positions in primer sequences cannot be accounted for. Hence, for loci with a wobble position in a primer sequence, alternative nucleotides of the wobble are erroneously recognized as different alleles. Moreover, the repeat motif needs to be specified in CHIIMP, but as repeat motifs can vary in the investigated species, correct (orthologous) reads remain unrecognized for some species if CHIIMP is fed with a wrong repeat motif. Due to these reasons, the output for all loci was checked manually and corrected if needed. Additionally, we screened the processed reads for the general level of amplification per locus and the occurrence of PCR artifacts (off-target amplification, primer dimer, false primer pairings, etc.).

3 | RESULTS

3.1 | In silico selection of microsatellite loci

In total, 217 of the 269 investigated loci were not optimal for microsatellite genotyping of catarrhines. For 147 of them, one or both primer binding sites or the complete locus were located in repetitive elements. This increases the likelihood to amplify various off-target PCR products, particularly in multiplex settings when many primers that can bind multiple times in the respective genome are combined in a single PCR reaction. For an additional 32 loci, we could not find conserved primer binding sites near the microsatellite and a further 15 loci contained relatively long microsatellite repeat regions for one or more species, resulting in long PCR products (>250 bp). Longer PCR products are often difficult to generate if only degraded DNA material is available and can result in null alleles. Further problems included, for instance, the location of loci directly next to each other on the same chromosome and thus increasing the risk of linkage. Additionally, double entries of loci under different names or gaps in some of the reference genomes (especially for Y-chromosomal loci) impeded the screening process. A full list of screened loci including the respective reasons for their exclusion is provided in Table S6. Of the 52 loci which fulfilled our criteria, we selected 45 (1–3 loci per human chromosome including gonosomes) for downstream analyses. The chromosomal locations of the chosen loci in the genomes of *H. sapiens*, *N. leucogenys*, *M. mulatta*, and *C. sabaeus* are provided in the supplement (Table S2). We found no indication for the presence of linkage between any of the loci in any of the four investigated species (minimal distance between two loci 5.35 million bp).

The newly designed primers for the 45 loci (consisting of di-, tri-, and tetra-repeats) amplify PCR products between 56–215 bp (according to available genome data; Table S2). Compared to the original published primers, we were able to reduce PCR product sizes by 2–225 bp (mean 75.9 bp) in 37 loci whereas for five loci, the new primers amplify a moderately longer fragment (elongation by 2 – 15 bp; mean 7.6 bp). PCR product size for the remaining three loci did not change. As primer binding sites were not always perfectly conserved among the 17 investigated catarrhine reference genomes, primers for 21 loci contain wobble positions. Mismatches in primer binding sites, found only in a few (1–2) of the investigated species, were neglected in primer design and probably result in less efficient or no amplification of the respective locus in the given species (0–12 loci with mismatches per species, mean 3.4; Table S2).

3.2 | Singleplex PCR test

Singleplex PCR reactions of the 45 loci in ten species representing all major lineages of catarrhines were run on agarose gels and resulted, for all loci and species, in PCR products within the expected size range with no signs of amplifying any off-target PCR products (data not shown). Thus, locus specificity and universal applicability of our primer set to catarrhine primates was indicated.

3.3 | Multiplexing approaches

Sequenced alleles ranged in size from 71 bp (D3s1768) to 211 bp (D12s372) and nine loci contained cryptic alleles in at least one species (Tables S7–S10). The level of amplification and obtained sequence reads varied across samples/species and loci in all three approaches. The amplification of all loci in one pool (1-pool approach) was least effective, resulting in the lowest number of amplified loci (mean 25.9) and alleles (mean 36.9; Table 2). In some cases, the reason for allelic dropouts could be attributed to wrong primer pairing/primer mismatches (primer dimer or off-target amplification of short products). Most loci amplified less efficiently than in the other two approaches and some ($N = 11$) failed to amplify at all. Only nine loci recovered the same number of alleles as in the 5-pool approach. Interestingly, even though the number of amplified alleles was reduced from a mean of 60.1 to 36.9 compared to the 5-pool approach, the level of heterozygosity was not affected to the same extent with a reduction from 49.8% to 43.5% (Table 2).

The best results, that is, the highest amplification levels for loci (mean 40.2) and alleles (mean 60.1), were generated applying the 5-pool approach (Table 2). Nevertheless, we observed again primer dimers and short off-target PCR products potentially as a result of interacting primers from different loci. Moreover, three loci (D11s1366, D12s67.2, and D15s1007) neither amplified in the 1-pool nor in the 5-pool approach and were excluded from further testing. To further improve amplification success and to reduce primer interactions among primers of different loci (based on the knowledge obtained from the 1-pool and 5-pool approaches), we distributed the 42 remaining loci into three amplification pools containing 18, 12 and 12 loci, respectively (Table S5). Using the 3-pool approach, we were able to largely minimize primer interactions, but amplification success for loci (mean 37.8) and alleles (mean 55.5) per species was slightly reduced compared to the 5-pool approach, but higher than in the 1-pool approach (Table 2). The reduced amplification success was due to allelic dropouts of single alleles or whole loci in some species (see Table S9).

3.4 | Degraded DNA samples

For the degraded DNA samples, we applied the 3-pool approach as this represented the best compromise between amplification efficiency and laboratory effort and costs (see Results Multiplex approaches). The amplification from fecal samples was successful except for four (out of 42) loci (two autosomal and two gonosomal loci; Table S10). The number of loci and alleles amplified per sample was comparable to the results obtained from high-quality DNA samples (Table 2). However, 10 of the 42 amplified loci were monomorphic in our *P. papio* population, that is, all twelve individuals showed the same allele. The remaining 32 loci showed a level of 46.3% heterozygosity (Table 2).

All autosomal loci were in accordance with Mendelian inheritance besides D7s503 and D13s1291. For D7s503, the two alleles with the highest read counts for male MRX (99/109) did not match one of the two alleles of his offspring THL (111/113; mother MMI: 103/113). A closer look at the data revealed that MRX also had many reads for allele 111 (only 23 reads less than for allele 109), indicating that the allele 109 of MRX was likely an overamplified stutter sequence. A genotype with the allele combination 99/111 also corresponds to the genotype derived from FLA for this locus (152/164; 12bp distance between alleles, based on >20 amplifications; Dal Pesco, 2019). For D13s1291, the two alleles of male MLK (130b/132b) did not match with his offspring PTC (130a/132a; mother LCY: 128/130a). MLK was the only individual with these two potential cryptic alleles (each with a G→A point mutation) and further showed reads with 130 and 132 bp length without this mutation. At this point, we can neither exclude the occurrence of a PCR artifact in this particular case, nor that this locus does not follow the rules of Mendelian inheritance.

4 | DISCUSSION

From a set of 269 microsatellite loci widely applied in catarrhine primates, we selected a total of 45 loci that can be universally applied to genotype catarrhine primates. Due to the relatively small amplicon sizes, even low-quality DNA could be genotyped and since the selected loci were evenly distributed throughout the genome (at least according to the human genome), the risk of linkage was significantly reduced. Moreover, our panel could be multiplexed to a great extent. The testing of different multiplex settings revealed that a 5-pool approach produced the best result, but that a 3-pool approach containing one pool of 18 and two of 12 loci is the best compromise between locus amplification efficiency and laboratory effort and costs.

We tested the panel with high-quality DNA samples from all major lineages of catarrhines in multiplex settings and revealed successful amplification rates of 33 to 41 (average 38) loci per species (Table 2). We additionally showed the applicability of the 3-pool approach to degraded DNA samples such as fecal samples, which is a common material in many noninvasive wildlife studies (Carroll et al., 2018; Waits & Paetkau, 2005). The results for fecal samples were similar to the results of the high-quality samples with respect to the mean number of loci and alleles amplified per sample (Table 2). All loci, besides D13s1291, were in accordance with Mendelian inheritance, demonstrating the suitability of the new microsatellite panel for kinship and relatedness analyses. To ensure high-quality genotypes from fecal samples, and depending on DNA quality, further adaptions to the protocol might be necessary. Quantifying the endogenous DNA content via quantitative PCR prior to genotyping will help to select only those samples with sufficient endogenous DNA content (e.g., >25 pg endogenous

DNA as suggested by Barbian et al., 2018). Additionally, multiple samples per individual can be analyzed or the number of PCR replicates per sample can be increased.

Through multiplexed GBS, cryptic alleles can be detected (Barbian et al., 2018; Sarhanova et al., 2018; Vartia et al., 2016), and even in our test panel of only ten catarrhine species with one individual each, we found cryptic alleles at nine loci (Tables S7–S10). Although our results are based on only two or three replicates per approach (depending on the sample type) and hence should be interpreted with caution, we are confident that these alleles are indeed cryptic alleles and not PCR artifacts. In case of PCR artifacts, we would expect mixed sequence reads showing more than two alleles or highly imbalanced sequence read counts for the "true allele" and the "artifact allele," as it is highly unlikely that the same PCR artifact occurs in all replicates. As more individuals per species get tested, the number of cryptic alleles will most likely increase and provide further accuracy and a higher statistical power of our panel.

Another advantage of GBS is that the resulting genetic data, in form of allele sequences, are independent of the used sequencing platform. Thus, data produced by different laboratories can be easily shared and compared. By applying validated bioinformatics pipelines, such as the CHIIMP pipeline (Barbian et al., 2018), one can further ensure that the resulting data are reproducible and less prone to arbitrary allele calling by different researchers while still allowing the customization of, for example, filtering parameters to fit different datasets.

Although we recommend the 3-pool approach, the amplification success of individual loci can be improved, for example, by amplifying all loci in individual reactions and then pooling before or after the indexing PCR. However, this would largely increase workload in the laboratory and costs. It is also important to check which loci are polymorphic in the species of interest, so that monomorphic loci can be excluded from large-scale population genetic investigations. Likewise, as several species exhibit mismatches in primer binding sites (0–12 loci with mismatches per species), primer design for a given species can be adjusted and optimized, which becomes easier to do with an increasing number of sequenced catarrhine genomes.

In summary, with our microsatellite panel, we provide a tool to universally genotype catarrhine primates via GBS from samples of varying DNA quality in a cost- and time-efficient way, with higher resolution, better comparability among laboratories, and largely mitigated problems of traditional FLA.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTION

Franziska Trede: Investigation (equal); Writing-original draft (equal); Writing-review & editing (equal). **Niels Kil:** Investigation (equal); Writing-review & editing (equal). **James Stranks:** Investigation (equal); Writing-review & editing (equal). **Andrew Jesse Connell:** Software (lead); Writing-review & editing (equal). **Julia Fischer:** Funding acquisition (equal); Writing-review & editing (equal). **Julia Ostner:** Funding acquisition (equal); Writing-review & editing (equal). **Oliver Schülke:** Funding acquisition (equal); Writing-review & editing (equal). **Dietmar Zinner:** Writing-original draft (equal); Writing-review & editing (equal). **Christian Roos:** Conceptualization (equal); Investigation (supporting); Writing-original draft (equal); Writing-review & editing (equal).

DATA AVAILABILITY STATEMENT

The sequencing data have been submitted to the NCBI Sequence Read Archive (SRA) under BioProject number PRJNA672243 (http://www.ncbi.nlm.nih.gov/bioproject/672243). Input files for the bioinformatics analysis (config-, sample-, and locus-attributes-files) are available online in the supporting information (Appendix S1).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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Chapter 3: The dynamics of sociality and glucocorticoids in wild male Assamese macaques

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Abstract

For males of gregarious species, dominance hierarchy status and the strength of their affiliative relationships can have major fitness consequences. Social dynamics also impose costs by affecting glucocorticoids, key mediators of homeostasis and indicators of the physiological response to challenges and within-group competition. We investigated the relationships between dominance rank, social bonds, seasonal challenges, and glucocorticoids in wild Assamese macaques (*Macaca assamensis)* at Phu Khieo Wildlife Sanctuary, Thailand, combining behavioural data with more than 4,100 faecal samples from 62 adult males collected over 15 years. Our previous work on this population suggested that increased competition during the mating season induced elevated glucocorticoids and that, unusually for male primates, lower rank position correlated with higher glucocorticoids (cost of subordination). With a much larger dataset and dynamic measures of sociality, we re-examined these relationships and tested for an association between social bonding and attenuated glucocorticoids (social buffering hypothesis). Contrary to our prediction and previous work, dominance rank had a positive relationship with glucocorticoids, as high status correlated with elevated glucocorticoids. We demonstrated a social buffering effect in males and showed that dynamics in affiliative relationships can correlate with dynamics in physiological responses. Glucocorticoids were upregulated at the onset of the mating season, replicating our previous study. Taken together, our results suggest that even in a relaxed competitive regime, high dominance status can impose physiological costs on males that may potentially be moderated by social relationships. We highlight the need to consider the dynamics of sociality and competition that influence hormonal processes.

KEYWORDS

Glucocorticoids; dominance; social bonds; social buffering; seasonality; male-male competition; primates

Introduction

In group-living animals, dominance ranks and affiliative relationships play a crucial role in shaping an individual's fitness with a high dominance rank, central position in the affiliation network, and access to supportive affiliative ties or social bonds, resulting in increased mating or reproductive success (Ostner and Schülke, 2018; Silk, 2007; Snyder-Mackler et al., 2020; Thompson, 2019). The extent to which the benefits of dominance and affiliative relationships are associated with costs can be investigated by quantifying the underlying hormonal responses (Abbott et al., 2003; Cohen and Wills, 1985; Goymann and Wingfield, 2004). Here, we demonstrate the allostatic load of dominance and the potential for buffering effects of close affiliative relationships. In a longitudinal study, we quantify HPA axis activity from faecal glucocorticoid metabolite levels and explicitly track the dynamic nature of social relationships by employing Elo-rating for both dominance and affiliation.

In vertebrates, glucocorticoids (GCs) correlate with aspects of sociality such as social isolation, affiliative relationships, and dominance rank (Beehner and Bergman, 2017; Seyfarth et al., 2012). GCs are metabolic hormones that act as a physiological response to decreased energy availability or increased demand (MacLeod et al., 2023). They are upregulated during periods of increased energetic need to promote mobilisation of stored energy while simultaneously limiting processes with less immediate benefits such as energy storage or growth (MacDougall-Shackleton et al., 2019), allowing an individual to return to homeostasis (Creel et al., 2013). At sustained elevated concentrations, when an individual is under chronic physiological stress or "homeostatic overload" (Romero et al., 2009), GCs can cause adverse health effects (Hostinar et al., 2014). Elevated GCs have also been associated with reduced survival in long-lived species, suggesting an accumulation of negative effects from chronic stress or repeated wear and tear as somatic maintenance is neglected (Campos et al., 2021; Schoenle et al., 2021). Despite this, it has been argued that wild populations may not be chronically stressed to the same extent as captive populations, or if they are, their stress responses are still adaptive and fitness promoting (Boonstra, 2013).

Agonistic dominance

The links between HPA axis activity and dominance or affiliation were conceptualised in separate bodies of literature. The directionality of the association between dominance rank and GCs has been theorised in two hypotheses: the costs of dominance and the costs of subordination hypotheses (Abbott et al., 2003; Goymann and Wingfield, 2004). While higher social status is associated with numerous benefits such as preferential access to resources, reduced predation risk, improved health, and ultimately increased reproductive success and longevity (Bulger and Hamilton, 1987; Krause, 1994; Snyder-Mackler et al., 2020); the physiological costs or benefits of a high rank are thought to vary depending on the type of competitive regime that underlies the rank position. If acquiring and maintaining a higher dominance rank is energetically costly, then GC levels are expected to increase with dominance rank (*cost of dominance* hypothesis (Goymann and Wingfield, 2004)). For example, in male rock hyraxes (*Procavia capensis*) who use an energetically costly (and predator attracting) singing behaviour, dominance was positively correlated with GC production (Koren et al., 2008).

Opposite effects are predicted by the *cost of subordination* hypothesis (Abbott et al., 2003). If dominance ranks are inexpensive to attain and maintain, higher GCs are predicted to correlate with subordinate positions, due to a lack of social support in agonistic interactions and a lack of control, because dominants use random acts of aggression to intimidate subordinates (Abbott et al., 2003; Sapolsky, 2005; Silk, 2002). Subordinate female meerkats (*Suricata suricatta*), for example, had elevated GC secretions that were dependent on the rates of aggression directed to them by dominant females, if they lacked the support of close kin in their group (Dantzer et al., 2017). Together these two hypotheses highlight that the competitive regime generating the dominance hierarchy, rather than rank position itself, influences rank-differential HPA axis activity.

In group-living primates, males typically compete aggressively for dominance, resulting in frequent changes to their agonistic relationships and dominance ranks over time (Foerster et al., 2016). In a review of primate endocrinological field work, the vast majority (12 out of 15) of studies that found a direct relationship between dominance rank and male GC levels reported a positive correlation (Beehner & Bergman, 2017), and more recent studies have confirmed this pattern (Milich et al., 2018; Muller et al., 2021; Rudolph et al., 2020). In addition to agonistic behaviours directly involved in dominance competition, higher ranking males often engage more in energetically salient behaviours such as group defence (Kitchen and Beehner, 2007; Wittig et al., 2016), anti-predator defence (van Schaik et al., 2022), or mate guarding (Ostner et al., 2011), which have been shown to be associated with increased GCs (Emery Thompson and Georgiev, 2014; Girard-Buttoz et al., 2014). The strength of the relationship between rank and energetic demand is also determined by the intensity of direct mating competition between males, conceptualised as monopolisation or contest potential (Emlen and Oring, 1977). Contest potential depends on a single male's ability to monopolise fertile females against rivals, which itself is dependent on both female reproductive synchrony and the number of males present in a group (Cowlishaw and Dunbar, 1991; Gogarten and Koenig, 2013; Mitani et al., 1996; Ostner et al., 2008c). The stronger the male-male competition, the higher the potential benefit of increased energy mobilisation and dominance status which, in evolutionary terms, has to counter-balance the detrimental effects of homeostatic overload. In sum, the energetic demands of rank competition, mate defence, and male services make dominance physiologically costly for males in most primate species (Beehner and Bergman, 2017; Goymann and Wingfield, 2004).

Affiliation

One way to alleviate the costs of sociality is via social support. Beyond its role in explaining the direction of the dominance rank-GC relationship discussed above, social support can be defined as a phenomenon whereby an individual benefits either physically or emotionally from the presence of a companion (Cohen and Wills, 1985). A mechanism by which these benefits can occur is proposed by the *social buffering hypothesis*, which predicts that the presence of a close partner attenuates the activation of the HPA axis and therefore reduces GC levels (Hennessy et al., 2009). In a group context, individuals with stronger affiliative relationships have greater predictability or stability in their social interactions and are therefore predicted to have a lower GC production because they can rely more on their companions (Cohen and Wills, 1985; MacLeod et al., 2023). The presence of a social partner or even just sensory stimuli that evokes the partner can provide passive support, complemented by active behaviours such as physical touch to reinforce the buffering effect (Wu, 2021). The stronger the affiliative relationship with the social partner, the greater the attenuation on physiological correlates is predicted to be (Kiyokawa and Hennessy, 2018).

The social buffering hypothesis was derived from human (Gunnar and Hostinar, 2015) and laboratory studies (Masis-Calvo et al., 2018), with research initially focused on the role of parent-offspring relationships or pair-bonds, but has since expanded to include social bonds between other group members. Evidence for social buffering comes from wild group-living fish (Gilmour et al., 2022), birds (e.g. Greylag geese (*Anser anser*) (Szipl et al., 2019)), and mammals (e.g. Black-tailed prairie dogs (*Cynomys ludovicianus*) (Kusch et al., 2023) and colonial tuco-tucos (*Ctenomys sociabilis*) (Woodruff et al., 2013)). Given their pronounced gregariousness, primates are among the most commonly studied taxa in social buffering research (Beehner & Bergman, 2017). Studies are particularly prominent on female primates, as they are typically the philopatric sex and can rely on a network of supportive, genetically related partners (Clutton-Brock and Lukas, 2012; De Moor et al., 2020a). Indeed, evidence supporting a buffering effect of female social bonds comes from chacma baboons (*Papio ursunis*) (Crockford et al., 2008; Engh et al., 2006; Wittig et al., 2008) and macaques (Brent et al., 2011; Sonnweber et al., 2015). If bonds are formed among primate males, as the dispersing sex they are typically are not as long lasting (Schoof and Jack, 2014; Schülke et al., 2023) and social buffering of the stress response may consequently be less effective for male partners. Consistent with this, evidence for social buffering in males has so far only been found in two primate species, Barbary macaques (*Macaca sylvanus*) and male-philopatric chimpanzees (*Pan troglodytes schweinfurthii*) (Wittig et al., 2016; Young et al., 2014a).

Seasonality

Social challenges may occur in seasonally reproducing species with predictable dynamics, as competition for access to mates (Higham et al., 2013; Ostner et al., 2008b) and increased infanticide risk (Ostner et al., 2008b) are concentrated in a few months of the year. During the mating season, rates of energetically costly behaviours are increased such as aggression (Gesquiere et al., 2011; Pappano & Beehner, 2014), mate guarding (Higham et al., 2011), and overall mating effort (Pavitt et al., 2015), leading to an increased frequency of injuries (Cords and Arguelles, 2023). Therefore, following the *energy mobilisation hypothesis* (Romero, 2002), during the mating season males are predicted to have, on average, higher GCs compared to the non-reproductive season. This has been consistently reported across vertebrates (Casagrande et al., 2018; Romero et al., 2017), including primates (Charpentier et al., 2018; Lynch et al., 2002; Ostner et al., 2008a; Rudolph et al., 2020). However, the frequencies of energetically demanding behaviours are not consistent throughout the entire mating season. In primates, spikes of aggressive behaviour often occur early in the mating season, male immigration increases the potential for conflict, and rates of mate guarding peak (Borries, 2000; Cords, 2002, 2000; Girard-Buttoz et al., 2014). Therefore, the *energy mobilisation* hypothesis more specifically predicts a sharp rise in GC concentrations during the peak of costly behaviours, which frequently occur at the start of the mating season.

The increase in GC could also be due a preparatory phase; increasing GC levels may mobilise energy before the onset of the mating season to prime males for the period of intense competition to come, as has also been suggested for testosterone (*preparative hypothesis* (Brockman and van Schaik, 2009; Sapolsky et al., 2000). Long-tailed macaques (*Macaca fascicularis*), for example, exhibit maximal GC levels one to two months before the onset of the mating season (Girard-Buttoz et al., 2009). Thus, seasonally breeding primates may show short-term dynamic responses to mating competition in addition to the broad mating to non-mating season split in average hormonal responses. The temporal dynamics of GCs can act synergistically with the correlates of both dominance rank and affiliative relationships, compounding the costs of dominance or subordination and highlighting the role of social buffering in homeostatic regulation.

Assamese macaques

Contrary to the general trend across primate species (Beehner & Bergman 2017), in our study species, the Assamese macaque (*Macaca assamensis*), dominance rank was negatively rather than positively associated with GCs in adult males (Ostner et al., 2008a). Assamese macaques are seasonal breeders, with mating and mate-guarding behaviours restricted to a 4-month period during which rates of male-male aggression are increased (Ostner et al., 2011, 2008a). To explain why dominance rank is not positively associated with GCs, it has been argued that the competitive regime may provide adult males with sufficient agonistic support and rank stability that the burden of competition falls on the subordinates who receive most of the aggression. As a crucial part of the competitive regime, males of the study group were found to form differentiated affiliative relationships or social bonds with each other (Kalbitz et al., 2016), that were formed somewhat independently of kinship (De Moor et al., 2020b). These bonds functioned as longer-term agonistic alliances such that strongly bonded males were more successful in attaining and maintaining high dominance positions (Schülke et al., 2010). However, the vast majority of coalitions were directed down the hierarchy at lower ranked individuals to stabilise the hierarchy at the expense of subordinates (Ostner et al., 2008a; Young et al., 2014b). Here, we aim at replicating the initial analyses with a markedly larger data set from several different groups of the same population.

Relationship dynamics

An individual's sociality is not static; instead it is constantly changing either as a result of their own actions or those of other group members. The HPA axis is a dynamic system too, mediating homeostatic responses and phenotypic flexibility. There are numerous examples where a single change in sociality predicts a change in GCs, such as the sudden loss of a strong affiliative relationship resulting in higher GCs in female chacma baboons (Engh et al., 2006). However, dominance and affiliation metrics typically summarise and conjugate these changes into composite measures over a specific timeframe to represent relationships (Silk et al., 2013; Strauss and Shizuka, 2022), missing the social dynamics that occur (Mielke et al., 2017; Neumann et al., 2011). Recently developed sociality metrics can capture short-term dynamics in both dominance and affiliative relationships by updating to dominance success or affiliative relationship scores throughout the group after each observed interaction (Goffe et al., 2018). Since Elo ratings are cardinal measures (Levy et al., 2020b), they can not only capture rank changes more precisely in time, but also track a narrowing or widening of dominance difference without a rank reversal (Foerster et al., 2016). Similarly, Elo-rating allows to track effects of changes to affiliative relationship strength without requiring the complete loss of a partner as a unit of analysis. Here, we investigate dynamic measures of both dominance and affiliative relationships as predictors of variation in male GCs.

We tested the predictions of the *cost of subordination*, *social buffering*, and *energy mobilisation/preparative hypotheses* with long-term data on wild male Assamese macaques. Specifically, we predicted that (i) following the *cost of subordination* hypothesis, dominance rank will have an *inverse relationship* with glucocorticoids; (ii) following the *social buffering* hypothesis, dynamics in the strength of affiliation will have an *inverse relationship* with glucocorticoids; an increasing strength of the top affiliative bond will come with decreasing GC values and a decrease in strength of top bond will be associated with increased GC levels. Finally, we predicted that there will be strong temporal dynamics of glucocorticoids and investigate *energy mobilisation/preparative* hypotheses, making no specific predictions as to which hypothesis we expected: (iii) if GC upregulation occurred *before* the start of the mating season, this would be evidence for the *preparative* hypothesis, and (iv) if peak GC levels occurred *during* the mating season, this would be evidence for the *energy mobilisation* hypothesis. Because of a change in the hormone extraction protocol three years into the study (see below), all analyses were run separately for the before and after periods.

Methods

Study Site and Population

This study is part of a long-term research project taking place in Phu Khieo Wildlife Sanctuary (PKWS, 16° 05′–35′ N, 101° 20′–55′ E, 1573 km^2), part of the Western Issan Forest Complex in northeastern Thailand, a contiguous protected forest area of > 6500 km^2. The forest at the study site Huai Mai Sot Yai (16° 27′ N, 101° 38′ E, 600–800 m above sea level) is composed mostly of hill evergreen vegetation and bamboo stands with a diverse community of large mammals (Borries et al., 2002).

We collected data on 62 adult males in six groups of fully habituated Assamese macaques, from 2006 to 2021. Assamese macaques live in multi-male multi-female groups, with male dispersal prior to sexual maturity and female philopatry. Adult males subsequently migrate multiple times throughout their life time. Males were considered adult and therefore included in the data collection when they had fully developed testes and canines, as well as full body length. Note that this definition includes males that were classified as large subadults in a previous publication (Ostner et al. 2008a); since then such large subadults have been found to sometimes outrank prime adult males, sire offspring, and attain alpha rank. Therefore, they do not constitute a distinct age class in this study. Groups ranged in size from 20 to 97 macaques, with 2 to 15 adult males (mean = 9.9), and three group split events occurred during the study. Assamese macaques are seasonal breeders, with a mating season from October to February followed by a non-mating season from March to September (Fürtbauer et al., 2010). Three time periods were excluded from the study due to a lack of either behavioural or hormonal data (March 2009 - September 2011, May 2017 - September 2019, and May 2020 - September 2020). Accounting for this, we analysed data collected in 117 out of the 180 months of the study or 21 out of 30 season-years.

Ethics Statement

Data collection and export of samples were authorized by the Department of National Parks, Wildlife and Plant Conservation (DNP) and the National Research Council of Thailand (NRCT) with a benefit sharing agreement (permit numbers: 0004.3/3618, 0002.3/2647, 0002/17, 0002/2424, 0002/470, 0002/4137, 0402/2798, 0402/8707). The study was purely observational, strictly non-contact/non-invasive, and adhered to the guidelines for the treatment of animals in teaching and research of the ASAB Ethical Committee/ABS Animal Care Committee SAB (2023) and the EU directive 2010/63/EU.

Data collection – Behaviour and Faecal Samples

All subjects were identifiable by differences in size, stature, coat colour, natural body markings such as facial skin pigmentation patterns, injuries, wounds and scars with knowledge about identity maintained by a team of long-term Thai research assistants. Behavioural data were recorded using 40-minute continuous protocols (Altmann, 1974), following one adult male at a time covering all daylight hours. During these protocols, we recorded the frequency and duration of all affiliative and agonistic (aggressive and submissive) interactions including the identity of the actor and receiver. We attempted to balance protocols across individuals and time of day. Agonistic interactions were also recorded ad libitum. In total, 16,261.8 hours of behavioural data (mean ± standard deviation per male 262.3 ± 258.4) were recorded. In parallel, faecal samples were collected from focal males for analysis of glucocorticoid metabolite output, our measure of HPA axis activity. Samples were collected immediately after defection, and only if not contaminated with urine (for further details, see Hormone Analysis section). A total of 4,129 faecal samples were analysed, with a mean of 66 per male (± 73.2 standard deviation). Nine subjects were excluded from analysis due to a lack of either behavioural or hormonal data, leaving 62 focal males.

Dominance Hierarchy

Dominance ranks were derived from submissive behaviours in decided dyadic conflicts recorded in focal protocols or ad libitum. In order to capture the dynamics of the hierarchy, we used the Elo-rating method to calculate the dominance ranks, which takes into account the sequence or history of the interactions (Albers and De Vries, 2001). We used the “elo.seq” function from the package EloRating (Neumann and Kulik, 2020) to calculate dominance elo ranks in *R 4.1.0* (R Core Team, 2021). Following (De Moor et al., 2020b) we set the start value at 1000 with the gain constant k at 100. Elo ranks were considered to be accurate after a burn-in period of one month, and after group splits, males kept their Elo score from the original group as the start value in the new group. When a new male immigrated into the study groups or matured into the adult male age class, we used an individual burn-in of one month and ranks for the new male were assessed only after this. The absolute values of the Elo score were used for statistical analysis.

Social Relationships – Dynamic Dyadic Sociality Index

To assess the strength of dyadic affiliative relationships between males and their dynamics, we used the dynamic dyadic sociality index (DDSI; Kulik, 2015), a modification of the DSI method (Silk et al., 2013) and based on the principles of Elo-ratings. We will use the term DDSI and affiliative Elo rating interchangeably. We focused exclusively on male-male dyads and only included interactions between adult males in our calculations. The DDSI is based on the time each male-male dyad spent on three primary affiliative behaviours; grooming, body contact and spatial proximity within 1.5m. Dyads started with a score of 0.5, representing a neutral relationship (range of DDSI scores 0-1). Each time one of the affiliative behaviours was recorded, the given DDSI for a dyad increased: $\mathrm{DDSI}\textit{new} = \mathrm{DDSI}\textit{old} + (G - G*\mathrm{DDSI}\textit{old}) * W$, with G the gain factor (between 0 and 1, set at 0.5) and W the weight of the behaviour. Therefore, the increase in DDSI score was dependent on both the dyad’s score before the interaction and how frequently the behaviour was observed, with weight being the inverse of frequency. A lower DDSI score prior to the interaction resulted in a proportionally larger increase, reflecting the significance of interacting without a prior strong relationship, whereas a single affiliative interaction between individuals that already have a strong relationship will affect the relationship less. Simultaneously, the score of all other male-male dyads that included either of the interacting dyad members decreased: $\mathrm{DDSI}\textit{new} = \mathrm{DDSI}\textit{old} * (1 - (G/n-2))$, with n the number adult males in the group at the time of the interaction. Through this, the DDSI is able to capture the decline of relationships if they are not maintained with regular affiliative interactions. DDSI scores were considered to represent the actual dyadic relationship strength after a burn-in period of one month. When a new male immigrated into a study group or matured into the adult male age class, we used an individual burn-in of one month and scores of all dyads including the new male were only considered after this period. After group splits, dyads kept their score from the original group as the start value in the new group.

Glucocorticoid metabolite (GC) analysis

For glucocorticoid metabolite analysis, faecal samples were extracted following one of two previously established methods (lab and field extraction). First from October 2006 to February 2009, samples upon collection in the field were stored at minus 20°C until transfer to hormone laboratory of the German Primate Center where they were lyophilized, pulverized and an aliquot of 0.05-0.08g was extracted with 80% methanol in water (details in Ostner et al., 2008a). This sampling period is called Period 1 throughout. For Period 2, from October 2011 to April 2021, samples were extracted at the field camp using a method validated for several primate species, including Assamese macaques (Berghänel et al., 2016; Nugraha et al., 2017; Rimbach et al., 2013; Shutt et al., 2012). Briefly, upon collection, faecal material was homogenized and approximately 1g was placed into 5ml of 80% ethanol in water. After return to camp, GCs were extracted by vigorously shaking the samples manually for two minutes before centrifuging the samples 6000upm for 5 min (c.f. Rimbach et al., 2013). Then 2ml of the resulting faecal extract were pipetted off and stored at minus 20°C until transport to the hormone laboratory for GC metabolite analysis.

For GC metabolite measurement, faecal extracts were diluted in assay buffer (1:10-1:3,000 depending on concentration) and analysed in duplicate for immunoreactive 11ß-hydroxyetiocholanolone, a major metabolite of glucocorticoids in primate faeces (Heistermann et al., 2006). The assay, carried out as described earlier (Heistermann et al., 2004; Ostner et al., 2008a), has previously been validated and successfully used to track adrenocortical activity in numerous primate species (Heistermann et al., 2006), including the study species (Anzà et al., 2023; Berghänel et al., 2016; Fürtbauer et al., 2014; Ostner et al., 2008a). Intra- and inter-assay coefficients of variation (CVs) of high and low-value quality controls were <10% and <15%, respectively. Faecal GC metabolite levels are expressed as ng per g faecal dry mass (Period 1) or ng per g wet weight (Period 2).

Social Metric Selection

In the present study, we aimed to investigate the dynamics in male-male social bond strength on the social buffering effect. Using an aggregated metric such as the strength of the top 3 relationships or social integration may obscure the dynamics of bonding and social buffering.

However, it is also key to ensure that our selected metric accurately reflects the social bonding of male Assamese macaques. Therefore prior to selecting the social metric for subsequent analysis, we correlated a number of metrics representing differing aspects of the social bonding dimension of sociality (Schülke et al., 2022). We ran correlations using the *cor* function from the package *stats* in *R 4.1.0* (R Core Team, 2021) and examined correlations at the individual level for social bonding metrics of all males in the groups, at specific time points in each season-year. We correlated the following metrics: strength of the top affiliative relationship, sum strength of the top two relationships, sum strength of the top three relationships, sum total strength of all relationships, mean strength of affiliative relationships, number of relationships above the 50% strength value in the group, number of relationships above 75%, number of relationships above 90%, number of relationships above the group median strength value, sum strength of relationship above 50%, sum strength of relationships above 75%, sum strength of relationships above 90%, number of top three relationships that were reciprocal. The strength of the top affiliative male-male relationship (as measured by the DDSI) was consistently correlated with the summed strength of the top two or three relationships, across all groups and season-years (mean correlation coefficient ± standard deviation: top two = 0.90 ± 0.11; top 3 = 0.80 ± 0.19). We therefore selected the strength of the top affiliative relationship, as we could represent the social bonding dimension of sociality in male Assamese macaques without using an aggregated metric.

Subsequently, we calculated the change in strength of the top affiliative relationship in the 30 days prior for each faecal sample (ΔTopAff), to capture the dynamics of social bonding. We chose to use 30 days as it allows for the relatively rarity of some male-male affiliative behaviours like grooming (Kalbitz et al., 2016) and for changes in relationships to become meaningful. Each faecal sample and associated GC value therefore has a unique matched ΔTopAff value which will be our metric for examining the dynamics of social buffering.

In addition, to ensure the dominance Elo values represented the true rank and value in our analysis, for each faecal sample we calculated the average dominance Elo score for that male over the previous fourteen days. This allowed us to assess the dynamics of dominance rank, but minimised Elo changes that happened on the day of the sample, which would be outside of the peak excretion window of faecal glucocorticoids (Behringer and Deschner, 2017).

Statistical Analyses

All statistical analyses were run in *R 4.1.0* (R Core Team, 2021). To test for a relationship between dominance rank and change in social bonding with faecal glucocorticoid levels, we constructed Bayesian linear mixed models with a Gaussian response distribution and identity link function.

We ran a separate model for each period (defined by the extraction method). Both models used the same predictors and control variables, with one exception (see below).

For model 1 covering Period 1, the response was glucocorticoid metabolite concentration (ng/g dry weight) with test predictors of ΔTopAff and dominance Elo score (average over the past two weeks prior to the sample). We added control predictors that have previously been shown to influence GCs in male primates (Gesquiere et al., 2011; Rudolph et al., 2020); a continuous variable of aggression received in the two weeks prior to the sample (corrected for observation time) and fixed variables of season (mating and non-mating) and alpha status (yes or no). We included the random effects of male identity and season-year to control for multiple observations and repeated sampling, as well the month of sample collection to account for temporal dynamics. We also included a maximal random slope structure and correlation parameters between random intercepts and random slopes for all predictors that varied within each random effect: ΔTopAff, dominance rank, season, alpha status, and aggression received (Barr, 2013; Harrison et al., 2018). For both models, we initially tested for an interaction between dominance rank and alpha status as well as dominance rank and ΔTopAff. Neither had a substantial effect on the model and so were removed (see Suppl. Mat., Tables 1 - 4). As aggression received was highly skewed with a lot of zero values in both datasets, we used a square root transformation to generate a more symmetrical distribution. All predictors in both models were z-transformed to a mean of 0 and standard deviation of 1 to make model estimates easier to interpret and more stable (Harrison et al., 2018).

For model 2 and Period 2, the response was glucocorticoid metabolite concentration (ng/g wet weight), with the same predictors and random effects as model 1 with the addition of the random effect of group identity (Period 1 only included one group). Model 2 also had a maximal random slope and correlation structure.

Both models were run using the function *brm* in the package *brms* (version 2.19.0; Bürkner, 2018) which calls on the computational framework Stan (https://mc-stan.org) to fit Bayesian models (Bürkner, 2018). Each model was run using four MCMC chains of 4000 iterations per chain with adapt_delta set at 0.99 and a max_treedepth of 12, including 1000 "warm up" iterations during which no divergent transitions were reported. This resulted in 12,000 posterior samples per model. The convergence and stability of the models were assessed using R-hat values, which were below 1.01 (Vehtarh et al., 2021) and a visual inspection of the plots of the chains (Gabry et al., 2019). In addition, all Bulk and Tail Effective Sample Sizes (ESS) for the estimated posteriors in both models were greater than 1000 (Bürkner, 2018; Vehtarh et al., 2021). We report model estimates as the mean of the posterior distribution with 95% credible intervals (CI). To help assess which predictor variables substantially affected glucocorticoid levels (the response), we report the proportion of posterior samples that fell on the same side of 0 as the mean (Pr). The Pr ranges from 0.5 to 1.0 where Pr = 1.0 indicates that based on the model, the effect of a predictor was entirely positive or negative. By contrast, a Pr = 0.5 indicates that the effect was centred around zero (Rincon et al., 2020).

In order to understand the temporal dynamics of glucocorticoids in male Assamese macaques, we first examined the Pr values for month of sample collection in Model 1 and Model 2. The proportion of posterior samples that fall on the same side as the mean can also be applied to random effects (Martin et al., 2021), so for each model we report Pr values for the random intercepts of month to assess if any month had a substantial effect on the response.

Results

Descriptive Statistics

The two study periods, which were dictated by a change in hormone sample processing, also mark differences in behaviour sampling: in Period 1, a single large study group was followed almost daily, whereas in Period 2, up to five groups of varying male and female group size were followed in consecutive observation blocks. A total of 1,777 faecal samples were collected during Period 1 from October 2006 to March 2009, spanning five season-year combinations with 355 samples on average (range: 283 – 450) from a total of 15 males. The majority of males (12) were present in all five season-years, with the other three only present in one. Each male had at least 27 samples (range: 27 – 164) and for the males present throughout at least 84 samples, with a mean of 118. On average 250 hours of focal animal data were collected per male after burn-in phases (range: 2 – 450 hours), see Table 1 for more details.

There were 2,352 faecal samples collected during Period 2 from October 2011 to April 2021. Accounting for gaps in data collection (May 2017 - September 2019 and May 2020 - September 2020), this period spans 16 season-year combinations, with an average of 147 samples collected each season-year (range: 36 – 267). Six groups were followed during this period and data was collected on a total of 58 males. Males were present in the groups for 5.4 season-years on average (range: 1 – 16) with a majority present for at least four season-years (41 out of 58). On average, 40 samples were collected for each male across the 16 season-years (range: 2 – 159) which rises to 53 for the individuals present for at least 4 season-years (range: 12- 159). On average 207 hours of focal data was collected per male after burn-in (range: 16 – 699 hours), see Table 1 for more details.

Table 1. Information on number of males, study groups, samples collected and observation effort for each season-year combination in the study. Mean samples per male and mean observation time per male show the range for all males in that season-year in brackets. All values are after burn-in periods for Elo scores.

Season Year	**Period**	**No. Groups**	**Male Group(s) size (range)**	**Total No. Males**	**Total No. Samples**	**Mean samples per male**	**Total obs. (hrs)**	**Obs. time per male (hrs)**
Mating 2006-07	1	1	12-12	12	283	24 (17-32)	173	14 (10-16)
Non-Mating 2007	1	1	12-12	12	342	28 (16-38)	342	28 (21-37)
Mating 2007-08	1	1	11-12	12	348	29 (2-37)	399	33 (2-39)
Non-Mating 2008	1	1	12-15	15	354	30 (20-39)	310	26 (14-33)
Mating 2008-09	1	1	13-15	15	450	30 (7-38)	907	60 (21-79)
Mating 2011-12	2	1	9-9	9	130	14 (8-19)	450	50 (27-76)
Non-Mating 2012	2	3	3-9	19	151	17 (11-21)	685	76 (28-105)
Mating 2012-13	2	2	3-7	11	55	6 (3-9)	373	41 (6-64)
Non-Mating 2013	2	2	7-10	19	117	8 (1-20)	1146	82 (50-100)
Mating 2013-14	2	2	8-10	19	221	12 (1-19)	253	14 (3-25)
Non-Mating 2014	2	3	5-10	24	227	12 (2-24)	977	51 (8-88)
Mating 2014-15	2	3	5-10	25	75	5 (1-8)	798	50 (18-67)
Non-Mating 2015	2	4	4-9	25	267	11 (6-22)	1519	63 (24-87)
Mating 2015-16	2	4	2-7	24	236	11 (5-18)	972	46 (22-64)
Non-Mating 2016	2	4	3-9	28	137	7 (2-11)	566	27 (7-40)
Mating 2016-17	2	4	3-10	30	81	3 (1-6)	367	15 (6-26)
Non-Mating 2017	2	3	3-13	23	36	2 (1-3)	80	5 (2-9)
Mating 2019-20	2	3	6-12	32	259	8 (3- 13)	807	25 (4-38)
Non-Mating 2020	2	3	6-12	27	69	3 (1-4)	285	11 (2-18)
Mating 2020-21	2	6	3-10	45	188	6 (2-11)	773	26 (8-51)
Non-Mating 2021	2	5	4-10	32	103	4 (1-8)	387	14 (8-22)

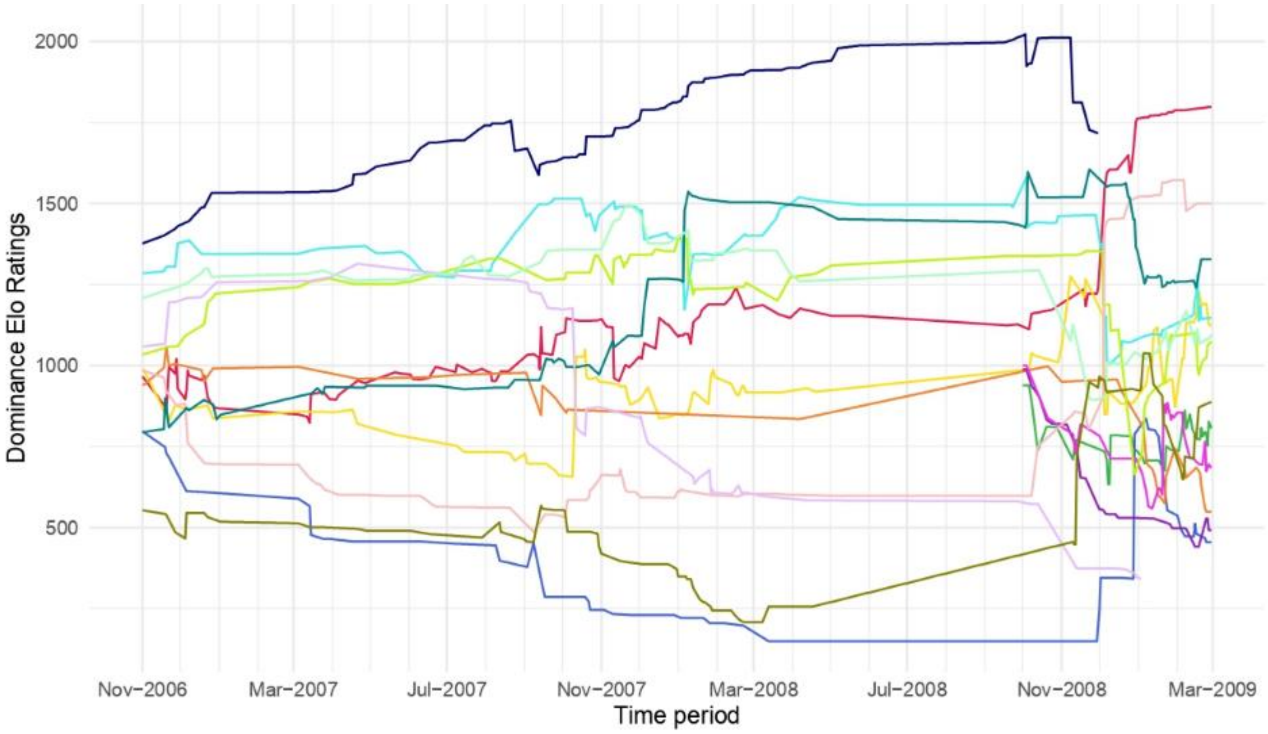

Figure 1. Dominance hierarchy of the group AS from November 2006 to March 2009, covering Period 1. Colours refer to the 15 different adult males in the group during the time period. See Supplementary Material Figures 1 - 10 for other groups and time periods.

Dominance Hierarchy

In contrast to our prediction based on the cost of subordination hypothesis, dominance rank was positively correlated with GC values (Period 1: Estimate = 0.18, 95% CI = 0.01, 0.38, Pr = 0.98; Period 2: Estimate = 0.07, 95% CI = -0.05, 0.20, Pr = 0.90; Tab. 2-3, Fig. 2-3; prediction i). This was the case for both datasets, with higher GC levels in males of a higher dominance rank. In addition, for Period 1 (model 1), alpha male status also predicted GC, with lower GC values in alpha males (Estimate = -0.44, 95% CI = -1.14, 0.19, Pr = 0.92). We did not find any effect of this predictor in model 2 for Period 2 (Estimate = 0.01, 95% CI = -20, 0.24, Pr = 0.55).

Table 2. Glucocorticoid levels in relation to dominance rank and dynamics of top affiliation (ΔTopAff) for Period 1 (model 1). Number of males = 15, number of samples = 1,777. CI = 95 % credible intervals, Pr = proportion of the posterior samples that fall on the same side of 0 as the mean. Predictors with a higher certainty of effect (above 0.9) are in bold.

Predictor	Estimate	SD	CI lower	CI upper	Pr
Intercept	0.08	0.35	-0.62	0.77	0.61
Alpha (yes)	**-0.44**	**0.34**	**-1.14**	**0.19**	**0.92**
Season (non-mating)	-0.25	0.43	-1.08	0.63	0.73
Dominance rank	**0.18**	**0.09**	**0.01**	**0.38**	**0.98**
Aggression received	0.05	0.11	-0.16	0.26	0.71
ΔTopAff	**-0.18**	**0.14**	**-0.47**	**0.11**	**0.92**

Predictor	Estimate	SD	CI lower	CI upper	Pr

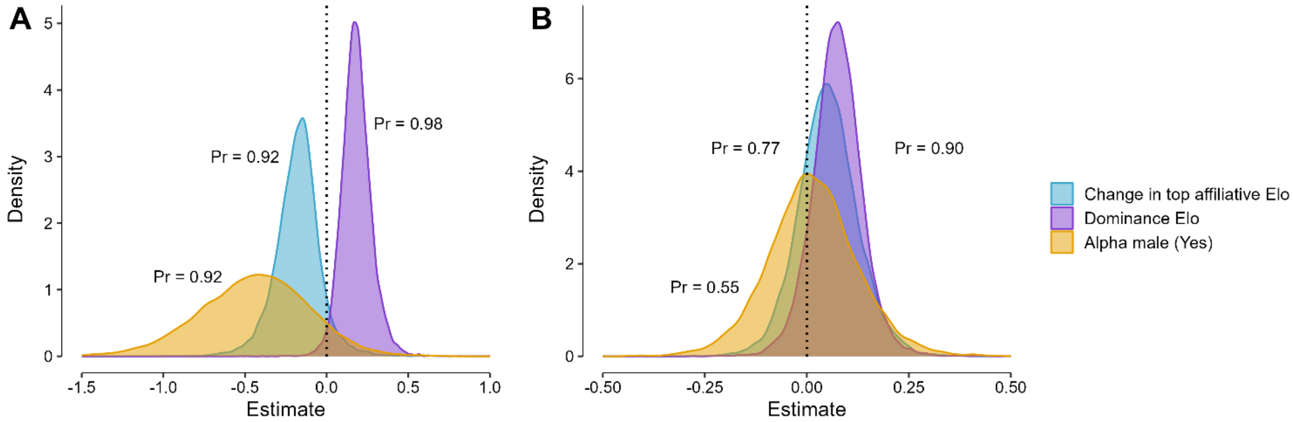

*Figure 2. Effects of dominance rank, dynamics in strength of top affiliation and alpha status on GC – posterior probability distributions of the slope estimates resulting from **A:** model 1 (Period 1) and **B:** model 2 (Period 2). Pr = proportion of the posterior samples that fall on the same side of 0 as the mean.*

Table 3. Glucocorticoid levels in relation to dominance rank and dynamics of top affiliation (ΔTopAff) for Period 2 (model 2). Number of males = 58, number of samples = 2352. CI = 95 % credible intervals, Pr = proportion of the posterior samples that fall on the same side of 0 as the mean. Predictors with a higher certainty of effect (above 0.9) are in bold.

Predictor	Estimate	SD	CI lower	CI upper	Pr
Intercept	0.07	0.26	-0.43	0.58	0.62
Alpha (yes)	0.01	0.11	-0.20	0.24	0.55
Season (non-mating)	0.04	0.32	-0.59	0.68	0.55
Dominance rank	**0.07**	**0.06**	**-0.05**	**0.20**	**0.90**
Aggression received	0.02	0.06	-0.08	0.14	0.65
ΔTopAff	0.05	0.07	-0.09	0.20	0.77

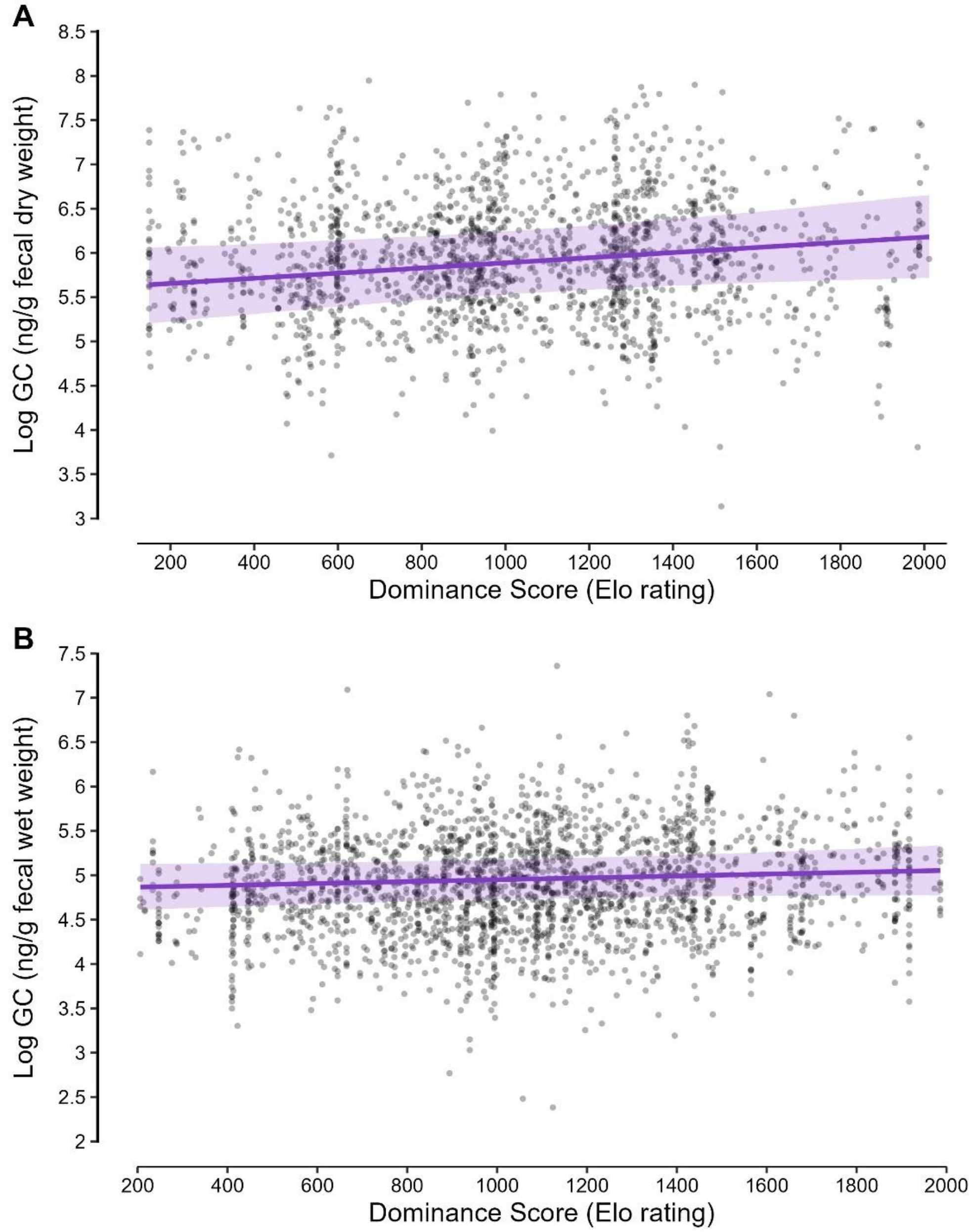

Figure 3. Correlation between glucocorticoid levels and dominance rank. ***A:*** *model 1 (Period 1). Depicted are the fitted values from model 1 (solid line) and 95 % credible intervals (shaded area), with other predictors at mean values. Circles indicate raw data points (N = 1777).* ***B:*** *model 2 (Period 2). Depicted are the fitted values from model 2 (solid line) and 95 % credible intervals (shaded area), with other predictors at mean values. Circles indicate raw data points (N = 2352).*

Social Buffering

Following our prediction, dynamics in the strength of the top affiliative relationship were inversely related to GC levels in Period 1. An increase in the strength of the top relationship correlated with a decrease in subsequent GC values, whereas a decrease in relationship strength corresponded to elevated GCs (prediction ii) (Estimate = -0.18, 95% CI = -0.47, 0.11, Pr = 0.92;

Tab. 2, Fig. 2, 4). However, we did not find any correlation between the dynamics of top affiliation strength and GC values in Period 2 (Estimate = 0.05, 95% CI = -0.09, 0.20, Pr = 0.77; Tab. 3, Fig. 2).

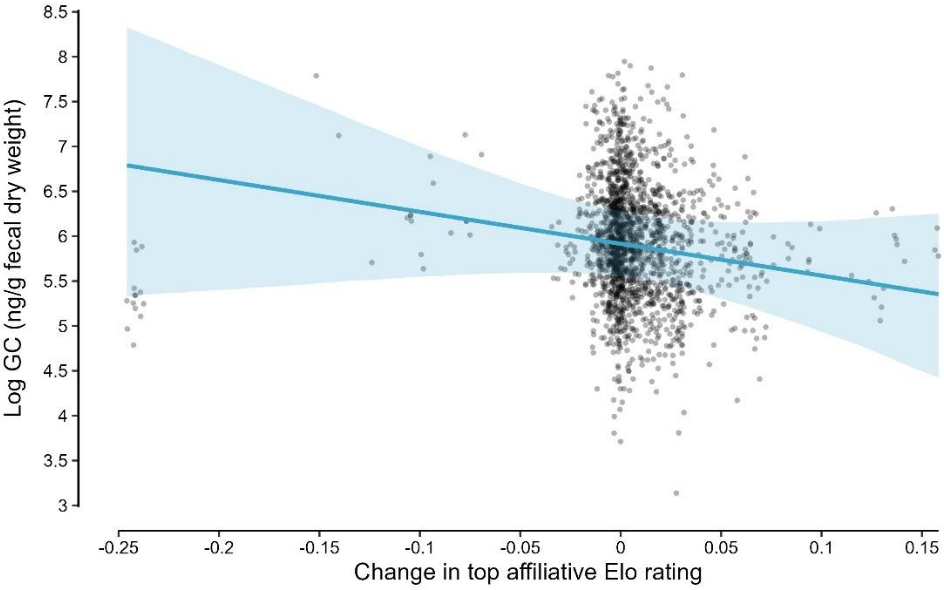

Figure 4. Correlation between glucocorticoid levels and dynamics in top affiliative strength for Period 1. Depicted are the fitted values from model 1 (solid line) and 95 % credible intervals (shaded area), with all other predictors at mean values. Circles indicate raw data points (N = 1777). ΔTopAff on the x axis.

Seasonal Dynamics of GC

Following our predictions, we found evidence for temporal dynamics in glucocorticoids (prediction iii/iv). While there was no effect of season overall, i.e. mating compared to non-mating season (Tab. 2-3), the period around the onset of the mating season (September in Period 1; September-October in Period 2) was associated with a high certainty with higher values of GC, consistent with the preparative and/or energy mobilisation hypothesis (Tab. 4-5). When samples were pooled across years in each period, the upregulation of GC in September is evident (Fig. 5) and of the seven full calendar years with data for each month, a clear spike in GC levels during September can be seen in five of them (Figure 6). As the mating season starts in October (based on birth dates, (Fürtbauer et al., 2010)), the spike in September matches the prediction of the *preparative hypothesis* (prediction iii) and suggests that this is not solely a consequence of energetic demand.

Table 4. Glucocorticoid levels in relation to the month of sample collection for Period 1 (model 1). Number of males = 15, number of samples = 1778. Estimate = random intercept for the predictor, CI = 95 % credible intervals, Pr = proportion of the posterior samples that fall on the same side of 0 as the mean. All predictors shown have a higher certainty of effect (above 0.9), see Supplementary Materials Table 5 for all months.

Predictor	Estimate	SD	CI lower	CI upper	Pr
February	-0.71	0.26	-1.22	-0.19	0.99
March	-0.55	0.23	-1.02	-0.10	0.99
July	-0.60	0.24	-1.08	-0.14	0.99
September	1.07	0.24	0.61	1.55	1.00

Table 5. Glucocorticoid levels in relation to the month of sample collection for Period 2 (model 2). Number of males = 58, number of samples = 2352. Estimate = random intercept for the predictor, CI = 95 % credible intervals, Pr = proportion of the posterior samples that fall on the same side of 0 as the mean. All predictors shown have a higher certainty of effect (above 0.9) see Supplementary Materials Table 6 for all months.

Predictor	Estimate	SD	CI lower	CI upper	Pr
January	-0.36	0.18	-0.73	-0.005	0.98
July	-0.37	0.16	-0.70	-0.05	0.99
September	0.65	0.18	0.31	1.01	1.00
October	0.59	0.18	0.23	0.96	1.00
December	-0.28	0.18	-0.65	0.07	0.95

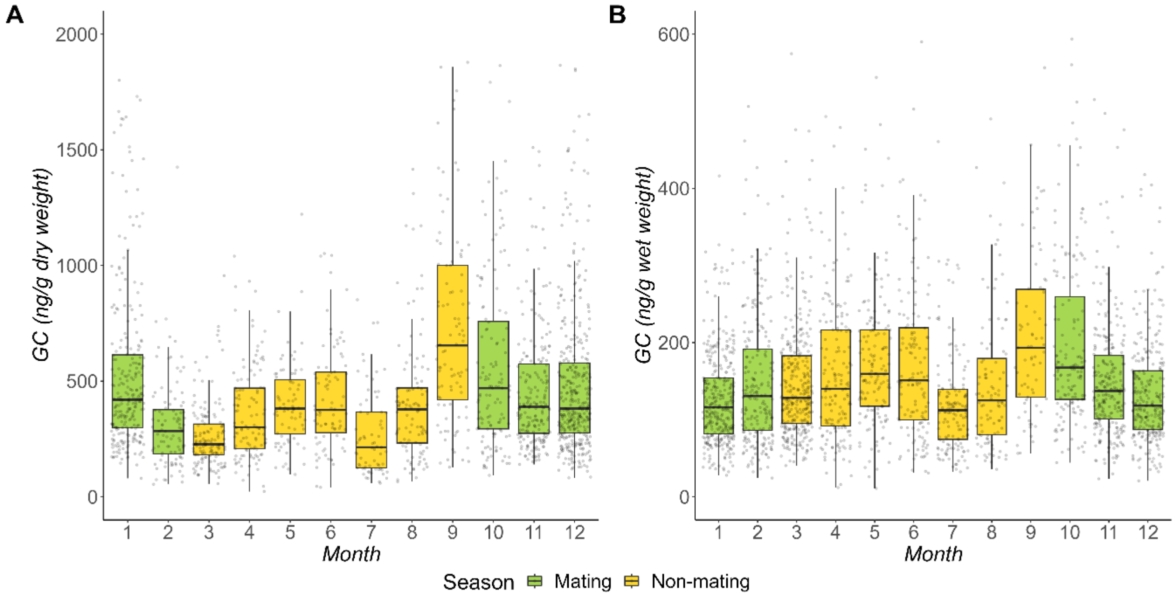

*Figure 5. **A:** GC values (ng/g dry weight) per month, pooled across years in Period 1. Samples collected in September correlated to higher GC values in model 1 (Estimate = 1.07, 95% CI = 0.61, 1.55, Pr = 1.00). **B:** GC values (ng/g wet weight) per month, pooled across years in Period 2. Samples collected in September (Estimate = 0.65, 95% CI = 0.31, 1.01, Pr = 1.00) and October (Estimate = 0.59, 95% CI = 0.23, 0.96, Pr = 1.00) correlated to higher GC values in model 2. Boxes depict the median and interquartile range of each month; the whiskers show 1.5*the interquartile range. Points are raw data (samples collected) with 15 large values not shown in A and 20 large values not shown in B for ease of plotting.*

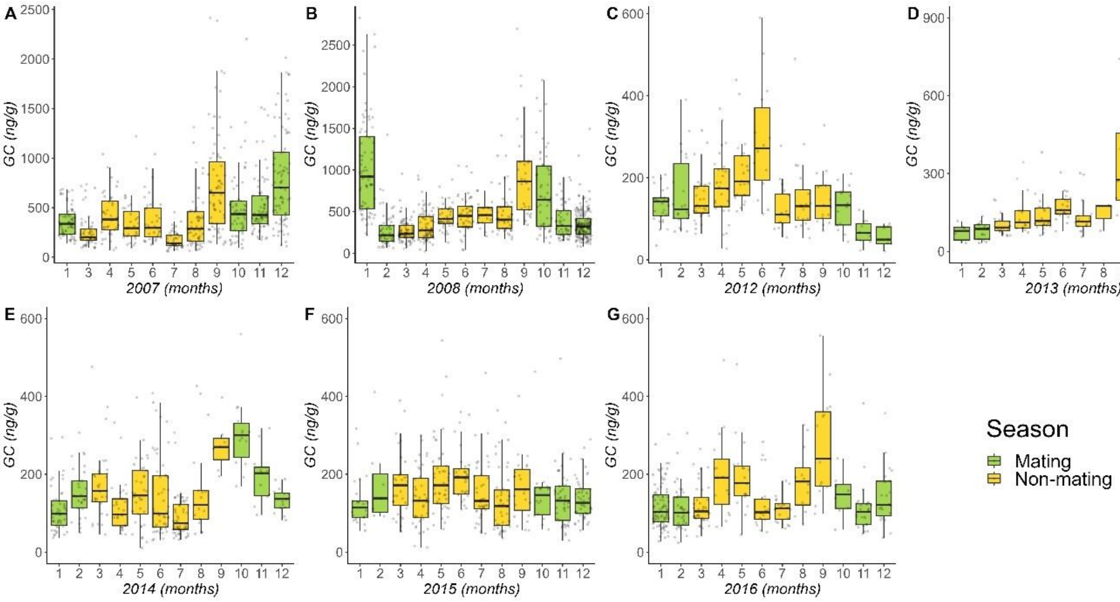

Figure 6. Annual dynamics in GC values in years when samples were collected in each month. Overall, 5 of the 7 years with samples in each month show an elevation in GC during September, before the start of the mating season. ***A, B:*** *GC values (ng/g dry weight) per month for the first period (model 1) in 2007 (A) and 2008 (B).* ***C, D, E, F, G:*** *GC values (ng/g wet weight) per month for the second period (model 2) in 2012 (C), 2013 (D), 2014 (E), 2015 (F) and 2016 (G). Boxes depict the median and interquartile range of each month; the whiskers show 1.5*the interquartile range. Points are raw data (samples collected) with 1, 3, 4, and 2 large values removed from D, E, F, G respectively for ease of plotting. See Supplementary Material Figure S11 for other years where samples were not collected each month.*

Discussion

In the present study, we assessed the relationship between social and seasonal dynamics and the glucocorticoid response in male Assamese macaques across multiple years and groups. We used a dynamic method, matching individual hormonal samples to the fluctuations of male sociality. We found evidence for the cost of dominance hypothesis, where a higher dominance rank was associated with higher glucocorticoid values in both datasets. In contrast to our prediction (i), we did not replicate the results of Ostner et al. 2008a in finding a cost of subordination in this population, although in Period 1, alpha males had lower GC values. In line with our prediction (iii/iv), in both datasets we demonstrated an upregulation of GCs at the onset of the mating season. The costs associated with a higher rank or the energetic demands of the mating season may be mitigated by the presence of a social support system. Following our prediction (ii), we found evidence for the social buffering effect in Period 1, but not in Period 2.

Period 1, from late 2006 to early 2009, covers data collection on a single group of Assamese macaques about which we have substantial amount of information. Males form and maintain strong bonds with each other independent of kin (De Moor et al., 2020b; Kalbitz et al., 2016), aided by male-infant-male interactions (Kalbitz et al., 2017). These bonds provide a pathway to higher dominance status through coalitions, resulting in a greater reproductive success (Schülke et al., 2010). Although the highest ranking males engage extensively in mate guarding behaviours (Ostner et al. 2011), mate guarding males do not appear to incur energetic costs (Schülke et al., 2014), and overall there is a low paternity skew within the group (Sukmak et al., 2014). This study adds evidence for a social buffering effect in Period 1.

Dynamics in the strength of the top affiliative relationship were correlated with the GC response, to our knowledge the first time this has been demonstrated in a wild primate. Males who did not maintain the strength of their top affiliative relationship showed an increase in GCs. By contrast, investing in their top social bond and increasing its strength correlated with lower GC values. Males with stronger top affiliative relationships are likely to have had more predictable and frequent social support, which can reduce the stress of a challenge, either perceived or actual (Cohen & Wills, 1985; Hennessy et al., 2009). In an ongoing conflict, male macaques attempt to solicit support from their most closely bonded partners among bystanders and the closer the affiliative relationship the less likely the solicited male will refuse to help (Young et al. 2014b). Males in the present study preferentially formed social bonds with compatible males based on factors such as personality and dominance rank similarity (De Moor et al., 2020b; Ebenau et al., 2019; Kalbitz et al., 2016). These factors could also impact social buffering, if males can increase bond strength more quickly with more compatible partners (Baxter et al., 2023; Verspeek et al., 2019).

Social buffering in male primates through male-male relationships has so far been reported twice. Using a single aggregate score of dyadic relationship strength per season year, male Barbary macaques were shown to exhibit increasing attenuation of the GC response to aggression received from male group members (Young et al., 2014a). Male chimpanzees also showed a reduction in GC response when interacting with or in the presence of a closely bonded partner (also using an aggregated sociality score), and this attenuation occurred both during highly stressful events (intergroup encounters) as well as during every-day social interactions (grooming events; (Wittig et al., 2016)). Here, we add to these earlier findings that dynamics in the top male-male affiliative relationship can influence the effectiveness of the social buffering effect. A stronger attenuation of a GC response may ensure that the upregulation of GCs does not induce short-term costs due to homeostatic overload (Milewski et al., 2022) and that the hormonal responses to challenges faced by strongly bonded males are adaptive (MacDougall-Shackleton et al., 2019).

The association between alpha male status and lower GCs in Period 1 may therefore be due to a social buffering effect from the strong affiliative relationships that alpha males maintained. Additionally, support from coalitionary partner(s) could have allowed alpha males to reduce their engagement in energetically costly competitive behaviours, producing the opposite pattern to species where alphas compete more intensely to maintain their rank (Gesquiere et al., 2011;

Girard-Buttoz et al., 2014; Milich et al., 2018). Alternatively, having alpha status could minimise the quantity of stressful rank changes a male was exposed to, which is the proposed reason for a reduced GC production in top ranked female savannah baboons (Levy et al., 2020a). A caveat on our study is that one male held the alpha rank for the majority of Period 1 (Fig. 1), who may not have been representative of the overall population. The buffering benefit of a relationship is predicted to be most effective with strong and stable partners (Kikusui et al., 2006) which may explain why we did not find evidence for the social buffering effect later in our long-term study of the same population. Given that Period 2 covers more years, males, and groups; some of the males may have pursued alternative rank acquisition strategies, resulting in less investment in social bonds and therefore less effective social support (Kiyokawa and Hennessy, 2018).

Across all data for both periods, male dominance rank was positively correlated to GC levels, matching the predictions of the cost of dominance hypothesis (Goymann and Wingfield, 2004) and patterns observed across primate species (Beehner and Bergman, 2017; Cavigelli and Caruso, 2015). Although male Assamese macaques may not compete as intensely for rank as some other primate species, males still engaged in energetic behaviours in order to establish their position in the dominance hierarchy. Assamese macaques form coalitions against rival males, the majority of which are "all-down", where two high-ranking males direct aggression down the hierarchy (Young et al., 2014b). Frequently engaging in coalitions could therefore incur energetic costs in a similar manner to the intense competition for ranks faced by high-ranking baboons, chimpanzees, and other male primates (Beehner and Bergman, 2017; Kalbitzer et al., 2015; Muller et al., 2021). In addition, while rare, the threat of a coalitionary attack from lower-ranked males could induce physiological stress in highly ranked males (Feng et al., 2016) or at least reinforce the need for regular all-down coalitions to maintain their status, which therefore incurs energetic demands on higher ranked males.

Beyond social bonding for alliance formation, Assamese macaque males may also use alternative strategies for attaining and maintaining high rank that involve more direct competition and greater energetic demands. The male career framework, as suggested by van Noordwijk and van Schaik (2004), posits that male dominance strategies are determined by the contest potential. In groups with fewer males, the highest ranked males are able to monopolise access to a larger share of the reproductive females. Given that the potential rewards of a high rank are therefore greater, dominance status is predicted to be competed for by more direct challenges (van Noordwijk and van Schaik, 2004). Equally, in smaller groups there might be a lack of suitable, compatible bonding and coalition partners (Noë, 1994) and males may have no choice but to compete directly with each other (Bissonnette et al., 2014). Alternative strategies for rank acquisition, dependent on the contest potential, have been reported for both Japanese (*Macaca fuscata*) and rhesus macaques

(*Macaca mulatta*) (Georgiev et al., 2016; Sprague et al., 1998). In Period 2 of our study, where male group size ranged substantially, more direct competition could therefore have resulted in a greater energetic cost of high rank acquisition and maintenance.

While the exact mechanisms are beyond the scope of this study, overall and across both periods, a higher dominance rank was correlated to elevated GC levels in male Assamese macaques which is in contrast to our previous work (Ostner et al., 2008a). This difference is likely due to an improved statistical methodology combined with a significantly larger sample size, as has been suggested for varying results from female baboons (Levy et al., 2020a), and also due to a greater understanding of our study species. Previously adult males were split into two aged-based categories and analysed separately, however genetic paternity analyses have shown that the younger males are reproductively active and fully embedded in the adult male hierarchy (Sukmak et al., 2014). Including these males may go towards explaining our contrasting results. Our previous work also reported a seasonal change in GCs, with higher values in the mating season compared to the non-mating season over a single season-year comparison (Ostner et al., 2008a), which we replicated and expanded on in the present study.

For males of seasonally breeding species, the mating season comes with an increase in contest potential as females enter their fertile phase, invoking an increase in mating effort (Pavitt et al., 2015) and competition for access to females (Clutton-Brock and Huchard, 2013). As such, males often show an upregulation in GCs when energetically expensive behaviours peak at the onset of the mating season (Corlatti et al., 2012; Milich et al., 2018; Romero et al., 2017). However, we demonstrate that in male Assamese macaques, the upregulation of GC occurs before the start of the mating season and therefore follows the predictions of the preparative hypothesis (Romero, 2002), as has been reported in long-tailed macaques (Girard-Buttoz et al., 2009) and other mammals such as Asian elephants (*Elephas maximus*) and degus (*Octodon degus*) (Bauer et al., 2014; Menargues Marcilla et al., 2012). GCs not only mobilise energy for immediate use but can have a range of preparative actions including stimulating food intake, the building of fat reserves, and augmenting catecholamine production to respond to anticipated stressors (Landys et al., 2006; Sapolsky et al., 2000). A preparative increase in GCs therefore allows for appropriate allostatic adjustments to predictable challenges, prior to the onset of the changing energetic requirements of the challenge (Vera et al., 2017). Given that Assamese macaques do not seem to incur an energetic cost from mate guarding (Schülke et al., 2014), this upregulation may be in preparation for increased male aggression during the mating season (Ostner et al., 2011). In Period 2, GC concentrations were also elevated in October (Table 3, Figures 6 and 7) which indicates that males also incurred a greater energetic demand from mating competition, supporting the energy mobilisation hypothesis in addition to the preparative hypothesis

(Romero, 2002). In order to further distinguish between the two hypotheses, physiological markers with a narrower energetic function such as C-peptides or triiodothyronine might be required (Behringer et al., 2023; Surbeck et al., 2015; Touitou et al., 2021a). A lack of food is unlikely to be the driver of the observed spike, as it is only later in the mating season that the high food availability from the peak rainy season from August to October begins to disappear (Heesen et al., 2013; Touitou et al., 2021b). The upregulation of GCs is therefore most likely driven by social competition, either as a preparative measure or as a consequence of energy mobilisation, with the seasonal challenges for male Assamese macaques concentrated at the start of the mating season.

The dynamics within the mating season are likely the reason for a lack of evidence for a general seasonal effect, as the mating season overall was not correlated to higher GCs. Inconsistent seasonal differences over multiple years or seasons, either in magnitude or pattern, have been found in a number of longer-term studies; including snowshoe hares (*Lepus americanus*) (Sheriff et al., 2011), sifakas (*Propithecus verreauxi*) (Rudolph et al., 2020), and agile gracile opossums (*Gracilinanus agilis*) (Hernandez et al., 2018). This was the case in our data too with some years not showing an upregulation of GC values. Due to the multifunctional nature of GCs, variation in additional environmental factors such as predation rates (Monclús et al., 2009), food availability (Emery Thompson, 2017) or temperature (Santos et al., 2018) can impact on the dynamics of GC; as can rare stressful events such as a group split, which occurred during one of the study years without a seasonal spike (Figure 6C, 2012). While the broader pattern of seasonal upregulation in GCs was detected, the interannual variation in seasonal dynamics highlight the importance of multi-year and multi-group studies to allow for patterns to be elucidated.

The need to have multiple groups, a sufficient sample size, and an extended study period when examining hormonal corelates from wild populations is evident from the complex nature of our results. Equally, our method linking the dynamics in rank and affiliation to a specific GC sample allowed for a more accurate understanding of the competitive regime influencing individuals and its effect on their physiological responses. Dominance hierarchies and affiliative relationships are dynamic systems with multiple feedback loops (Dehnen et al., 2022; Fisher et al., 2017) and dynamic methods are needed to understand them. While both ranks and social bonding are broadly stable in male Assamese macaques (Kalbitz et al., 2016; Ostner and Schülke, 2014), the use of cardinal metrics demonstrated that there are underlying competitive actions occurring that while not rank changing, can widen or narrow the gap between males, affecting the structure of the dominance relationships. The improved accuracy may partially explain why we detected a positive relationship between rank position and GCs. Equally, by matching a male's hormone samples to the dynamics in their top affiliative relationship at that specific time, we were able to show changes in the social buffering effect in action, where the strengthening or weakening of a top relationship correlated to a modified GC response over a short time-frame. Combining dynamic cardinal metrics with matched individual samples, rather than averaging and conjugating hormonal responses or measures of sociality, provides an exciting way to further develop our knowledge of the hormonal correlates of competition and sociality.

Conclusion

We demonstrate that in Assamese macaques, a species where dominance ranks are not competed for with the same intensity as in primates with higher contest potential, males match the predictions of the cost of dominance hypothesis, showing a positive relationship between dominance rank and GCs. Assamese macaques thus add more weight to the theory first put forward by Goymann and Wingfield (2004) that for males, life is tough at the top or at the very least energetically demanding. We also found evidence for the social buffering effect, adding a third primate species for which this has been reported among males (Wittig et al., 2016; Young et al., 2014a), and we show that the dynamics in affiliation can correlate to dynamics in the physiological response, suggesting a mechanism for social bond maintenance. Although we were able to report the same seasonal effect as previous work on our study population, with an upregulation in GCs at the start of the mating season, we found evidence for a contrasting relationship between dominance rank and GCs between our earlier study and this one. Our study highlights the need in behavioural ecology for repeated research into the same study populations, with a broad variety of social groups and subjects. Much has been written about the replication crisis within scientific research in general (Korbmacher et al., 2023; Shrout and Rodgers, 2018) and behavioural ecology research from wild animals is not immune to this (Filazzola and Cahill, 2021; Kelly, 2006).

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Supplementary materials

1: Output of models 3, 4, 5, 6.

For Period 1, model 3 tested for an interaction between dominance rank and alpha status. Model 4 tested for an interaction between dominance rank and ΔTopAff. Neither interaction a high certainty or size of effect (significance in frequentist statistics) and were removed from the main model.

Table S1. Glucocorticoid levels in relation to dominance rank and dynamics of top affiliation (ΔTopAff) for Period 1 (model 3) with an interaction between dominance rank and alpha male status. Number of males = 15, number of samples = 1,777. CI = 95 % credible intervals, Pr = proportion of the posterior samples that fall on the same side of 0 as the mean. Predictors with a higher certainty of effect (above 0.9) are in bold.

Predictor	Estimate	SD	CI lower	CI upper	Pr
Intercept	0.07	0.35	-0.65	0.75	0.59
Alpha (yes)	-0.19	0.62	-1.41	1.06	0.63
Alpha*Dominance Rank	-0.24	0.49	-1.26	0.69	0.69
Season (non-mating)	-0.21	0.45	-1.07	0.70	0.70
Dominance rank	**0.19**	**0.10**	**0.001**	**0.41**	**0.98**
Aggression received	0.05	0.11	-0.16	0.27	0.71
ΔTopAff	**-018**	**0.14**	**-0.48**	**0.09**	**0.93**

Table S2. Glucocorticoid levels in relation to dominance rank and dynamics of top affiliation (ΔTopAff) for Period 1 (model 4) with an interaction between dominance rank and ΔTopAff. Number of males = 15, number of samples

= 1,777. CI = 95 % credible intervals, Pr = proportion of the posterior samples that fall on the same side of 0 as the mean. Predictors with a higher certainty of effect (above 0.9) are in bold.

Predictor	Estimate	SD	CI lower	CI upper	Pr
Intercept	0.05	0.35	-0.65	0.74	0.55
Alpha (yes)	**-0.44**	**0.34**	**-1.14**	**0.19**	**0.92**
Season (non-mating)	-0.15	0.45	-1.03	0.75	0.64
Dominance rank	**0.16**	**0.09**	**0.007**	**0.36**	**0.97**
Aggression received	0.05	0.11	-0.17	0.28	0.70
ΔTopAff	-0.14	0.13	-0.42	0.10	0.89
ΔTopAff*Dominance Rank	-0.11	0.16	-0.43	0.21	0.78

For Period 2, model 5 tested for an interaction between dominance rank and alpha status. Model 6 tested for an interaction between dominance rank and ΔTopAff. Neither interaction had a high certainty or size of effect (significance in frequentist statistics), and were removed from the main model.

Table S3. Glucocorticoid levels in relation to dominance rank and dynamics of top affiliation (ΔTopAff) for Period 2 (model 5) with an interaction between dominance rank and alpha male status. Number of males = 58, number of samples = 2352. CI = 95 % credible intervals, Pr = proportion of the posterior samples that fall on the same side of 0 as the mean. Predictors with a higher certainty of effect (above 0.9) are in bold.

Predictor	Estimate	SD	CI lower	CI upper	Pr
Intercept	0.07	0.26	-0.43	0.60	0.61
Alpha (yes)	-0.06	0.18	-0.42	0.31	0.64
Alpha*Dominance Rank	0.09	0.15	-0.19	0.40	0.73
Season (non-mating)	0.03	0.33	-0.62	0.69	0.54
Dominance rank	0.07	0.06	-0.06	0.19	0.86
Aggression received	0.02	0.05	-0.08	0.13	0.64
ΔTopAff	0.05	0.08	-0.09	0.21	0.78

Table S4. Glucocorticoid levels in relation to dominance rank and dynamics of top affiliation (ΔTopAff) for Period 2 (model 6) with an interaction between dominance rank and ΔTopAff. Number of males = 58, number of samples = 2352. CI = 95 % credible intervals, Pr = proportion of the posterior samples that fall on the same side of 0 as the mean. Predictors with a higher certainty of effect (above 0.9) are in bold.

Predictor	Estimate	SD	CI lower	CI upper	Pr
Intercept	0.07	0.26	-0.43	0.58	0.61
Alpha (yes)	0.01	0.11	-0.20	0.24	0.54
Season (non-mating)	0.04	0.32	-0.58	0.69	0.55
Dominance rank	**0.08**	**0.06**	**-0.05**	**0.20**	**0.90**
Aggression received	0.02	0.05	-0.08	0.14	0.62
ΔTopAff	0.06	0.08	-0.09	0.21	0.79
ΔTopAff*Dominance Rank	-0.02	0.06	-0.14	0.09	0.66

2: Plots of Dominance scores (Elo ratings) for all groups and periods

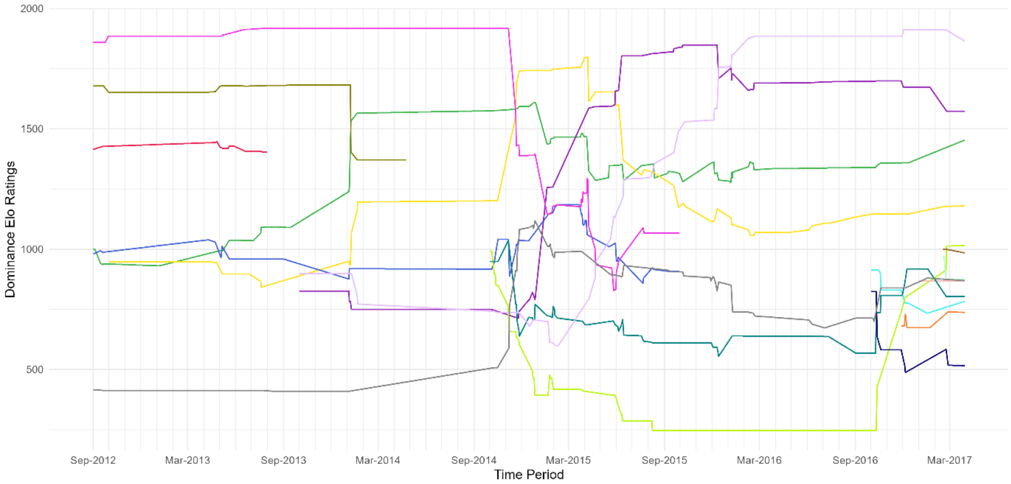

Figure S1. Dominance hierarchy of the group ASM from September 2012 to March 2017. Colours refer to the different adult males in the group during the time period.

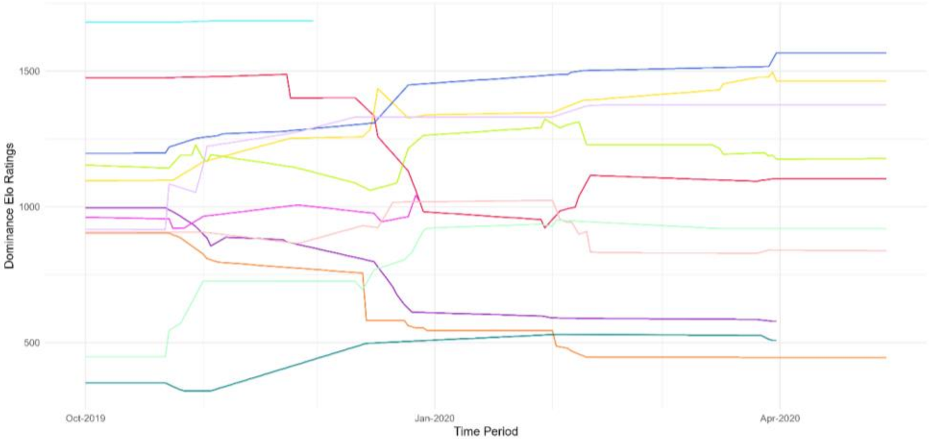

Figure S2. Dominance hierarchy of the group ASM from October 2019 to Apr 2020. Colours refer to the different adult males in the group during the time period.

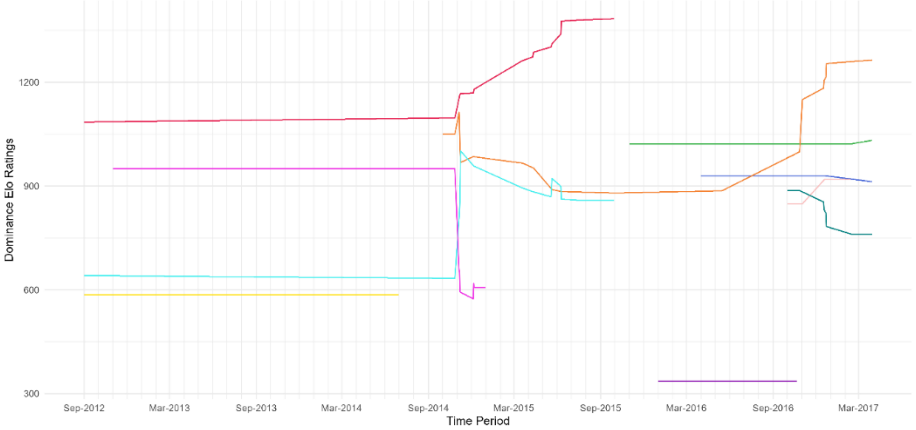

Figure S3. Dominance hierarchy of the group ASS from September 2012 to March 2017. Colours refer to the different adult males in the group during the time period.

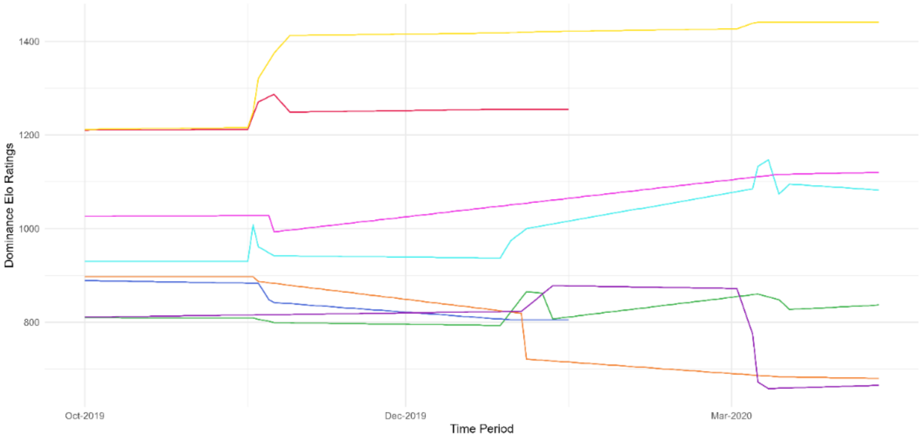

Figure S4. Dominance hierarchy of the group ASS from October 2019 to March 2020. Colours refer to the different adult males in the group during the time period.

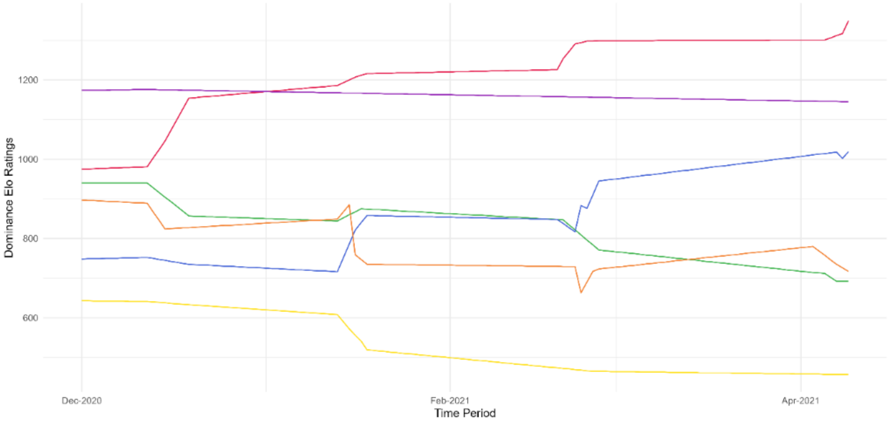

Figure S5. Dominance hierarchy of the group ASS from December 2020 to April 2021. Colours refer to the different adult males in the group during the time period.

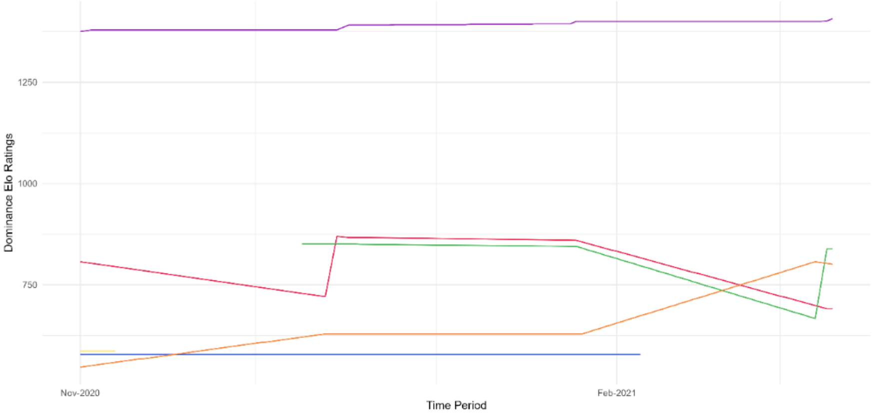

Figure S6. Dominance hierarchy of the group MS1 from November 2020 to March 2021. Colours refer to the different adult males in the group during the time period.

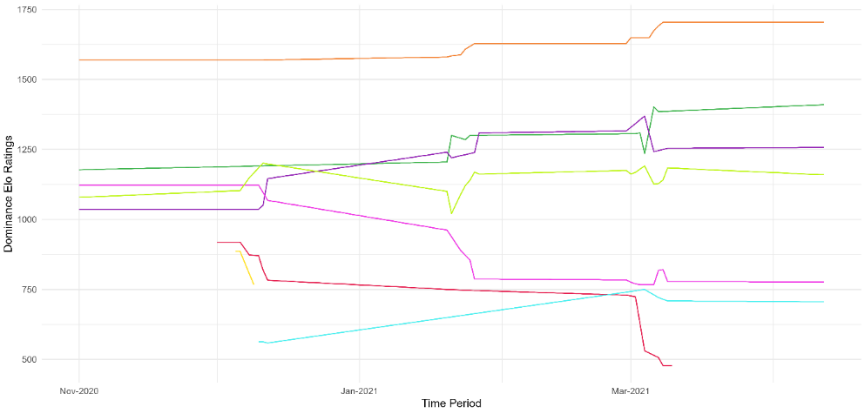

Figure S6. Dominance hierarchy of the group MS2 from November 2020 to April 2021. Colours refer to the different adult males in the group during the time period.

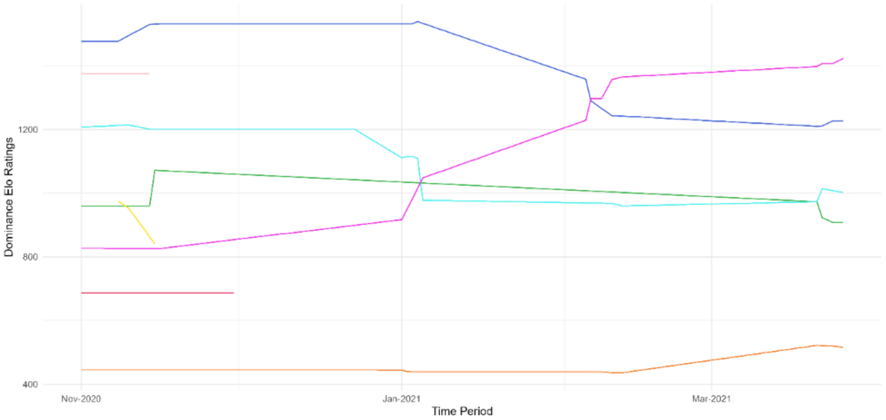

Figure S7. Dominance hierarchy of the group MS3 from November 2020 to April 2021. Colours refer to the different adult males in the group during the time period.

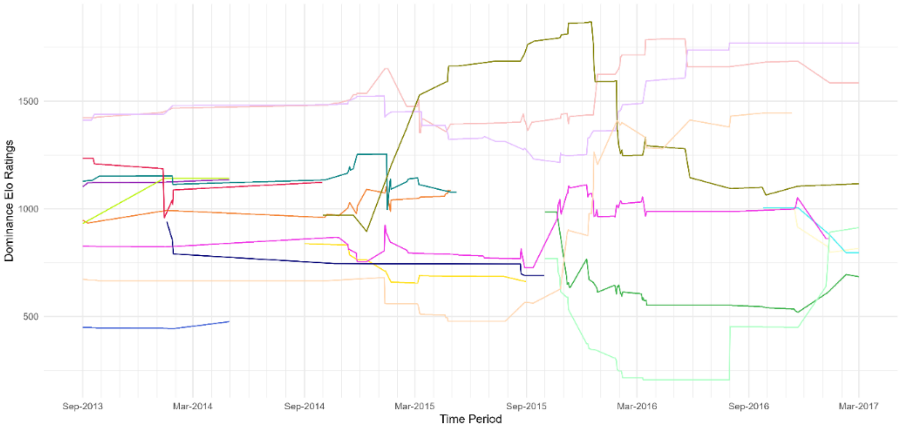

Figure S8. Dominance hierarchy of the group OTH/MOT from September 2013 to March 2017. Colours refer to the different adult males in the group during the time period. This is one group but a sub-group splintered off in 2014, hence the name change.

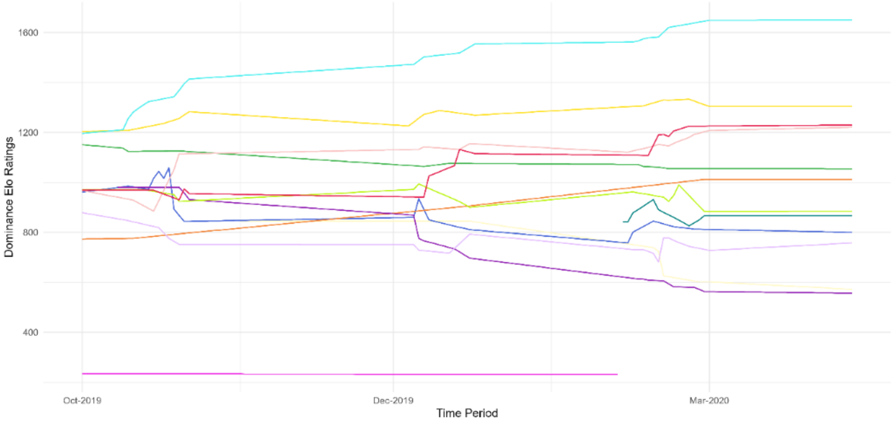

Figure S9. Dominance hierarchy of the group MOT from October 2019 to April 2020. Colours refer to the different adult males in the group during the time period.

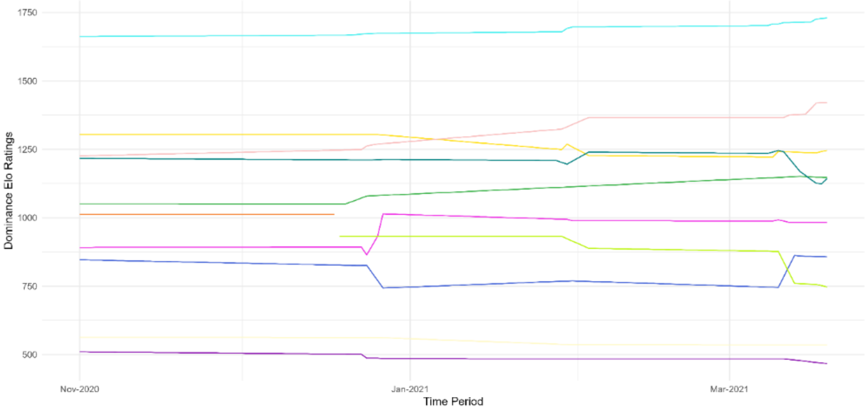

Figure S10. Dominance hierarchy of the group MOT from November 2020 to April 2021. Colours refer to the different adult males in the group during the time period.

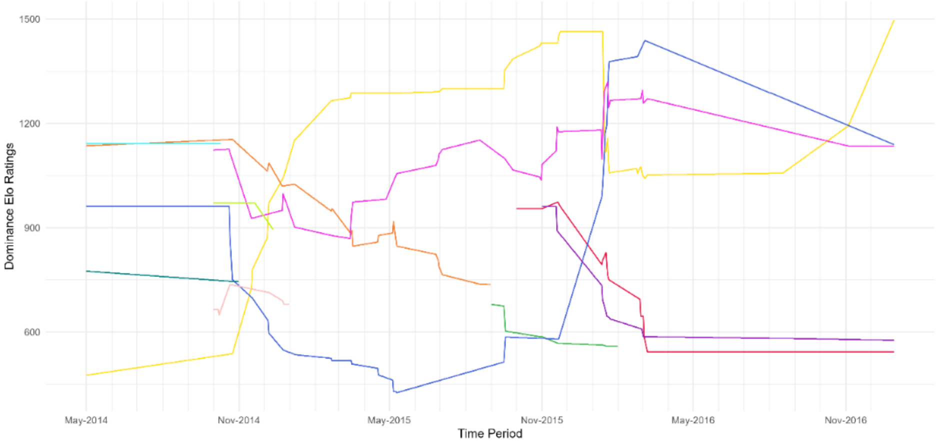

Figure S11. Dominance hierarchy of the group SOT from May 2014 to December 2016. Colours refer to the different adult males in the group during the time period.

3: Output for all months for Period 1 (model 1) and Period 2 (model 2)

Table S5. Glucocorticoid levels in relation to the month of sample collection for Period 1 (model 1). Number of males = 15, number of samples = 1778. Estimate = random intercept for the predictor, CI = 95 % credible intervals, Pr = proportion of the posterior samples that fall on the same side of 0 as the mean. Predictors shown have a higher certainty of effect (above 0.9) are in bold.

Predictor	Estimate	SD	CI lower	CI upper	Pr
January	0.27	0.25	-0.23	0.79	0.87
February	**-0.71**	**0.26**	**-1.22**	**-0.19**	**0.99**
March	**-0.55**	**0.23**	**-1.02**	**-0.10**	**0.99**
April	-0.21	0.23	-0.68	0.24	0.83
May	0.14	0.23	-0.32	0.61	0.75
June	0.15	0.24	-0.32	0.62	0.75
July	**-0.60**	**0.24**	**-1.08**	**-0.14**	**0.99**
August	-0.04	0.24	-0.51	0.43	0.57
September	**1.07**	**0.24**	**0.61**	**1.55**	**1.00**
October	0.25	0.26	-0.26	0.77	0.84
November	0.05	0.26	-0.45	0.57	0.57
December	0.18	0.25	-0.31	0.70	0.77

Table S6. Glucocorticoid levels in relation to the month of sample collection for Period 2 (model 2). Number of males = 58, number of samples = 2352. Estimate = random intercept for the predictor, CI = 95 % credible intervals, Pr = proportion of the posterior samples that fall on the same side of 0 as the mean. Predictors shown have a higher certainty of effect (above 0.9) are in bold.

Predictor	Estimate	SD	CI lower	CI upper	Pr
January	**-0.36**	**0.18**	**-0.73**	**-0.005**	**0.98**
February	-0.08	0.18	-0.44	0.28	0.67
March	-0.18	0.16	-0.51	0.14	0.89
April	-0.10	0.16	-0.43	0.22	0.75
May	0.16	0.16	-0.17	0.48	0.84
June	0.16	0.17	-0.17	0.50	0.85
July	**-0.37**	**0.16**	**-0.70**	**-0.05**	**0.99**
August	-0.17	0.17	-0.51	0.16	0.86
September	**0.65**	**0.18**	**0.31**	**1.01**	**1.00**
October	**0.59**	**0.18**	**0.23**	**0.96**	**1.00**
November	0.03	0.18	-0.32	0.39	0.58
December	**-0.28**	**0.18**	**-0.65**	**0.07**	**0.95**

4: Plots of monthly GC levels from years where samples were not collected in every month

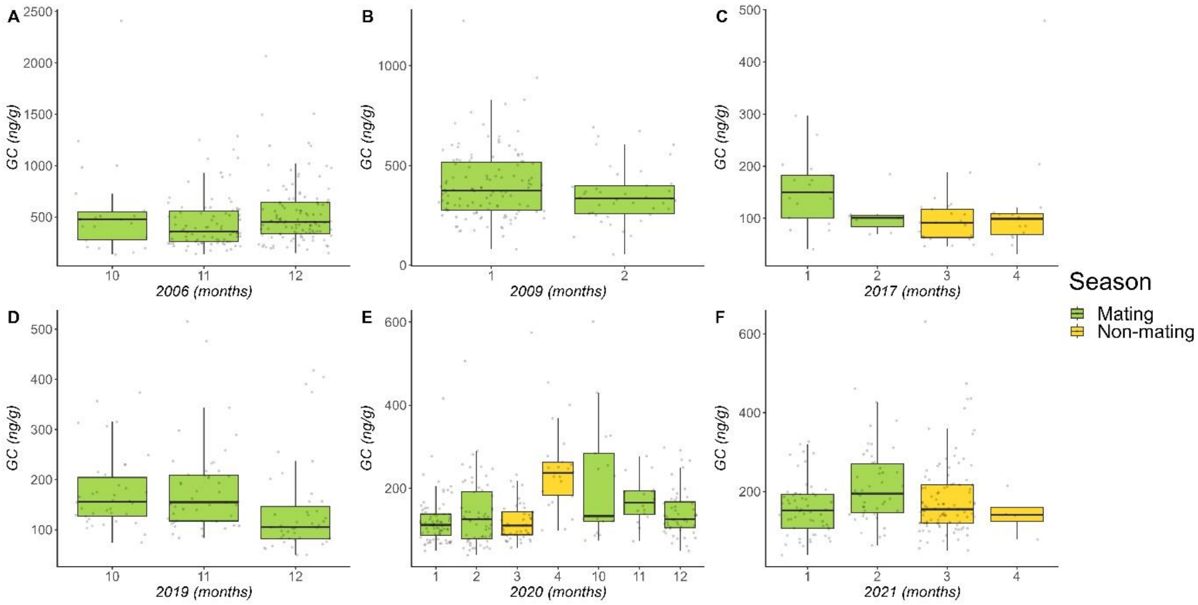

Figure S12. Monthly levels of GC values in years when samples were not collected in every month. ***A, B:*** *GC values (ng/g dry weight) per month for the first period (model 1) in 2006 (A) and 2009 (B).* ***C, D, E, F:*** *GC values (ng/g wet weight) per month for the second period (model 2) in 2017 (C), 2019 (D), 2020 (E), and 2021 (F). Boxes depict the median and interquartile range of each month; the whiskers show 1.5*the interquartile range. Points are raw data (samples collected). Note the gap along the x axis in 2020 (E), samples were not collected from May – September.*

Chapter 4: General Discussion

In this thesis, I approached the costs and benefits of sociality from two angles. In Chapter 2 I described a refined panel of 42 microsatellites, conserved within catarrhine primates. Combined with genotyping-by-sequencing, the panel addresses methodological issues within microsatellites and allows for rapid, accurate quantification of genetic variation in addition to easier collaboration between researchers. In Chapter 3, I examined the short-term impacts of sociality and competition by assessing the correlated glucocorticoid response to social dynamics in wild male Assamese macaques. Contrary to previous work on this species and study population, I reported evidence for the cost of dominance hypothesis: high dominance status correlated to elevated GC values, across all groups and time periods. However, in Period 1, alpha male status was associated with lower GC output. I also found evidence for a social buffering effect in Period 1, as dynamics in the strength of a male's top affiliative relationship correlated to the dynamics in the GC response. Males who invested in their top relationship, increasing its strength, showed a subsequent decrease in GC values. I also reported a seasonal upregulation of GCs in my study species, likely to be both a preparative increase and due to the energetic demands of competition. In the current chapter, I discuss my results in a broader context, highlighting potential implications and applications of my work. I also briefly discuss the results of correlating 14 social bonding metrics in more detail, which was used in Chapter 3 to determine the suitability of the dynamic bonding metric.

4.1 Microsatellites of the future

Microsatellites are among the most popular methods for studying the genetic consequences of sociality, although as I discussed in Chapter 1, there is much debate over which genetic markers provide the optimal mix of accuracy, reproducibility, and cost-effectiveness (Flanagan and Jones, 2019). Many of the issues currently facing microsatellites can be ameliorated by the panel I present in Chapter 2, which is an excellent tool to further their use in catarrhine primates and has been validated using blood samples from ten catarrhine species and degraded faecal samples from Guinea baboons.

Individual studies of catarrhine primates involving microsatellites typically use bespoke panels that share similarities with those of closely related species (e.g. Engelhardt et al., 2017; De Moor et al., 2020) as a consequence of their imperfect cross-species amplifiability (De Barba et al., 2017). This approach hinders comparisons between studies or species, which may be of particular interest to researchers. Conservation strategies utilise genetic diversity metrics to asses which population or species is most at risk and therefore requires the most urgent management (Wang et al., 2017). However, if one panel of microsatellites contains loci that are significantly more polymorphic, this can result in an ascertainment bias and an overestimation of genetic diversity (Queirós et al., 2015). Similarly, fundamental research into primate sociality often combines microsatellite analysis with behavioural data to understand the relationship between genetics and sociality (Cords et al., 2018), with broader inferences about the evolution and fitness consequences elucidated through cross-species comparisons (Ostner and Schülke, 2018). However, different panels of microsatellites are under differing rates of selection and mutation (Bhargava and Fuentes, 2010) making such inferences difficult to draw. Finally, varying practices between labs including different methods of allele identification and calling through to PCR conditions result in most microsatellite data being unique to that particular lab or study species (Miller et al., 2019). The need for more comparable microsatellite data between and within species has been consistently recognized (Barbian et al., 2018; De Barba et al., 2017; Guichoux et al., 2011; Miller et al., 2019; Moran et al., 2006). This panel offers a pathway to resolving some of these problems in catarrhine primates.

4.1.1 Minimised errors and improved accuracy

Two of the primary sources of error in microsatellites, namely null alleles and allelic dropout (Rico et al., 2017; Silva et al., 2017) are minimised with this panel. Of the 275 previously published loci tested in Chapter 2 (see Chapter 2, Table S6: https://doi.org/10.1002/ece3.7069), only 18% met our strict criteria for cross-species amplification across catarrhine primates. Each loci excluded had one or more features that can result in allelic dropout; primarily mismatches in primer regions, large variation in PCR product size, and multiple binding sites or monomorphism (Fox et al., 2019). For over half of the screened loci (53%) one or both of the primers bound at least partially within a repeat region. Moreover, 12% of the loci produced PCR products of over 350bps, making them unsuitable for degraded DNA samples like hair or faecal material commonly used in primate genetic studies (Arandjelovic and Vigilant, 2018) and more prone to producing null alleles (Putman and Carbone, 2014). By redesigning the primers to ensure that the PCR lengths are comparable, of a similar length, and that there were no nucleotide polymorphisms or indel (insertion–deletion) mutations in the primers, the panel should have a lower error rate for Old world primates than many currently published.

Despite this, some modifications to the panel could improve its efficacy, like the inclusion of Y-chromosome and X-chromosome markers to facilitate sex and individual identification in one working step. Y-chromosomal markers are frequently difficult to develop for non-model species due to a number of reasons, including a lack of polymorphism (Lawson Handley et al., 2006) or the differing structure of the chromosome itself (Greminger et al., 2010). Moreover, the development of Y-chromosome markers is hindered by the lack of male reference genomes. For the in-silco primer development in Chapter 2, only five non-human Y-chromosome sequences were available at the time and only two (*Pan troglodytes* and *Macaca mulatta*) were subsequently able to be tested with blood samples. There are promising methods to include Y-chromosome markers such as to test human Y-chromosome markers as they are published (e.g. Li et al., 2020). Equally, de novo microsatellite markers are still being developed for primates and could be added to the panel. For example, a recent study that published new *Papio* and *Theropithecus* Y-chromosome microsatellites (Mutti et al., 2023) is a highly promising resource to be tested using the in-silco methods from Chapter 2, in order to incorporate a Y-chromosome marker into the panel.

The microsatellite panel in Chapter 2 is supplemented by the use of GBS for analysis. GBS consistently detects previously unknown alleles (Barbian et al., 2018; Šarhanová et al., 2018; Vartia et al., 2016) which increases the statistical power of each locus. For example, in Chapter 2, nine of the loci contained previously unknown cryptic alleles (alleles of the same length but with a different sequence). As more individuals and species get tested, this number is likely to increase and will provide a greater accuracy and a higher statistical power for the panel. The proportion of new cryptic alleles to those previously identified by fragment length analysis varies between study species but is often high; for example 31% in chimpanzees (Barbian et al., 2018) and 53% for a study in the mushroom *Armillaria ostoyae* (Lepais et al., 2020). The greater statistical power may be of particular relevance for species of conservation risk or with low genetic diversity (Hohenlohe et al., 2021; McLennan et al., 2018). Equally, the core panel of 20 loci is more than most primate studies use (Day et al., 2018; De Moor et al., 2020a; Li et al., 2020; Minkner et al., 2018) with the option to add up to 22 extra loci as needed (e.g. for paternity exclusion). Therefore, the panel can offer noticeably more statistical power to resolve research questions than many currently available.

4.1.2 Comparable genetics

Of equal importance is that GBS produces microsatellite data that is independent of the sequencing platform, which allows for the comparison and pooling of data across studies and labs (Miller et al., 2019). In Chapter 2, I added further evidence for the suitability of the CHIIMP bioinformatic pipeline (Barbian et al., 2018) for the genotyping and analysis of primate microsatellite data. The CHIIMP pipeline has the advantage of not needing any extra programs to call alleles, unlike other GBS options (Lepais et al., 2020; Pimentel et al., 2018; Šarhanová et al., 2018). GBS is also becoming more cost-efficient, particularly with increasing sample numbers

(Darby et al., 2016) and the decreasing cost of NGS technology (Metzker, 2010). Therefore, our panel in combination with CHIIMP can quickly generate accurate genetic data that is comparable across labs. However, GBS and CHIIMP are not without issues. A comparison of GBS programs including CHIIMP reported high rates of false alleles (an allele-like artifact generated by PCR) (Salado et al., 2021) and issues with false alleles have been reported in other GBS studies (Donaldson et al., 2020). Therefore, while much of the genotyping process has been automated, CHIIMP as yet does not provide a standardised analytical pipeline that fully minimises researcher error and the need for expert judgement in deciding what is an allele and what is not. In addition, to compare and share microsatellite data, the loci need to be analysed using the same (or close enough) methods; such as the same primers and downstream processing. To this end, I am part of an ongoing project with a Masters' student to develop a Python script and GUI to further automate this process and make a fully standardised and comparable pipeline for catarrhine primates and CHIIMP.

Many fundamental facets of primate sociality cannot be understood without genetic data, such as preferential bond formation with close kin to maximize the indirect genetic benefits of affiliative relationships (Eberhard, 1975; Hamilton, 1964). Despite the rise of SNPs and the increasing viability of whole genome sequencing (Ekblom and Wolf, 2014; Hauser et al., 2021; Zimmerman et al., 2020); the numerous advantages of microsatellites have meant that they remain a valuable method for investigating the long-term fitness consequences of sociality. For example, previous paternity analysis on my study population of Assamese macaques directly informed my research into the hormonal correlates of sociality (see this chapter, section 4.6). Equally, combining the microsatellite panel with my work in Chapter 3 on glucocorticoids suggests an interesting avenue of research. Glucocorticoids are repeatable within individuals (Tkaczynski et al., 2019) and also heritable (Stedman et al., 2017), including in primates (Fairbanks et al., 2011). Thus far there are relatively few field-based estimates of glucocorticoid heritability, which can help to elucidate how selection acts on GCs and the stress response (Taff et al., 2018). Combining the microsatellite panel with the long-term hormonal data in my study population would be an excellent way to address this.

To sum, the microsatellite panel developed in Chapter 2 is a promising step towards improving research, either applied or more theoretical into catarrhine species, with universally amplifiable loci that provides a greater accuracy of genetic variation, with higher statistical power and fewer errors. Combined with a standardised pipeline that I am helping to further develop, the panel provides an exciting tool to facilitate data sharing and collaborative work between labs or researchers, something that has been cited as a key step for future research into human genomics and wildlife conservation genetics (Ahmed et al., 2023; Hohenlohe et al., 2021) and could further our knowledge of the long-term consequences of sociality.

4.2 Tough at the top: GCs and dominance rank

In Chapter 3, I investigated the short-term consequences of sociality and in contrast to my prediction, I found a positive association between dominance rank and GC in male Assamese macaques, spanning 15 years of data from over 60 individuals in six groups, including the time period of the previous work on this population (Ostner et al., 2008a). While there are many examples of glucocorticoids showing no correlation to male rank position in vertebrates, including humans and primates (Beehner and Bergman, 2017; Edwards et al., 2020; Fedurek et al., 2023; Hudson et al., 2019; Preis et al., 2019), if a direct relationship was reported, there is a clear pattern. In male group-living mammals, when dominance status correlates with GCs there is more evidence for the cost of dominance hypothesis i.e. higher ranked males show elevated GC levels compared to subordinates (Beehner and Bergman, 2017). Male Assamese macaques are consistently cited in the primate literature as an exception that proves the rule (Cavigelli and Caruso, 2015; Thierry et al., 2023) as the first evidence from this species suggested that lower ranked males had, on average, higher GC values during the mating season (Ostner et al., 2008a). Assamese macaques were thought to be unusual and fulfilled the cost of subordination hypothesis (Abbott et al., 2003) but with good reasons: a low-contest competition potential (Ostner and Schülke, 2014), an inexpensive pathway to higher rank via strong social bonds (Schülke et al., 2010), and no energetic cost of mate guarding (Schülke et al., 2014). However, in my thesis I provide contrasting evidence and suggest that in line with many male primates and mammals more generally, Assamese macaques match the predictions of the cost of dominance hypothesis, with high status being physiologically costly.

4.2.1 Mechanisms for the cost of dominance

The relationship between high male dominance status and elevated GCs is thought to be driven by the energetic demands of competition with co-resident males to achieve and maintain dominance rank (Goymann and Wingfield, 2004). In male primates, the rate of aggressive behaviour has been suggested to be the mechanism behind the correlation between rank position and GCs, such as in chimpanzees (Muller et al., 2021) and gray-cheeked mangabeys (*Lophocebus albigena*) (Arlet et al., 2009). For Assamese macaques, aggression may be a saliently costly behaviour as elevated aggression rates are likely to be (at least partially) behind the observed upregulation of GCs at the onset of the mating season (see Section 4.5). For males in Period 1

(October 2006 – March 2009) coalitions between bonded male partners are a key pathway for rank acquisition and maintenance (Schülke et al., 2010). The majority of coalitions from this period were directed down the hierarchy at lower ranked individuals in conservative coalitions, used by high status males to maintain rank (Young et al., 2014c, 2014b). These coalitionary aggressions may have imposed an energetic cost on higher ranked males and partially be driving the observed relationship between dominance ranks and GCs.

As I discussed in Chapter 3, the varying numbers of males and sexually receptive females within the study groups over the years could have promoted the use of alternative tactics for achieving dominance status. This likely includes more direct competition but could also promote more levelling or rank-changing coalitions if partners were available. Males can increase their long-term status or short-term access to females by forming rank-changing coalitions or by temporarily decreasing the priority of access across ranks through levelling coalitions that break up mate-guarding by dominant males (Bissonnette et al., 2014; van Noordwijk and van Schaik, 2004; Young et al., 2014c). In groups with a greater monopolisation or contest potential, the profitability of rank-changing or levelling coalitions increases but the number of available partners decreases, making them harder to achieve (Noë, 1994; Pandit and Van Schaik, 2003; Van Schaik et al., 2004). The best evidence of male primates pursuing alternative dominance strategies, dependent on the contest potential, comes from comparisons between large, provisioned groups of Japanese and rhesus macaques with smaller, wild-foraging groups of the same species: males in the larger groups queued for dominance ranks whereas in the smaller groups they competed more directly (Georgiev et al., 2016; Sprague et al., 1998). Nepal gray langurs (*Semnopithecus schistaceus*) also show alternative competitive strategies (immigrant and wait vs. aggressive alpha takeover) but the drivers behind these are not yet clear (Borries et al., 2017). Two non-exclusive mechanisms could therefore be behind the relationship between rank and GCs in Assamese macaques. Firstly, the energetic costs of conservative coalitions, likely prevalent Period 1; combined with secondly, more direct, aggressive competition and rank-changing or levelling coalitions in Period 2.

4.2.2 Alpha male status

In Period 1, alpha male status was unexpectedly correlated to lower GCs, which may be a consequence of a social buffering effect (see Section 4.3) but could also be related to alternative strategies of dominance competition. The alpha male likely maintained his status through recruiting support from his bonded partners in coalitionary aggressions, with stronger bonds resulting in a greater success in soliciting support (Young et al., 2014b). The presence of reliable coalition partners may have allowed the alpha male to reduce his engagement in energetically costly aggressions, producing the opposite pattern to species where alphas compete more intensely (Gesquiere et al., 2011), or conferred a reduced exposure to psychologically stressful rank changes (Levy et al., 2020a). In addition, the social environment of Period 1 was predictable and stable, averaging only 0.38 adult male immigrations and 0.63 emigrations per season-year compared to 3.25 immigrations and 3.13 emigrations per season-year across the groups in Period 2. A stable social environment has been shown to minimise the stress response of humans in leadership positions (Sherman and Mehta, 2020) and was suggested to be why, in a recent study comparing Tonkean and long-tailed macaques, higher GC values were reported in the Tonkean macaques, who have less predictable social relationships (Sadoughi et al., 2021). However, as the association between alpha status and lower GCs is likely driven by one individual (Figure 1, Chapter 3), it should be interpreted with the appropriate degree of caution.

Given the wide range of group sizes and possible contest potentials in my study groups, elucidating the mechanisms behind the cost of dominance in male Assamese macaques should be feasible. In my study, I used the rates of aggression a male received as a predictor in my analysis, as it is a key variable in the cost of subordination hypothesis (Abbott et al., 2003), which I was explicitly testing. However, the cost of dominance hypothesis suggests that the energetic demands of competitive behaviours affect the correlation between GC and dominance status and thus rates of aggression given by an individual is often the primary variable linked to GC production (Creel, 2022; Muller et al., 2021). Therefore, further examination of the mechanisms in my study population could take this into account as well as additional factors such as the hierarchy stability (Higham et al., 2013), alpha male tenure, types of coalitionary aggressions, or utilising the dynamic method of assessing social changes I demonstrated for social bonding (see Chapter 3).

Dominance status: cost or benefit?

Maintaining a high dominance status is associated with some costs for males including a greater parasite or infection risk (Romano et al., 2022) or an accelerated epigenetic aging process (Anderson et al., 2021). Dominant individuals could also have an increased risk of oxidative stress, as has been reported in rhesus macaques (Georgiev et al., 2015) and mandrills (*Mandrillus sphinx*) during unstable dominance hierarchies (Beaulieu et al., 2014), which can lead to peripheral tissue damage and impairments to cell signalling (Metcalfe and Alonso-Alvarez, 2010). However, highly ranked male Assamese macaques sire a greater proportion of offspring (Sukmak et al., 2014) and high status for male primates provides numerous benefits that are worth the energetic investment in competition; such as an increased reproductive success, access to food, and mating opportunity (Majolo et al., 2012). There is no indication that higher ranked Assamese macaques have any negative fitness consequences as a result of their rank position, not least because they avoid the deleterious consequences of lower social status (Shively et al., 2023; Snyder-Mackler et al., 2016).

Nevertheless, the question remains: are the greater physiological demands of competition that dominant male Assamese macaques incur, i.e. elevated levels of GCs, indicative of homeostatic overload? If a GC response is sustained and elevated above adaptive concentrations, then this could induce short-term costs due to homeostatic overload and chronic stress (Romero et al., 2009), although there is little evidence for this in wild populations (Boonstra, 2013). Instead, the increased GC responses are likely to be adaptive, at least in the short-term, as they allow dominant males to respond to challenges (Schoenle et al., 2018) and maintain their high status; rather than indicative of chronic stress or homeostatic overload. However, over a longer timeframe, the elevated GCs could begin to incur costs for dominant Assamese macaques. Recent evidence has suggested that repeated upregulation can lead to somatic damage due to wear and tear, as has been reported in a recent meta-analysis (Schoenle et al., 2021) and in female baboons (Campos et al., 2021). Elevated GCs are linked to negative health consequences in humans, such as depression (Gillespie and Nemeroff, 2005) and dominant captive long-tailed macaques developed higher levels of coronary artery atherosclerosis under high levels of male-male competition (Kaplan et al., 2009). Any costs of elevated GCs in dominant Assamese macaques are likely to be cumulative and may only start to have consequences in later life, possibly after dominance status has been lost (Glucocorticoid Cascade Hypothesis: Sapolsky et al., 2002) . Additionally, glucocorticoids are only one part of a broad suite of physiological responses to sociality and can act synergistically (or antagonistically) with other hormones, including testosterone to affect costs or benefits.

Testosterone, the male sex hormone, cognitively primes individuals for competition (Oliveira, 2004) and is upregulated in response to periods of social challenges, such as during the mating season or when dominance hierarchies are unstable (Wingfield et al., 1990). Testosterone stimulates reproductive effort and competitive behaviour, which in male primates can manifest as promoting rates of male-male aggression (Muller, 2017). However, elevated testosterone can also impose costs on individuals as its anabolic function generates an energetic demand and may impair immune function (Foo et al., 2017; Muehlenbein and Bribiescas, 2005). Testosterone can also interact with GCs, as suggested by the Dual-Hormone hypothesis (Mehta and Josephs, 2010). Developed from research into humans, this hypothesis posits that high cortisol levels block testosterone from promoting competitive or status seeking behaviour (Knight et al., 2020). Although a recent meta-analysis found only weak evidence for the hypothesis (Dekkers et al., 2019), it has received little research in wild populations thus far (but see Goll et al., 2023) and provides another potential pathway by which elevated GCs could affect males. Previous research has shown that male Assamese macaques in Period 1 have no difference in testosterone output between dominant or subordinate individuals (Ostner et al., 2011). However, given the contrasting results of my thesis with our earlier GC work, a re-evaluation of the relationship might highlight additional hormonal costs or benefits for dominant male macaques.

4.3 Friends with benefits: GCs and social buffering

As I discussed in the previous section, it is unlikely that wild Assamese macaques are under chronic stress but if the challenges an individual faces are particularly extreme, unexpected, or compounded by group-wide stressors, they run the risk of inducing homeostatic overload (Taborsky et al., 2022). An attenuated HPA axis through the social buffering effect can therefore minimise the potential risks of elevated GCs (Hennessy et al., 2009). Assamese macaques are the third species of male primates for whom we have evidence of the social buffering effect in adult male-male affiliative relationships (Wittig et al., 2016; Young et al., 2014a). Previously an aggregate score of relationship strength in male Barbary macaques was shown to correlate with the attenuation of the GC response to aggression received from male group members (Young et al., 2014a). Also using an aggregated sociality score, male chimpanzees had a reduction in their GC production when interacting with or in the presence of a closely bonded partner and this attenuation occurred both during highly stressful events as well as during social interactions (Wittig et al., 2016). In Chapter 3, I found evidence of a dynamic social buffering effect in Period 1: dynamics in the strength of the top affiliative relationship were correlated with the GC response.

An attenuated GC response to a challenge may provide a pathway for bond maintenance in male Assamese macaques. An experimental study in humans demonstrated that feelings of “personal closeness” not only decreased cortisol levels but also that individuals with low cortisol had partners that desired to be closer to them (Ketay et al., 2017). Conversely, moderate increases in GCs can motivate individuals to engage in affiliative behaviour, possibly as a means to maintain or repair bonds and solicit social support (Raulo and Dantzer, 2018). Broadly, the buffering effect of a relationship or ability to attenuate GCs is predicted to be most effective with strong and stable partners (Kikusui et al., 2006). Therefore, given that I found evidence for dynamics in social buffering, with changes in an individual’s top social bond correlating to the GC response, it is possible that the buffered HPA axis (or loss of the buffering effect) from social support reinforced the need for bonds and acted as a mechanism for bond maintenance in my study population.

GCs may also have interacted with oxytocin, another hormone strongly linked to both social buffering and bonding (Wu, 2021). Bond maintenance (and formation) is thought to be driven partially by the effects of oxytocin (Rincon et al., 2020a; Ross and Young, 2009), a neuropeptide which can be released after positive affiliative interactions such as food sharing or grooming (Crockford et al., 2013; Samuni et al., 2018). Oxytocin could induce positive emotions through its interaction with the dopaminergic reward system (Dölen et al., 2013) and mediate social bonds through emotional bookkeeping (Schino and Aureli, 2009). For example, if oxytocin is released after interactions with bond partners, those interactions then become associated with positive emotions and reinforce the social bond (Romero et al., 2014). In addition, oxytocin has been shown to impact on the social buffering effect (Smith and Wang, 2014). An increase in hypothalamic oxytocin inhibits the activation of the HPA axis (DeVries et al., 2003) and oxytocin appears to limit GCs, although the exact pathway for this is still unclear (Crockford et al., 2018). Oxytocin may act synergistically with social support by not only enhancing the buffering effect (i.e. reduce the GC response) but could also encourage affiliative behaviour with bond partners, reinforcing the relationship and social support (Wu, 2021).

The social buffering of HPA activity due to social support (perceived or otherwise) is most likely related to fitness benefits that the partner can provide and as such preferred partners change over an individual's lifespan (Kiyokawa & Hennessy, 2018). In Period 1 of my study, there is a clear link between social bonds, support, and fitness (Schülke et al., 2010) and males who did not maintain the strength of their top affiliative relationship showed an increase in GCs. By contrast, investing in their top social bond and increasing its strength correlated with lower GC values, likely due to more predictable and frequent social support, which can reduce the stress of a challenge (Cohen & Wills, 1985; Hennessy et al., 2009). Males in other macaque species are aware of the relationships of their group members (Kubenova et al., 2017), thus strongly bonded Assamese males in Period 1 may have perceived that they could count on coalitionary support in conflicts more reliably than others, which could have contributed to the buffering effect. This might also be why I did not find evidence of a buffering effect in Period 2 if alternative dominance strategies with direct competition were more prevalent as suggested by the varying contest potentials. Males in Period 2 likely invested less in their social relationships, either due to a lack of partners or as a deliberate strategy and so did not have a reliable partner for coalitionary support who could also have provided a buffering effect. Equally, males preferentially bond with males that they are compatible with (Ebenau et al., 2019). The smaller group sizes and less stable social environment in Period 2 may have meant that males had fewer suitable partners to bond with and that they were unable to invest the time needed to build up the strength of their relationship.

Although males are typically the dispersing sex and may have fewer close kin for support or suitable partners, this is not the case for all primates. Male philopatry is found in a range of taxa (Milich, 2023) and was initially thought to be crucial for male-male bonds (Van Hooff and Van

Schaik, 1994). Many male philopatric species do form same-sex bonds (Bray et al., 2021; Dal Pesco et al., 2022; Verspeek et al., 2019) but even in species where males disperse, there is mounting evidence for male-male bonding (Berghänel et al., 2011; Neumann et al., 2022; Schoof and Jack, 2014; Stocker et al., 2020). It is therefore possible that the limited amount of evidence for male-male social buffering is simply that it has thus far not been discovered. It is also worth highlighting that the social buffering hypothesis is sometimes split into two, non-exclusive hypotheses (Ricci-Bonot et al., 2021): the main or direct effects hypothesis and the interaction hypothesis. The main effect hypothesis predicts that having a close social bond or bonds will have a general dampening effect on GC production, irrespective of the context (Wittig et al., 2016). The interaction effect hypothesis predicts that the attenuating effect of bonded social partner(s) on GC only occurs during a challenging or stressful event (Kikusui et al., 2006). Disentangling the two hypotheses can be complicated as changes to social bonding, stressors that induce a GC response, and the GC response itself can all impact an individual simultaneously but over different timescales (Hennessy et al., 2009; Wittig et al., 2016; Wu, 2021). By using the dynamic method I demonstrated in Chapter 3 and specifically linking GC responses to salient changes in social bonding, it may be possible to identify further examples of social buffering in male primates and to further refine the two hypotheses.

4.4 Dynamic social metrics

Social relationships can often appear stable, particularly if aggregated over a longer time period but, in reality they are constantly in flux and can be affected not only by an individual's behavioural choices but those of their fellow group mates too. Dominance hierarchies and affiliative relationships are dynamic systems with multiple feedback loops (Dehnen et al., 2022; Fisher et al., 2017) and dynamic methods are needed to understand them. In Chapter 3, I describe a method to include the dynamic nature of both affiliation and the GC response into questions about social buffering. By adapting the methods of Schülke et al. (2022) and correlating 14 metrics that compose the social bonding dimension of affiliative relationships, I found that the strength of a male's top affiliative relationship was consistently correlated to the summed strength of his top two or top three relationships across all groups and season-years (mean correlation coefficient ± standard deviation: top two = 0.90 ± 0.11; top 3 = 0.80 ± 0.19; Appendix, A1 – A10). An individual's top three relationships are frequently identified as key in studies of primate sociality (Ostner and Schülke, 2018); such as which relationships can be classified as social bonds (Silk et al., 2013) and have been used to assess social buffering (Young et al., 2014a). As might be expected, given that all of the metrics assessed broadly represent social bonding, many of the metrics showed positive correlations but the association between the top affiliative relationships was the most consistent. This is important in two respects. Firstly it allowed for the inclusion of more groups and data in Period 2. The group ASS at times dropped down to only two adult males present and often had less than five at a time so selecting a more traditional aggregated metric, like the summed strength of a males top two relationships would not have been possible (Appendix Figures A5 – A6). Secondly and perhaps more pertinently, as the top affiliative relationship is correlated to and representative of social bonding, changes to it represent salient changes in affiliation for the males. By matching these salient changes to specific hormone samples, ΔTopAff can capture the dynamics of social buffering. Rather than aggregated measures that may not accurately reflect the true costs and benefits of sociality, dynamic metrics like ΔTopAff can help to further our knowledge and improve our hypotheses. For male Assamese macaques, particularly in Period 1, a weakening top social bond has both fitness consequences and more immediate consequences, such as a lack of support in aggressions. Therefore ΔTopAff, which accounts for these types of relative changes in bonding rather than absolute values, may be able to better reflect the challenges individuals face and could be an exciting and biologically valid tool for future research.

4.5 Seasonal glucocorticoids

Attenuated HPA axis activity may be of particular importance during times of elevated social stress and competition; minimising any potential costs of elevated GCs while still allowing for an adaptive response to challenges. In Chapter 3, I showed that although there is not an overall seasonal difference in average GC levels between the mating and non-mating season, the start of the mating season corresponds to an upregulation of GCs for male Assamese macaques. The spike in GC production occurred more specifically just before the onset of the mating season in both periods, which matches the predictions of the preparative hypothesis. Additionally, elevated GC levels in Period 2 also extended into the mating season, likely due to the energetically demanding behaviours used in mating competition and providing evidence for the energy mobilisation hypothesis too.

A preparative increase in GCs allows for appropriate allostatic adjustments to predictable challenges, prior to the onset of the changing energetic requirements of the challenge (Sapolsky et al., 2000; Vera et al., 2017). Evidence of preparative spikes in GC production due to predictable challenges are more common in female mammals, for example due to the costs of lactation (Fürtbauer et al., 2014; Zhang et al., 2020) but it can also occur in males (Bauer et al., 2014; Girard-Buttoz et al., 2009). As Assamese macaques do not seem to incur an energetic cost from mate guarding (Schülke et al., 2014), this upregulation could be in preparation for increased male aggression during the mating season (Ostner et al., 2011, 2008a). A preparative spike, priming males for competition was suggested to be causing an upregulation in testosterone before the onset of the mating season in this population (Ostner et al., 2011) and similar patterns of testosterone excretion have been reported in other macaques (Higham et al., 2013; Rincon et al., 2017). Equally, the energetic costs of elevated competition, whether that is specifically aggressive behaviours or mating competition in general (Clutton-Brock and Huchard, 2013), appear to be at least partially driving the upregulation of GCs during the mating seasons of Period 2. There is compelling evidence for this across seasonally breeding mammals (Baker et al., 2013; Beehner and Bergman, 2017; Romero, 2002) but the distinction between the two hypotheses may be more blurred than it originally appears.

As GCs are highly multi-functional (MacDougall-Shackleton et al., 2019), neither hypothesis precludes the other. An argument could be made that GC upregulation as a consequence of energy mobilisation or as preparation for energetic demands both represent a supportive function; helping an organism to maintain homeostasis and respond to challenges (Vitousek et al., 2019). There appears to be a phylogenetically robust trend for the supportive functions of GCs in the face of both environmental and social challenges for tetrapods (Vitousek et al., 2019) and the distinction between preparative or energy mobilisation is less clear cut in birds, where seasonal elevations of GCs can fulfil both functions (Casagrande et al., 2018). The GC spike I reported in Chapter 3 therefore likely matches both hypotheses and the mechanism driving both could also be broadly the same i.e. elevated social competition. Further hormonal markers such as c-peptides or triiodothyronine which have a more specific energetic role could help to elucidate the specific drivers (Behringer et al., 2023; Surbeck et al., 2015; Touitou et al., 2021a) and may help to explain why in some years, no seasonal upregulation was observed (see Chapter 3, Figure 6). GCs can be influenced by a wide range of factors such as food availability or diet (Laver et al., 2020), temperature (de Bruijn and Romero, 2018), predation pressure (Monclús et al., 2009), and ranging patterns (Kaisin et al., 2023). Unusual events, either climatic (Young et al., 2019) or social, such as the three group splits that occurred during my study period, can have significant impacts on GC output. Long-term research projects involving multiple years, groups, and focal animals may be required to detect the true seasonal pattern (Sheriff et al., 2011) and the complex nature of my results highlights this.

4.6 The need for replication in long-term studies

As long-term field sites continue to accumulate data, more and more studies are built on top of groundbreaking work from decades ago (Alberts and Altmann, 2012; Chapman et al., 2017; Festa-Bianchet et al., 2017; Widdig et al., 2016). Advances in non-invasive and statistical techniques are opening up the possibility of asking ever more complex questions, using long-term data with repeated sampling of many individuals, often over the course of an animal's lifetime (e.g. Tung et al., 2016). The complex, multi-faceted nature of my results in Chapter 3 and many other studies show the value of long-term projects. However, it is equally important to re-evaluate older work on the same species, to utilise the wealth of data accumulated over the years. Differing results between populations of the same species are not unusual (e.g. in chimpanzees, Muller et al., 2021; Preis et al., 2019) but contradictory findings from the same population do occur. In a long-term study of male mountain gorillas (*Gorilla beringei beringei),* earlier research suggested a positive relationship between urinary testosterone and dominance rank but a recent re-analysis failed to detect any such relationship (see discussion in Rosenbaum et al., 2021). Similarly inconsistent results have been found in female baboons, suggested to be due to the methods of analysis, as correlations rather than mixed-models with random effects to control for variation were often used in earlier studies (Levy et al., 2020a).

In Chapter 3, I replicated and expanded on the result of seasonal changes in GC values from earlier work in my lab, with higher values in the mating season compared to the non-mating season over a single season-year comparison (Ostner et al., 2008a). However, I found contrasting evidence for the relationship between dominance rank and GC, which was initially reported to have a negative correlation: six lower ranked males had on average higher GCs during a single mating (Ostner et al., 2008a). As discussed in Chapter 3, there are a number of reasons behind the differing result such as more samples included in the study, an improved statistical methodology, and dynamic social metrics that have a greater precision and ability to capture the competitive structure. I also want to highlight the importance of re-analysing data with more knowledge about the study population. Further observations of the study population combined with genetic paternity analysis (using microsatellites) identified that younger males, who were previously excluded from analyses, were reproductively active and fully embedded in the adult male hierarchy (Sukmak et al., 2014). Including these males may go towards explaining my contrasting results.

My thesis shows the need for replication studies and re-analysis of long-term data, particularly if new biological insights gained over the years can be incorporated to improve the hypotheses and accuracy. Much has been written about the replication crisis within scientific research (Korbmacher et al., 2023; Shrout and Rodgers, 2018) and behavioural ecology is not immune from this (Filazzola and Cahill, 2021; Kelly, 2006). Long-term field studies provide an excellent opportunity to reassess old predictions and results, often on the same subjects but with a greater sample size and variation in data to detect patterns. For example, one male was present through all 15 years (as an adult!) of my study in Chapter 3 and many males remained in the study population for multiple years. Moreover, replications with a greater statistical power combined with long-term data can ensure that reported trends are consistent with the wider population and not a consequence of short-term or unusual environmental and social effects. In order to develop a firm understanding of the impacts of sociality, in both the long and short-term, repeated studies on long-term social data are essential.

4.7 A conservation toolkit

The methods I have discussed in Chapter 2 and 3 provide an exciting method for assessing the long-term and short-term consequences of sociality. In addition, both microsatellite and glucocorticoids are key markers for addressing conservation questions. They can be used non-invasively, as DNA and hormones can be extracted from a wide variety of animal matter like faeces or hair, making them suitable for use on rare or protected species (Costa et al., 2017; Palme, 2019)

Microsatellites are applicable to many of the key concerns in conservation including tracking the movement of wild animals (Hindrikson et al., 2017), illegal wildlife trade monitoring (Wasser et al., 2008), and resolving status or funding issues such as whether a population deserves unique protection status (Singh et al., 2015). By contrast, glucocorticoids are typically used to determine how a population responds to anthropogenic changes; ranging from habituation (Shutt et al., 2014), habitat degradation (Rimbach et al., 2013), and more general assessments of population health (Newediuk and Bath, 2023). Both markers are vital in the remote monitoring of populations (Boyle et al., 2021; Kerry et al., 2022) and aid with assessing the vulnerability of a species to climate change, habitat loss, or other anthropogenic disturbances. Microsatellites can identify risk factors including inbreeding depression or a low genetic diversity (Hohenlohe et al., 2021; Wang et al., 2019) whereas glucocorticoids highlight if a species is currently facing deleterious consequences from anthropogenic factors (Pérez-Ortega and Hendry, 2023); all of which confer a greater risk of extinction. Additionally, for some species, monitoring social relationships can have an in-situ conservation impact too; for example when faced with the removal of group members due to poaching (Parker et al., 2022). The use of dynamic, cardinal metrics could therefore be used to track the responses to such events more accurately and inform wildlife management actions. The integration of physiology, behaviour, and genetic methods will become increasingly important in the face of accelerated global biodiversity loss (Cooke et al., 2014; Galla et al., 2022) and in order to formulate appropriate conservation action plans and priorities, anticipating which species are most vulnerable to anthropogenic changes is vital (LeDee et al., 2021). The greater accuracy and cross-species applicability of the microsatellites I present in this thesis, in concert with non-invasive glucocorticoids and a dynamic social behaviour methodology could therefore be highly relevant for conservation decisions in catarrhine primates.

4.8 Conclusion

At the outset of this thesis, I aimed to investigate the costs and benefits of sociality from two angles. Firstly, I provide a microsatellite panel that can be used to assess the long-term consequences of sociality in Old world primates. Given its universal applicability to catarrhine species, the panel can facilitate comparative and integrative studies between species and studies. In addition, as it can more accurately assess genetic variation, the panel is an excellent tool for efficiently assigning parentage and determine kin relationships, which are key factors in the fitness outcomes of social relationships.

I also assessed the short-term impacts of sociality in male Assamese macaques. I demonstrated that male Assamese macaques are no longer an “exception that proves the rule” in male primates, who match the predictions of the cost of subordination hypotheses. Instead, they add further evidence for the cost of dominance hypothesis in male mammals. Even in a species with low-contest competition, such as Assamese macaques, dominant males in my study population showed elevated GC responses to competition and incurred a greater physiological cost. These physiological responses are likely to be adaptive, as was the preparative upregulation of GCs at the onset of the mating season, which may have primed males for the increase in competition to come. I also demonstrated dynamics in the social buffering response for the first time in a wild primate; which could have ameliorated the physiological demands of competition in my species and provide a mechanism for bond maintenance. By combining long-term data with a replication of earlier work from my lab and dynamic methods to assess sociality, I showed that life at the top of the hierarchy is a physiologically demanding place to be for male Assamese macaques but that having at least one friend might help while you’re there.

Future work could build on the foundations I have laid in this thesis and assess the interplay between sociality, physiological responses, and fitness. For example, dominant males who forgo social bonding may be able to gain a greater priority of access to females and an increased reproductive opportunity but could be at risk of a reduced lifespan due to the long-term consequences of elevated GCs. The microsatellite panel in Chapter 2, in concert with the dynamic matched-sample methods presented in Chapter 3 provide a pathway to assess if the physiological costs of competition and sociality affect long-term fitness in primates.

Appendix

1: Correlation plots of metrics representing aspects of the social bonding dimension of sociality, used to identify ΔTopAff (change in top affiliative Elo rating) as the metric of choice in Chapter 3.

The metrics are calculated at the individual level, based of affiliative Elo or DDSI values for the 15th of each month shown, February representing the mating season and September representing the non-mating season. May 2017 - September 2019 and May 2020 - September 2020 were excluded due to a lack of behavioural data. Figures A1 – A10 use the following abbreviations for the social metrics:

top_er = strength of the top affiliative relationship

sum_er = sum strength of the top two relationships

sum_t2 = sum strength of the top two relationships

sum_t3 = sum strength of the top three relationships

sum_er = sum total strength of all relationships

mean_er = mean strength of affiliative relationships (individual)

n_50 = number of relationships above the 50% strength value in the group

n_75 = number of relationships above 75%

n_90 = number of relationships above 90%

n_gm = number of relationships above the group median strength value

sum_50 = sum strength of relationship above 50%

sum_75% = sum strength of relationships above 75%

sum_90 = sum strength of relationships above 90%

n_r.t3 = number of top three relationships that were reciprocal

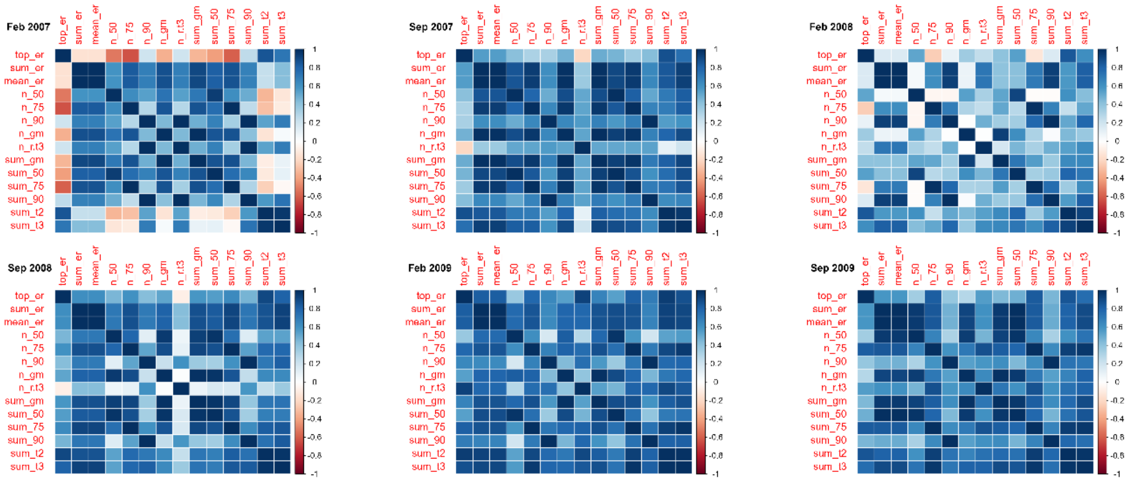

Figure A1: Correlation plots of 14 social metrics for the group AS that represent aspects of the social bonding dimension, based of affiliative Elo or DDSI values for the 15th of each month shown.

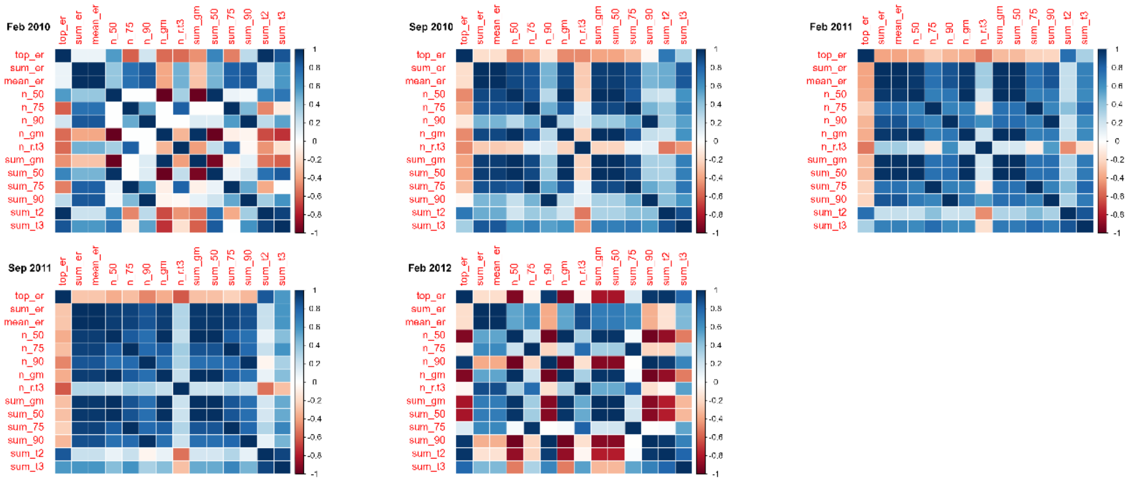

Figure A2: Correlation plots of 14 social metrics for the group AS that represent aspects of the social bonding dimension, based of affiliative Elo or DDSI values for the 15th of each month shown.

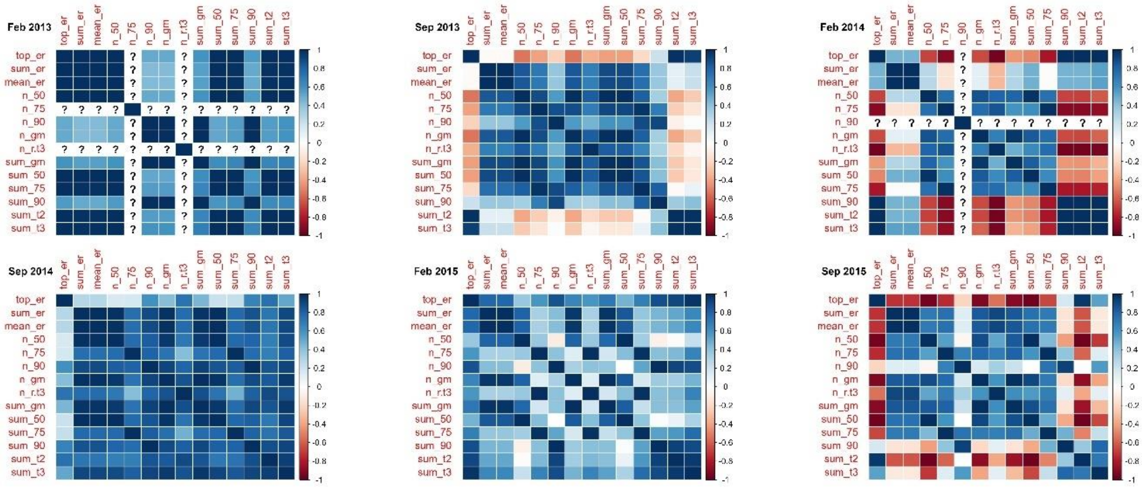

Figure A3: Correlation plots of 14 social metrics for the group ASM that represent aspects of the social bonding dimension, based of affiliative Elo or DDSI values for the 15th of each month shown.

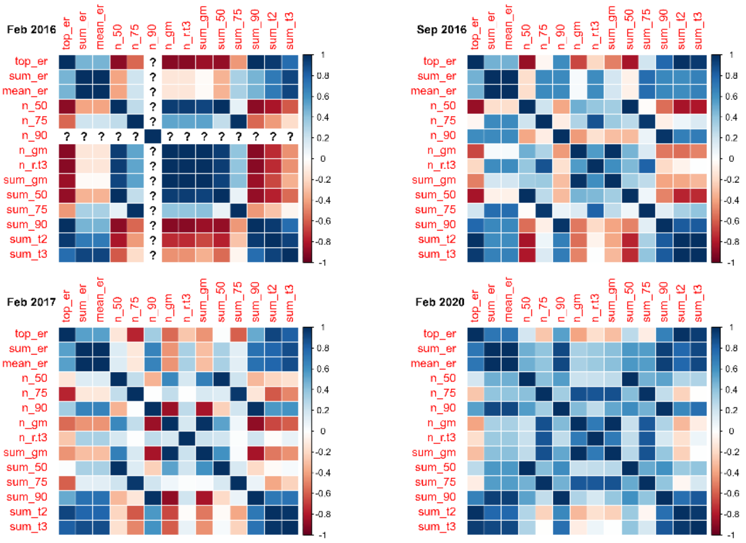

Figure A4: Correlation plots of 14 social metrics for the group ASM that represent aspects of the social bonding dimension, based of affiliative Elo or DDSI values for the 15th of each month shown.

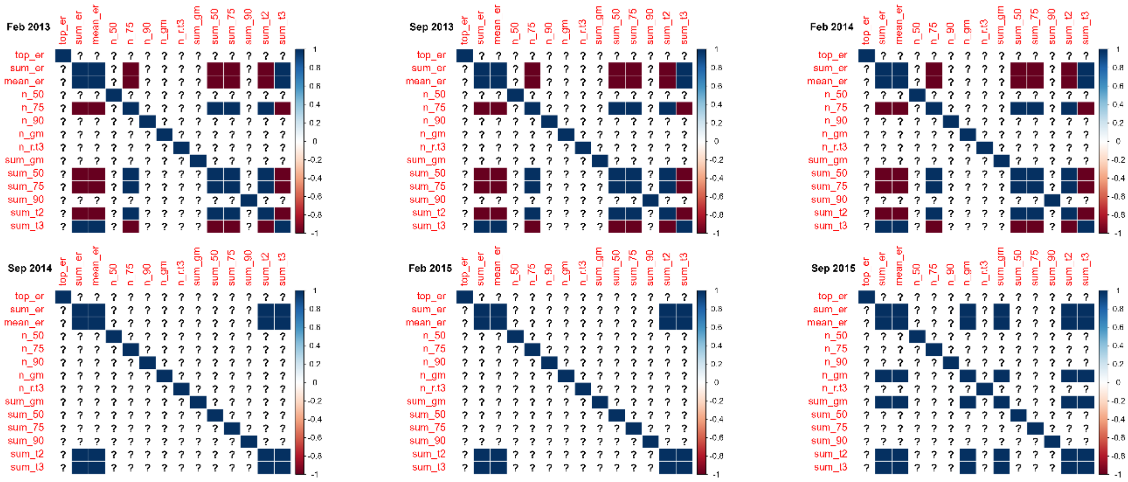

Figure A5: Correlation plots of 14 social metrics for the group ASS that represent aspects of the social bonding dimension, based of affiliative Elo or DDSI values for the 15th of each month shown.

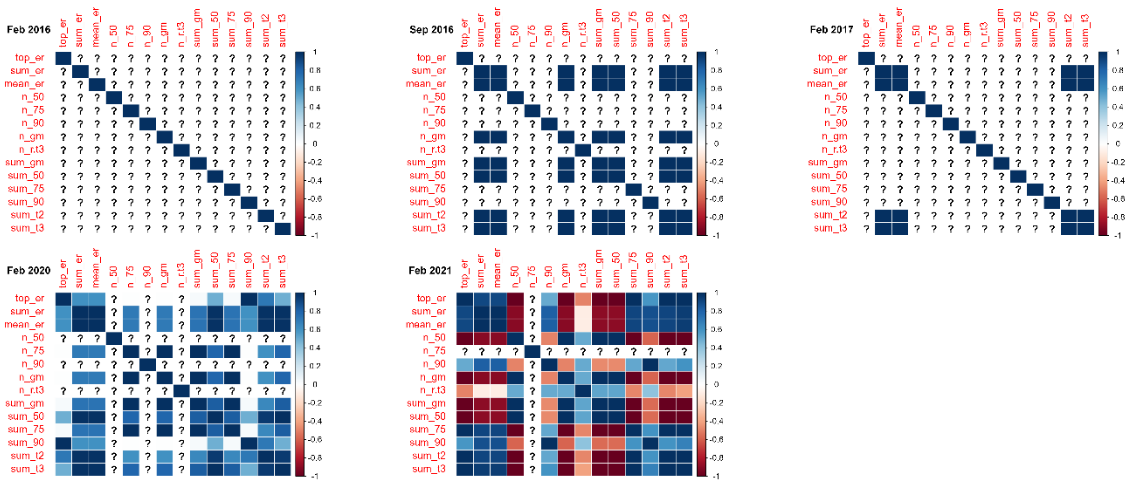

Figure A6: Correlation plots of 14 social metrics for the group ASS that represent aspects of the social bonding dimension, based of affiliative Elo or DDSI values for the 15th of each month shown.

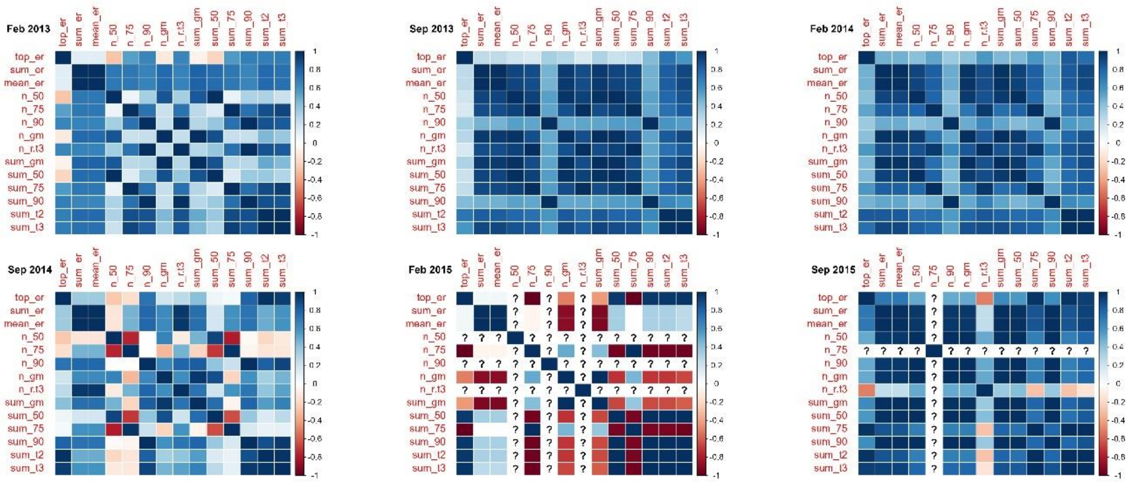

Figure A7: Correlation plots of 14 social metrics for the group OTH/MOT that represent aspects of the social bonding dimension, based of affiliative Elo or DDSI values for the 15th of each month shown. This is one group but a sub-group splintered off in 2014, hence the name change.

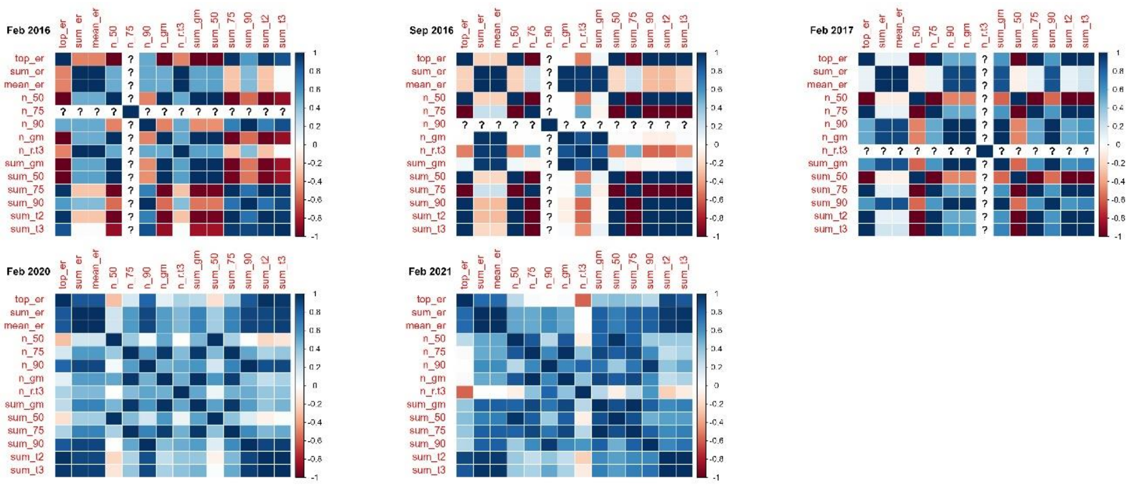

Figure A8: Correlation plots of 14 social metrics for the group MOT that represent aspects of the social bonding dimension, based of affiliative Elo or DDSI values for the 15th of each month shown.

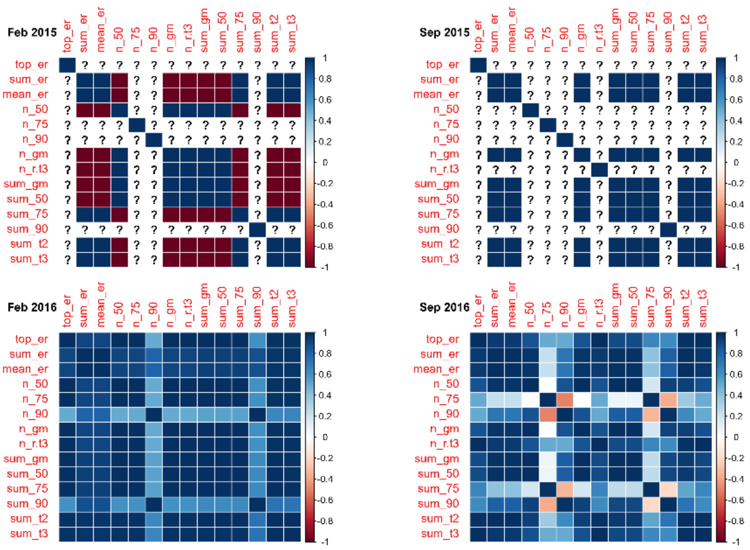

Figure A8: Correlation plots of 14 social metrics for the group SOT that represent aspects of the social bonding dimension, based of affiliative Elo or DDSI values for the 15th of each month shown.

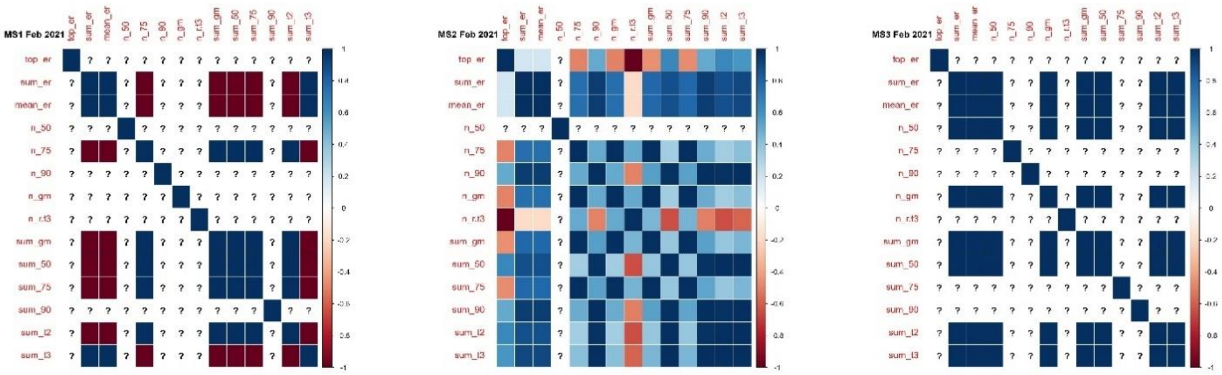

Figure A10: Correlation plots of 14 social metrics for the groups MS1 (left), MS2 (centre) and MS3 (right) that represent aspects of the social bonding dimension, based of affiliative Elo or DDSI values for the 15th of each month shown.

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"Some things came to you late, but late was better than never."

Jeff VanderMeer, Acceptance

Zusammenfassung

Um im Wettbewerb innerhalb einer Gruppe zu navigieren und die Fitness zu maximieren, haben sich Strategien bei Gruppentieren entwickelt, darunter soziale Dominanzränge und affilative Beziehungen. Beide spielen eine entscheidende Rolle bei der Gestaltung der langfristigen Fitness eines Individuums. Das Ausmaß, in dem die Fitnessergebnisse von Dominanzrängen und affilativen Beziehungen auch mit unmittelbaren Kosten verbunden sind, kann durch die Quantifizierung der zugrunde liegenden hormonellen Reaktionen untersucht werden. Dynamiken in der Sozialität können Kosten verursachen, indem sie Glukokortikoide (GCs), einen Schlüsselmediator der Homöostase und einen Indikator der physiologischen Reaktion auf Herausforderungen und Wettbewerb innerhalb der Gruppe, beeinflussen. Um das Kosten-Nutzen-Verhältnis der Sozialität zu verstehen, müssen sowohl die kurz- als auch langfristigen Konsequenzen des innergruppigen Wettbewerbs und der sozialen Beziehungen berücksichtigt werden, was ich in dieser Arbeit für Primaten tun wollte, wobei der Fokus auf Catarrhini-Arten und männlichen Assamese-Makaken (*Macaca assamensis*).

Um die langfristigen Fitnessfolgen der Sozialität zu bewerten, muss die genetische Variation einer Population genau quantifiziert werden. Mikrosatelliten, kurze repetitive DNA-Sequenzen in nicht-kodierenden Regionen des Genoms, sind ein häufig verwendetes Mittel dafür in freilebenden Arten, haben jedoch immer noch viele damit verbundene Probleme. Ich habe mich mit diesen methodischen Problemen auseinandergesetzt und eine verfeinerte Panel von 42 Mikrosatelliten für Catarrhini-Primaten beschrieben. Diese wurde entwickelt aus einer umfassenden Literaturübersicht über veröffentlichte Mikrosatelliten von Catarrhini, in Kombination mit einem Genotyp-für-Sequenzierung (GBS)-Pipeline. Die Mikrosatelliten-Loci wurden unter Verwendung verfügbarer veröffentlichter Catarrhini-Genome optimiert und sowohl an Blut- als auch an Kotproben validiert. Aufgrund ihrer universellen Anwendbarkeit auf Catarrhini-Arten kann das Panel vergleichende und integrative Studien zwischen Arten und Studien erleichtern. Darüber hinaus ist es aufgrund seiner genaueren Erfassung genetischer Variation ein ausgezeichnetes Werkzeug zur Bestimmung der Abstammung und zur Feststellung von Verwandtschaftsverhältnissen, die entscheidende Faktoren für die Fitnessergebnisse sozialer Beziehungen sind.

Um die kurzfristigen Kosten der Sozialität und des Wettbewerbs zu untersuchen, habe ich die korrelierten Glukokortikoid-Reaktionen auf Dynamiken in Dominanzrang und Affiliation bei wilden männlichen Assamese-Makaken untersucht, unter Verwendung von über 4.100 Kotproben von 62 erwachsenen Männchen über einen Zeitraum von 15 Jahren im Phu Khieo Wildlife

Sanctuary, Thailand. Unsere früheren Arbeiten an dieser Population legten nahe, dass erhöhter Wettbewerb in der Paarungszeit zu erhöhten Glukokortikoiden führte und dass ungewöhnlicherweise für männliche Primaten eine niedrigere Rangposition mit höheren Glukokortikoiden korrelierte, was der Hypothese der Kosten der Unterordnung entsprach. Unter Verwendung eines deutlich größeren Datensatzes und dynamischer Kardinalmetriken, die soziale Daten nicht aggregierten, sondern spezifische GC-Proben mit Dynamiken in sozialen Beziehungen verknüpften, habe ich diese Ergebnisse erneut untersucht. Im Gegensatz zu unserer früheren Arbeit zeigte der Dominanzrang eine positive Beziehung zu Glukokortikoiden, da ein hoher Status mit erhöhten Glukokortikoiden korrelierte. Die Replikation unserer früheren Ergebnisse zeigte, dass Glukokortikoide zu Beginn der Paarungszeit hochreguliert wurden, was eine vorbereitende Funktion vor dem Einsetzen des erhöhten Wettbewerbs gehabt haben könnte.

Zusätzlich habe ich die Hypothese der sozialen Pufferung getestet, die besagt, dass die Anwesenheit eines gebundenen sozialen Partners eine abschwächende Wirkung auf die Produktion von Glukokortikoiden haben kann. Wir fanden Hinweise auf den Effekt der sozialen Pufferung und fügten eine dritte Primatenart hinzu, bei der von einem Pufferungseffekt bei adulten Männchen berichtet wurde. Mit zunehmender Stärke der besten affilativen Beziehung eines Männchens verringerte sich die korrelierte GC-Reaktion; dies zeigt, dass Dynamiken in der Affiliation erstmals bei einem wilden Primaten mit Veränderungen in der physiologischen Reaktion korrelieren können. Die Investition in starke Bindungen könnte die physiologischen Anforderungen des Wettbewerbs gemildert und einen Mechanismus für die Bindungspflege bei männlichen Assam-Makaken bereitgestellt haben.

Declaration

I hereby declare that all parts of my thesis titled "Assessing sociality: catarrhine microsatellites and the dynamics of glucocorticoids with social relationships in wild male Assamese macaques (*Macaca assamensis*)" were written by myself. Assistance of third parties was only accepted if scientifically justifiable and acceptable in regards to the examination regulations. Assistance or contributions to the individual chapters are indicated and all sources have been quoted.

Göttingen, 30th of December 2023

James Stranks