Foundations of variation in male aggressiveness and tolerance between chacma baboons (*Papio ursinus*) in Botswana and Guinea baboons (*P. papio*) in Senegal

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In Memory of Moustapha Dieng (†2014)

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SUMMARY

The fitness limiting resource for most male primates is the indivisible fertilization of females. Therefore, males commonly compete aggressively with each other over access to receptive females. Among species, however, there is considerable variation in aggressiveness, and in some species males may even show cooperative behaviors, which is often associated with more relaxed and tolerant social relationships. The proximate and ultimate reasons for this variation may depend on several aspects of a social system, but are not yet entirely understood.

Baboons (*Papio* spp.) constitute a well-suited model for investigating the foundation of male aggressiveness and tolerance since different species show considerable variation in male-male competition and other aspects of their social systems. Male chacma baboons (*P. ursinus*) in southern Africa and male Guinea baboons (*P. papio*) in western Africa probably represent the opposite extremes in terms of male aggressiveness and tolerance in this genus. The purpose of my thesis was therefore to investigate several aspects of variation in male dominance relationships in these two species.

Chacma baboons live in stable multi-male multi-female groups in which mature males disperse into neighboring groups and aggressively compete for a high rank. High ranks confer ‘priority of access’ to fertile females and therefore determine individual reproductive success. Guinea baboons, in contrast, live in a multi-level society in which closely related males often remain in the same group. Male social relationships seemed to be characterized by lower rates of agonistic behaviors, high spatial tolerance, and cooperation; thus aggressiveness did not appear to represent the main factor regulating the access to females in this species.

Comparable quantitative data to corroborate these assumptions about differences in male aggressiveness between the two species were still lacking, however. Thus, one aim of my thesis was to compare aggressiveness and spatial tolerance between male chacma baboons living in the Moremi Game Reserve in Botswana, and male Guinea baboons living in the Parc National de Niokolo Koba in Senegal.

Differences in male-male competition are reflected in male reproductive trajectories which are associated with testosterone patterns in primates. In addition to these long-term patterns, the ‘challenge hypothesis’ predicts that short-term increases in testosterone levels promote aggression in the context of mate competition. The second aim of my thesis was therefore to investigate the link between testosterone and dominance-related aggression by comparing testosterone patterns between male chacma and Guinea baboons in relation to age, aggression and dominance relationships.

The competitive regime may also affect physiological costs, or allostatic load for individuals of different social status. These costs are reflected in inter-individual variation in glucocorticoid levels. The third aim of my thesis was therefore to obtain more information about the effects of male social relationships on allostatic load by comparing variation in glucocorticoid levels in relation to dominance status between chacma and Guinea baboons.

Among individuals of the same species, aggressiveness is a trait with a strong heritability. It is therefore likely that interspecific variation is also linked to differences in genetic architectures. The two length polymorphisms *5-HTTLPR* – in the gene of the the serotonin transporter - and *MAOALPR* -in the gene of the monoamine oxidase A - affect the activity of the serotonin neurotransmitter system and have been linked to variation in aggressiveness. Thus, interspecific variation in aggressiveness in baboons may be linked to different alleles in these two loci. The fourth aim of my thesis was to compare *5-HTTLPR* and *MAOALPR* alleles among five species of baboons.

By providing the first comparable data on behavior of male chacma and Guinea baboons, I could show that male chacma baboons were more often involved in agonistic interactions than male Guinea baboons, while male Guinea baboons showed a higher spatial tolerance towards other males and sometimes even exchanged affiliative behaviors. Furthermore, male chacma baboons formed linear hierarchies with highly consistent dominance relationships, while the linearity of hierarchies among male Guinea baboons was generally low. These observations seem to be consistent with previous studies on male social relationships in both species, indicating that the two species indeed vary in the intensity of male contest competition.

Testosterone levels were not correlated with age or dominance ranks in either species, but there was a trend that testosterone correlates with aggressiveness in chacma baboons. This is consistent with previous observations in this species during periods in which high ranks are challenged. This was not the case during this study but a recent fission event in the study group may have resulted in a similar situation driven by regular encounters between the two groups. In Guinea baboons, testosterone was not correlated with expressed agonistic behavior, which could be explained by the assumption that agonistic behaviors are less important to obtain mating opportunities in this species.

High ranking male chacma baboons showed higher levels of glucocorticoids than subordinate males. Again, this is consistent with previous observations during unstable periods, suggesting that the unusual event of group fission resulted in an unstable period. In Guinea baboons, glucocorticoid levels were not correlated with male dominance position further supporting the view that ranks are less important among male Guinea baboons.

A comparison of *5-HTTLPR* and *MAOALPR* alleles among five species of baboons suggested that *5-HTTLPR* genotype is not linked to interspecific variation in behavior as this locus was monomorphic in most species. A comparison among several papionin species indicated that this locus may have been under selection during the historical dispersal of macaques into Asia. The significance of this variation, however, remains to be investigated but may be related to environmental variation between different species.

By contrast, *MAOALPR* was polymorphic and the pattern of different alleles broadly mapped onto assumed behavioral variation among baboons. Overall, variation in this locus seen between and within species makes further investigation of this polymorphism in baboons promising to understand the genetic foundation of behavioral variation in primates.

In conclusion, with my thesis I provided insights into the proximate causes and costs of variation in male dominance relationships among different species of baboons. Behavioral variation among baboons may be linked to the *MAOALPR* genotype. The investigation of this locus with regard to neurotransmitter activity and behavior in baboons may reveal further insights into the proximate mechanisms underlying variation in aggressiveness in primates. Behavioral observations and measurements of glucocorticoid levels suggest that male reproductive strategies in Guinea baboons incur fewer ‘obvious’ costs. Studying the mechanisms regulating the access to receptive females in this species, and comparing the reproductive success among different individuals may ultimately reveal further insights into the evolution of reproductive strategies and variation in aggressiveness and tolerance among primate males.

ZUSAMMENFASSUNG

Die Fitness-limitierende Ressource für die meisten männlichen Primaten ist die unteilbare Befruchtung von Weibchen. Daher herrscht in der Regel ein aggressives Konkurrenzverhalten unter Männchen, um sich den Zugang zu fertilen Weibchen zu sichern. Jedoch zeigen Männchen unterschiedlicher Arten eine erhebliche Variation in ihrer Aggressivität. In manchen Arten kann sogar ein kooperatives Verhalten zwischen Männchen beobachten werden, das meist mit weniger angespannten und toleranteren Sozialbeziehungen verbunden ist. Die proximaten und ultimaten Ursachen für diese interspezifische Variation werden durch verschiedene Aspekte des Sozialsystems einer Art bedingt, jedoch sind die zugrundeliegenden Ursachen noch nicht vollständig geklärt.

Paviane (*Papio* spp.) stellen ein gut geeignetes Modell dar, um die Grundlage von männlicher Aggressivität und Toleranz zu untersuchen, da die unterschiedlichen Arten dieser Gattung eine erhebliche Variation in männlichem Konkurrenzverhalten und in anderen Aspekten ihrer Sozialsysteme zeigen. Männliche Bärenpaviane (*P. ursinus*) im südlichen und männliche Guineapaviane (*P. papio*) im westlichen Afrika scheinen dabei entgegengesetzte Extrema von Aggressivität und Toleranz darzustellen. Das Ziel meiner Promotion war daher, verschiedene Aspekte der männlichen Dominanzbeziehungen in den beiden Arten zu untersuchen und zu vergleichen.

Bärenpaviane leben in stabilen Gruppen mit mehreren Männchen und mehreren Weibchen, in denen geschlechtsreife Männchen in benachbarte Gruppen abwandern. Dort versuchen sie mit Hilfe von aggressivem Verhalten einen hohen Rang zu erlangen, da ihnen dieser ein Vorrecht („Priority of access“) auf fertile Weibchen verschafft und über den reproduktiven Erfolg eines Männchens bestimmt. Im Gegensatz dazu leben Guineapaviane in einer mehrschichtigen (“multi-level“) Gesellschaft, in der nahverwandte Männchen häufig in der gleichen Gruppe verbleiben. Die Sozialbeziehungen zwischen Männchen scheinen dabei vor allem durch eine niedrige Frequenz agonistischer Interaktionen und eine hohe räumliche Toleranz sowie Kooperation gekennzeichnet zu sein. Daher stellen Aggressionen in dieser Art scheinbar nicht das primäre Mittel in der Konkurrenz um den Zugang zu Weibchen dar.

Bisher gab es noch keine vergleichbaren Daten, um diese Vermutung über Verhaltensunterschiede zwischen den beiden Arten zu überprüfen. Daher war ein Ziel meiner Dissertation die Aggressivität und räumliche Toleranz zwischen männlichen Bärenpavianen im Moremi Game Reserve, Botsuana, und männlichen Guineapavianen im Parc National de Niokolo Koba, Senegal, zu vergleichen.

Unterschiede in männlicher Konkurrenz spiegeln sich auch in unterschiedlichen altersabhängigen Verläufen des Reproduktionserfolgs wider. Bei Primaten ist dieser Verlauf wiederum mit Variation im Testosteronspiegel verbunden. Neben diesen Langzeitverläufen wurde gezeigt, dass zusätzliche, kurzfristige Anstiege in Testosteronspiegeln ein aggressives Verhalten während der Konkurrenz um Paarungspartner fördern (‚Challenge hypothesis'). Das zweite Ziel meiner Dissertation war daher, den Zusammenhang zwischen Testosteron und dominanzbezogener Aggression zu untersuchen, indem ich die Variation in Testosteronspiegeln in Bezug auf Alter, Aggression, und Dominanzbeziehungen analysiert habe.

Die Art und Weise, wie Individuen konkurrieren, beeinflusst auch, wie physiologische Kosten (oder ‚allostatic load') zwischen Individuen unterschiedlichen Dominanzstatus verteilt sind. Diese Kosten spiegeln sich in inter-individuellen Differenzen in Glucocorticoidspiegeln wider. Das dritte Ziel meiner Arbeit war daher die Effekte von männlichen Sozialbeziehungen auf physiologische Kosten zu untersuchen, indem ich die Variation in Glucocorticoidspiegeln in Relation zu Dominanzstatus zwischen Bären- und Guineapavianen analysiert habe.

Inter-individuelle Unterschiede in Aggressivität sind stark erblich bedingt. Daher ist zu vermuten, dass auch Unterschiede zwischen Arten eine genetische Grundlage haben. Die beiden Längenpolymorphismen *5-HTTLPR* - im Gen des Serotonintransporters - und *MAOALPR* - im Gen der monoaminen Oxidase A - beeinflussen die Aktivität des serotonergen Neurotransmittersystems und wurden mit Variation von Aggressivität in Verbindung gebracht. Verschiedene Allele dieser beiden Loci könnten daher auch mit Artunterschieden bei Pavianen gekoppelt sein. Das vierte Ziel meiner Dissertation war daher, Allele dieser beiden Loci zwischen fünf Pavianarten zu vergleichen.

Durch die Erhebung der ersten unmittelbar vergleichbaren Verhaltensdaten für männliche Bären- und Guineapaviane konnte ich zeigen, dass männliche Bärenpaviane häufiger in agonistische Interaktionen verwickelt sind als Guineapaviane. Im Gegensatz dazu zeigen Guineapaviane eine höhere räumliche Toleranz gegenüber anderen Männchen und tauschen manchmal sogar affiliatives Verhalten aus. Des Weiteren zeigten männliche Bärenpaviane konsistente Dominanzbeziehungen und eine lineare Hierarchie, während die Linearität der Hierarchien von Guineapavianen allgemein niedriger war. Diese Beobachtungen stimmen mit vorherigen Beobachtungen über männliche Sozialbeziehungen in beiden Arten überein. Dies bedeutet, dass die beiden Arten sich tatsächlich in der Intensität von männlicher Wettbewerbskonkurrenz („contest competition") unterscheiden.

In keiner der beiden Arten konnte ein Zusammenhang zwischen Testosteronspiegel und Alter oder Dominanzrang gefunden werden. Es gab jedoch einen statistischen Trend, dass in Bärenpavianen der Testosteronspiegel mit Aggressivität korreliert. Dies wurde zuvor nur in Perioden beobachtet, in denen Männchen hoher Dominanzränge von anderen Männchen herausgefordert wurden (d.h. „unstabile Perioden“). Dies war in der vorliegenden Studie nicht der Fall. Jedoch könnten eine kurz zuvor beobachtete Teilung der Gruppe und darauf folgende regelmäßige Begegnungen der beiden neu entstandenen Gruppen eine ähnliche Situation verursacht haben. In Guineapavianen waren Testosteronspiegel nicht mit der Häufigkeit von agonistischen Verhalten korreliert. Dies könnte daran liegen, dass solche Verhalten in dieser Art keine bedeutende Rolle in der Konkurrenz um Paarungsmöglichkeiten spielen.

Hochrangige männliche Bärenpaviane zeigten höhere Glucocorticoidspiegel als niedrigrangigere Männchen. Auch dies wurde bei Bärenpavianen bisher nur während „unstabiler Perioden“ beobachtet und weist wieder darauf hin, dass die unübliche Teilung der Gruppe eine ähnliche Situation hervorgerufen haben kann. In Guineapavianen korrelierten Glucocorticoidspiegel nicht mit Dominanzpositionen, was die Vermutung unterstütz, dass Dominanzränge in dieser Art wenig oder keine Bedeutung haben.

Ein Vergleich von *5-HTTLPR* und *MAOALPR* Allelen zwischen fünf Arten von Pavianen lässt vermuten, dass der *5-HTTLPR*-Genotyp nicht mit interspezifischer Variation im Verhalten in Verbindung steht; dieser Locus war in fast allen Arten monomorph. Ein erweiterter Vergleich zwischen mehreren Arten von Pavianartigen (Papionini) deutete aber an, dass dieser Locus während der historischen Ausbreitung von Makaken nach Asien sehr wahrscheinlich unter Selektionsdrücken stand. Die Bedeutung dieser Variation muss noch untersucht werden, könnte aber eventuell mit Unterschieden in der Umwelt der jeweiligen Arten zusammenhängen.

Im Gegensatz dazu war der Locus *MAOALPR* polymorph und das Muster verschiedener Allele passte überwiegend mit den vermuteten Verhaltensunterschieden zwischen Pavianarten zusammen. Die beobachtete Variation in diesem Locus bietet daher eine gute Möglichkeit, um genetisch bedingte Verhaltensunterschiede zwischen verschiedenen Pavianen genauer zu untersuchen und dadurch die genetischen Grundlagen der Variation in Aggressivität bei Primaten besser zu verstehen.

Zusammengefasst hat meine Dissertation grundlegende Einblicke in die proximaten Ursachen und Kosten der Unterschiede in männlicher Dominanzbeziehungen zwischen Pavianarten geliefert. Erste Daten weisen darauf hin, dass Verhaltensunterschiede in Bezug auf Aggressivität zwischen Pavianen mit dem *MAOALPR*-Genotyp verbunden sind. Eine Untersuchung dieses Locus im

Zusammenhang mit Neurotransmitter-Aktivität und Verhalten könnte daher weitere Aufschlüsse über die proximaten Mechanismen geben, die unterschiedlichen Aggressivitätsmustern in Primaten unterliegen. Verhaltensbeobachtungen und Glucocorticoid-Messungen lassen vermuten, dass die reproduktive Strategie von männlichen Guineapavianen mit weniger „offensichtlichen“ Kosten verbunden ist. Daher könnten eine Untersuchung der Mechanismen, die den Zugang zu Weibchen bei Guineapavianen regeln, und ein Vergleich des reproduktiven Erfolgs zwischen unterschiedlichen Männchen weitere Einblicke in die Evolution von reproduktiven Strategien und damit von Aggressivitäts- und Toleranzunterschiede zwischen männlichen Primaten liefern.

CHAPTER ONE - General Introduction

Variation in male aggressiveness and tolerance

In order to compete over resources, animals commonly employ aggressive behaviors. In most mammals, in particular the social relationships among males are mainly characterized by aggressive interactions and lack of affiliative behaviors. There is, however, considerable variation in male aggressiveness among species, and in some species males even show cooperative, tolerant, and affiliative behaviors. In the following introduction to my thesis, I will outline how several aspects of the social system shape male reproductive strategies and therefore male-male competition, which is again reflected in different degrees of aggressiveness and tolerance. Furthermore, I will describe how differences in competition are thought to be regulated by testosterone levels, and how they affect physiological costs of individuals of different social status. As variation in aggressiveness is likely to have a genetic foundation, I will describe candidate genes that might be relevant in this context. Finally, I will introduce baboons as a model to investigate the causes and consequences of interspecific variation in male-male competition and present the aims of my thesis.

Sex differences in reproductive strategies

In the ‘struggle for existence’ (Darwin 1859), individuals have to compete over limited resources to maximize their reproductive success – or more generally, their fitness. In most mammalian species, males and females differ regarding their respective fitness-limiting resources as sexes differ in reproductive strategies (Trivers 1972). Females can only reproduce with one male at a time and, due to gestation and lactation, they usually provide the majority of parental care. Accordingly, female reproductive success is primarily determined by access to food and protection. Males, in contrast, benefit from increasing the number of receptive females to which they have access and male reproductive success is determined primarily by increasing mating opportunities rather than parental effort (Trivers 1972).

Food and protection as the fitness-limiting resources for females are mostly sharable, while fertilization as the fitness limiting resource for males cannot be shared. As a consequence, intrasexual competition among males is usually characterized by aggressive competition and intolerance (e.g. van Hoof & van Schaik 1994, van Hooff 2000). Nevertheless, there is considerable interspecific variation in the intensity of aggressive competition and cooperation (e.g. Plavcan & van Schaik 1992, Plavcan et al. 1995). This variation is closely correlated with variations in male reproductive strategies.

Variation in competition and cooperation among male primates

To investigate the causes for variation in male-male competition and cooperation, several aspects of a social system have to be considered (reviewed in Ostner & Schülke 2014). In primates, three different components of the social system are typically distinguished: the social organization, the mating system, and the social structure of a society (*sensu* Kappeler & van Schaik 2002).

The social organization describes the size, sexual composition and cohesion of a society. Some primates live solitary or in pairs but more commonly they form bisexual groups including at least three adult individuals (Kappeler & van Schaik 2002). According to socio-ecological models (Wrangham 1980, van Schaik & van Hooff 1983, Sterck et al. 1997; reviewed e.g. in Janson 2000, Koenig et al. 2013), major benefits of group-living include the ability to defend high-quality food resources and to decrease the risk of predation and infanticide (see below). Consequently, females are thought to benefit more from forming groups. To avoid inbreeding, members of one sex, in primates predominantly the males, emigrate from their group after maturation (Packer 1979b).

The mating system describes mating patterns and their reproductive consequences. Primate mating systems comprise all the main categories described for mammals (Clutton-Brock 1989), including monogamy, polyandry, polygyny, and promiscuity. As the fitness of males mainly depends on the number of fertilized females, they should try to monopolize (and exclusively mate with) as many females as possible. This strategy is likely the ‘major determinant of primate mating systems’ (Kappeler & van Schaik 2002).

Mating system and social organization are strongly interdependent. Males usually do not provide parental care, and thus it would be beneficial for a male to only associate with females during their receptive period. This strategy is only realized in solitary species in which males may either roam around to find receptive females (i.e. ‘scramble competition polygyny’) or defend territories including several females (i.e. ‘spatial polygyny’) (see Kappeler & van Schaik 2002). However, many primates live in permanent bisexual groups rather than temporary associations. This is likely the consequence of the high infanticide risk in the primate order (van Schaik & Kappeler 1997). Infanticide is considered as a sexually selected male strategy to increase the number of receptive females by interrupting lactation and thereby shortening the interbirth-interval (Hrdy 1974). Males may therefore benefit from permanently associating with females and protecting their progeny against other males rather than seeking new mating partners. Given this scenario, males should try to maximize the number of females with which they are associated. The ability of a male to monopolize several fertile females depends on their spatial and temporal distribution and their estrous synchrony (Emlen & Oring 1977, Altmann 1990). However, in case that too many females live together, or if they are highly synchronous, males may not be able to exclude additional males from their group (Nunn 1999, Carnes et al. 2011), or males may even benefit from additional males, for example by ameliorated infant protection or by communal defense of females or territories (reviewed in Koenig et al. 2013, Ostner & Schülke 2014). In the resulting multi-male, multi-female groups, males often mate-guard females during their receptive periods. Still, males are often unable to completely monopolize receptive females and potential competition for fertilization continues even after copulation (i.e. sperm competition; Moeller 1988).

Among primates, male contest competition appears to be the primary strategy in order to monopolize sexual access to receptive females, but some males may also employ alternative strategies such as furtive (sneak) copulations or the formation of long-lasting affiliative relationships with females, which may increase the mating success of competitively disadvantaged males (e.g. in *P. anubis*: Strum 1982, Smuts 1985; reviewed in Alberts 2012). Moreover, males may avoid direct confrontation with other males by forming coalitions (see below). As a consequence of the indivisibility of fertilization, in primates and other mammals a large potential for inter-individual variation in reproductive success among males exist, often resulting in a high reproductive skew (Trivers 1972).

Finally, the social structure describes the pattern of interactions among individuals within a group and the resulting social relationships (Hinde 1976). As outlined above, relationships among males are usually characterized by aggressive competition. Since aggression may also come with high costs, most importantly the risk of injury (e.g. Drews 1996, MacCormick et al. 2012), conflicts are not always resolved by physical fighting. As in many group-living mammals, individuals in primate groups avoid the costs of fighting by establishing ritualized dominance hierarchies based on differences in competitive abilities (e.g. Drews 1993, Zinner & Wheeler 2012). Ritualized signaling plays an important role in maintaining these dominance hierarchies (Preuschoft & van Schaik 2000, Fischer et al. 2004, Kitchen et al. 2003). Among males, the rank that an individual occupies in such a hierarchy is thought to depend mainly on its fighting ability (e.g. Alberts 2012) and determines the access to mating partners (Altmann 1962, Cowlishaw & Dunbar 1991). Yet, as mentioned earlier, males can circumvent 'one against one' competition (i.e. male-male contest competition) to obtain mating opportunities, and therefore do not have to rely exclusively on their fighting abilities. Subordinates may also cooperate with other males by forming coalitions to challenge a dominant male in order to gain temporary access to a female (i.e. leveling coalitions; Pandit & van Schaik 2003). In some species, males may even form coalitions to increase their rank, which means that the obtained rank does not necessarily reflect their fighting abilities (i.e.

'rank-changing' coalitions; reviewed in Ostner & Schülke 2014). Coalitions can be formed rather opportunistically or males may form long-lasting bonds characterized by high tolerance and the exchange of affiliative behavior (reviewed in: van Hoof & van Schaik 1994, Ostner & Schülke 2014). Cooperation is thought to be facilitated by kin selection (Hamilton 1964), and accordingly should be more common in species with male philopatry (i.e. males stay in their natal groups). However, cooperation also has been shown to occur among non-related males, which is most likely to be explained by mutual benefits (e.g. *Macaca assemensis*: Schülke et al. 2010; *Pan troglodytes*: Langergraber et al. 2007; *Papio anubis*: Bercovitch 1988).

In summary, males may follow different strategies to increase their fitness; solitary males may roam around to find receptive females, which increases the importance of post-copulatory (mainly sperm) competition. Most often, primate males engage in contest competition in order to defend a territory with several females, to exclude other males from a group of females, or to obtain a high rank in a multi-male group which regulates the access to receptive females. Some males may also engage in sneak copulations or cooperate with other males to obtain or defend access to females.

These strategies will be reflected in male social relationships, such as in the degree of aggressiveness, tolerance, and affiliation among males. Furthermore, the type and intensity of male-male competition may also affect male morphology, as sexual selection should favor traits that increase their reproductive success (reviewed in Muller & Emery Thompson 2012). For instance, the intensity of contest competition has been shown to affect sexual dimorphism in canine length (Plavcan & van Schaik 1992, Thorén et al. 2006) and body weight (Plavcan & van Schaik 1997) while intense sperm competition seems to increases relative testis size (e.g. Moeller 1988, Jolly & Phillips-Conroy 2006).

Physiological correlates of male reproductive trajectories, dominance, and aggression

Differences in social organization, mating system, and social structure are reflected in male reproductive trajectories, including age at emigration (in species where males disperse), age at first reproduction, length of reproductive career, number of produced offspring, and the extent of parental care (reviewed in Alberts 2012). Levels of the steroid hormone testosterone seem to be associated with these reproductive trajectories in primates (e.g. in *Cebus capucinus*: Jack et al. 2014; *Pan* spp.: Wobber et al. 2013; reviewed in Muller & Emery Thompson 2012). This androgen promotes traits associated with male mating effort, including muscle growth (e.g. in rhesus macaques, *M. mulatta*: Kemnitz et al. 1988) and spermatogenesis (e.g. reviewed in McLachlan et al. 1996) at the costs of parental behavior (e.g. in *Callithrix kuhlii*; Nunes et al. 2001) and immune function (reviewed in Muehlenbein & Bribiescas 2005). In addition to these long-term effects, a subtle, short-term increase in testosterone secretion has been proposed to facilitate aggressive behaviors in the context of mate competition; this 'challenge hypothesis' has been initially formulated for seasonally breeding birds (Wingfield et al. 1990), and was later adopted for primates (Muller & Wrangham 2004). In line with this idea, testosterone levels of males have been shown to increase during the mating season in several seasonally breeding primate species (e.g. *Eulemur fulvus rufus*: Ostner et al. 2002; *Lemur catta*: Cavigelli & Pereira 2000; *M. assamensis*: Ostner et al. 2011; *M. fascicularis*: Girard-Buttoz et al. 2009). In non-seasonally breeding primates, testosterone levels generally increase during periods of intense competition for mates or higher ranks (e.g. *Pan troglodytes*: Muller & Wrangham 2004; *Mandrillus sphinx*: Setchell et al. 2008).

Allostatic load of dominance status

Dominance status does not only convey benefits or disadvantages in relation to reproductive success, it can also affect physiological costs, or 'allostatic load' (Goymann & Wingfield 2004), which can be assessed by comparing glucocorticoid levels between individuals of different status (Goymann & Wingfield 2004, Abbott et al. 2003). These adrenal steroid hormones mobilize energy reserves and suppress non-essential metabolic processes; therefore increases in response to acute stressors can be adaptive while chronically high levels may be detrimental for health (Sapolsky 2005). Allostatic load of dominant individuals is related to the manner in which high ranks are acquired and maintained, while allostatic load of subordinates is related to the degree of threat that they have to suffer from dominant conspecifics, the availability of coping mechanisms (i.e. opportunities to avoid these threats), and disadvantages in resource availability (Goymann & Wingfield 2004). Accordingly, variation in allostatic load of dominance status is affected by competitive regimes among males.

Genetic foundation of variation in aggressiveness

Variation in aggressiveness between species likely correlates with different genetic architectures. Indeed, within many species, including humans (Yeh et al. 2010), vervet monkeys (*Chlorocebus pygerythrus*, Fairbanks et al. 2004), mice (*Mus musculus*, e.g. van Oortmerssen & Bakker 1981), silver foxes (a melanistic form of *Vulpes vulpes*: Belyaev 1979), inter-individual variation in aggressiveness has been shown to have a strong genetic component. Since aggressiveness is a quantitative trait, multiple segregating genes are thought to be involved, but the relationship between specific genes and aggressiveness is not yet well understood (reviewed in Anholt & Mackay 2012). As the system controlling the neurotransmitter serotonin (5-Hydroxytryptamine; 5-HT) has been linked to aggressiveness in mammals (e.g. in humans: Coccaro 1989; rhesus macaques, *M. mulatta*: Higley et al. 1992, Mehlmann et al. 1994; reviewed in Nelson &

Chiavegatto 2001), genes encoding for proteins controlling this neurotransmitter system are potential candidates to affect aggressiveness (Popova 2006, Craig & Halton 2009).

The 5-HT transporter (5-HTT) and the monoamine oxidase A (MAOA) are two important proteins in the 5-HT system (e.g. Lesch & Merschdorfer 2000); 5-HTT is responsible for the reuptake of the 5-HT from the synaptic cleft back into the neuron, and MAOA oxidizes 5-HT into its metabolite 5-hydroxyindoleacetic acid (5-HIAA). In both genes, functional length polymorphisms within promoter (i.e. regulatory) regions have been reported for several species of primates (e.g. Wendland et al. 2006a, Wendland et al. 2006b, Lesch et al. 1996). In the 5-HTT gene, the genotype of the *5-HT*-linked polymorphic region (*5-HTTLPR*) affects the *in vitro* transcription rate in humans (Heils et al. 1996) and in rhesus macaques (Bennett et al. 2002), and has been suspected to affect aggressiveness in rhesus macaques (Barr et al. 2003, Schwandt et al. 2010). Similarly, the genotype of the MAOA-linked polymorphic region (*MAOALPR*) in the MAOA-gene affects the transcription rate in humans (Sabol et al. 1998) and rhesus macaques (Newman et al. 2005), and is thought to be linked to variation in aggressiveness in rhesus macaques (Karere et al. 2009). Furthermore, these two loci have been suggested to be linked to interspecific variation in aggressiveness in macaques (Suomi 2006, Wendland et al. 2006b, Chakraborty et al. 2010).

As outlined in the last sections, males of different species may vary in their reproductive strategies, and this may correlate with differences in dominance relationships, and therefore aggressiveness and tolerance. As variation in dominance relationships and mating effort is assumed to be physiologically regulated by testosterone, and to incur specific physiological costs, different species should show varying patterns of testosterone and glucocorticoid levels. Furthermore, inter-individual variation in aggressiveness has been shown to have a strong genetic component, therefore variation between species is likely linked to different genetic architectures. Up to date, only a few studies have directly compared different species in this regard to further investigate the foundations of male aggressiveness and tolerance.

Baboons as a model

Baboons (*Papio* spp.) constitute a well-suited model for investigating the foundation of male aggressiveness and tolerance since different species show considerable variation in male-male competition and other aspects of their social systems. As outlined below in more detail, male chacma baboons (*P. ursinus*) and male Guinea baboons (*P. papio*) are considered to represent the opposite extremes of male aggressiveness and tolerance in this genus. In the following, I will use the term 'tolerance' referring to *spatial* tolerance, meaning that individuals stay within close proximity without showing agonistic behaviors though, for example, *social* tolerance may refer to many different dimensions of social relationships (e.g. Thierry 2013). Thus, the purpose of my thesis was to investigate several aspects of variation in male dominance relationships, including the associated physiological mechanisms and costs, in these two species and to compare genetic polymorphisms previously linked to variation in aggressiveness in the genus.

In the following, I will summarize the knowledge about social organization and mating system of different species of baboons, and how this is thought to be linked to variation in male social relationships and male life-histories. Furthermore, I will summarize previous studies on variation in testosterone and glucocorticoid levels in male baboons with regard to reproductive trajectories and dominance relationships. Finally, I will specify the aims and predictions underlying my thesis.

Baboon social systems

The genus *Papio* most likely originated in southern Africa and is thought to share a common ancestor dating from approximately two million years ago (Newman et al. 2004, Zinner at al. 2009). During the Pleistocene, the genus dispersed over large parts of sub-Saharan Africa and the Arabian peninsula (Benefit 1999, Newman et al. 2004, Zinner et al. 2009). Nowadays, baboons are widely distributed through most parts of sub-Saharan Africa and south-western Arabia, only excluding the west and central African rainforest (Fig. 1.1). They constitute clusters of allopatric populations with six distinct morphotypes, which have been recognized as species in several recent studies (e.g. Groves 2005, Zinner et al. 2013). Chacma baboons live in southern Africa, Kinda baboons (*P. kindae*) in parts of Zambia, Angola and the Democratic Republic of Congo, yellow baboons (*P. cynocephalus*) in eastern Africa, olive baboons (*P. anubis*) are widely distributed from western to north-eastern Africa, hamadryas baboons (*P. hamadryas*) live in northeastern Africa and a small part of the Arabian peninsula, and Guinea baboons at the western edge of the genus' distribution in West Africa.

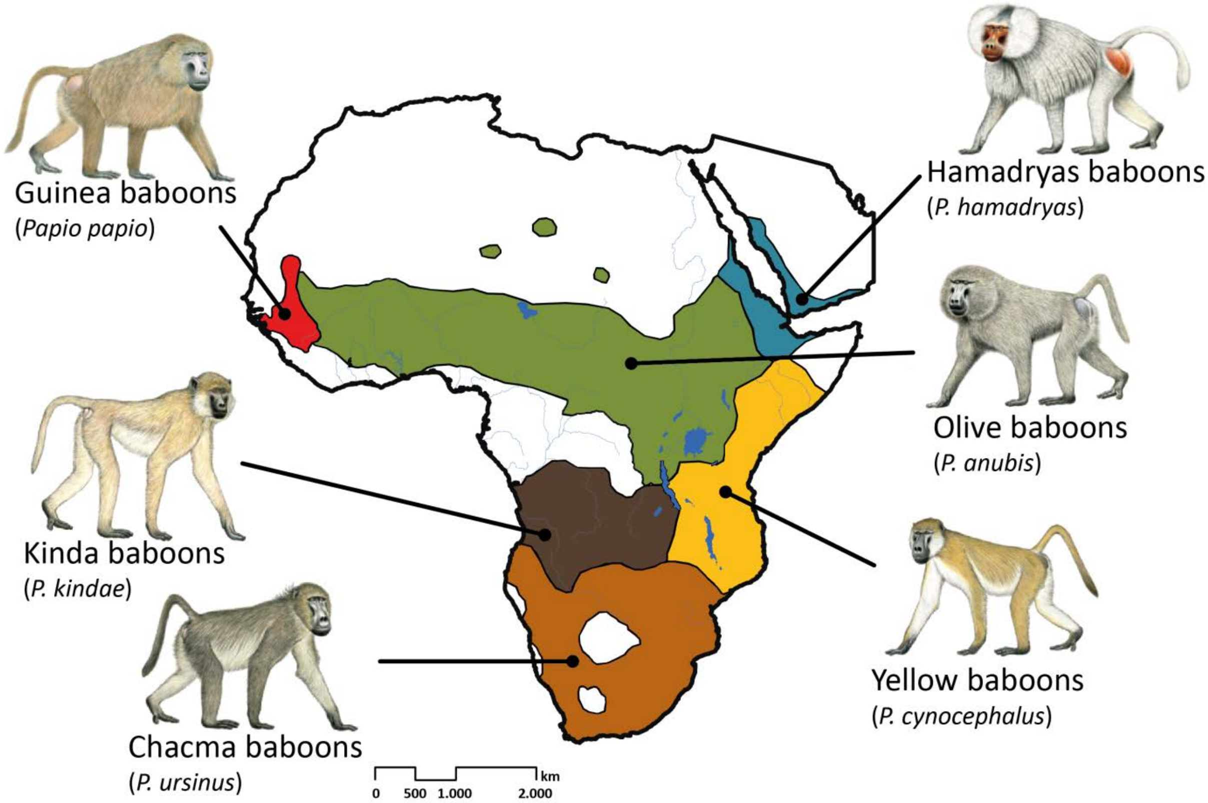

Fig. 1.1: Geographical distribution of baboons. Distribution taken from Zinner et al. 2013b; illustrations © 2013 Stephen D. Nash/IUCN/SSC Primate Specialist Group. Used with permission.

Social organization and mating systems of baboons

Chacma, yellow, and olive baboons share many similarities concerning their social organization and mating systems and were therefore traditionally collectively referred to as ‘savanna baboons’ (Barrett & Henzi 2008). All three species live in multi-male, multi-female groups, in which philopatric, - and thus related - females constitute the stable core, while males emigrate into neighboring groups. During females’ receptive periods, males form sexual ‘consortships’ characterized by aggressive mate guarding of associated females (Hausfater 1975, Smuts 1985). Males of all three species form linear dominance hierarchies, in which the rank confers the ‘priority of access’ (Altman 1962) to form such consortships. This leads to a high mating skew, which is more pronounced in chacma than in olive or yellow baboons (chacma baboons: Bulger 1993, Weingrill et al. 2003, Beehner et al. 2009; yellow baboons: Alberts et al. 2003; olive baboons: Packer 1979a). The observed mating frequency is not automatically associated with reproductive success, but it appears that time spent by a male in consort with an estrous female is a good predictor for paternity in baboons (Alberts et al. 2006, Moscovice et al. 2010). Researchers have only started to recognize Kinda baboons as a distinct species during the last few years (e.g. Jolly et al. 2011) and knowledge about this species is almost absent. I will therefore not further consider them hereafter.

Hamadryas baboons, in contrast to savanna baboons, live in a multi-level society with 'one-male units' (OMUs) as the smallest entities. OMUs consist of one reproductively active male, several females, (Kummer 1968), and sometimes an additional 'follower' male which has no sexual relationship with the females within the unit (Swedell 2006). Associations between two or three OMUs constitute a clan (Schreier & Swedell 2009). Several clans and additional solitary males form a band, which is a stable and exclusive unit and constitutes the next layer of social organization. Males show a strong tendency to stay in their natal band (Swedell & Leigh 2006), while females are sometimes usurped and transferred by males between bands. As a result, males are assumed to be more philopatric than females (Swedell et al. 2011). Females in OMUs are forcibly herded by the leader male and interact and mate only with him (Kummer 1968). Consequently, the mating skew within OMUs is extremely high, but the overall mating skew within bands is unknown.

Until recently, observations on Guinea baboons were limited to unidentified (Boese 1973, Boese 1975, Sharman 1981, Galat-Luong et al. 2006, Patzelt et al. 2011), or captive (Boese 1973, Boese 1975, Maestripieri et al. 2007) individuals. These studies suggested either a social organization similar to that of hamadryas baboons (Boese 1973), or multi-male, multi-female social groups in which smaller subgroups, potentially of varying composition and size (Patzelt et al. 2011), frequently break away and forage independently (Sharman, 1981). More recent observations on individually identified baboons and data obtained from GPS collars suggest that Guinea baboons live in a multi-level society in which the smallest entities are 'parties' consisting of several males and females (Patzelt 2013, Patzelt et al. in revision). Certain parties regularly associate and form 'gangs' which forage together or share a sleeping site. Several gangs sharing the same territory constitute the 'community', though they do not spend much time within close proximity of each other (Patzelt et al, in revision), and it is not yet known whether such communities represent exclusive units.

Genetic data from unknown individuals indicate that, as suspected for hamadryas baboons, Guinea baboon females contribute more to the gene flow among communities than males (Kopp et al. under review). Within communities, kinship analyses of individually identified animals suggest that males are more closely related within than between gangs, though the relatedness is relatively low; this is probably explained by the observation that closely related male dyads exist within but also between gangs (Patzelt et al. in revision).

With regard to the mating system, preliminary observations suggest that most adult males within parties are associated permanently with one to six females, though rarely with more than four females at a time (Patzelt 2013; personal observation). Such associations last for several months or years and even though the spatial association is often loose, females apparently only mate with the associated male. Given the observation that most adult males are involved in such reproductive units, the short-term mating skew is expected to be low. However, the genetic component of the mating system is still entirely unclear.

Variation in male social relationships

The outlined differences in baboon social organization and mating systems are closely linked to variation in male social relationships. Chacma baboons, which exhibit the highest mating skew, show the highest intensity of direct male-male competition, as males have regular fights that often result in severe injuries (Kitchen et al. 2005), they do not form coalitions (Henzi & Barrett 2003), the spatial tolerance is presumably low and male-male affiliation, such as grooming, has not been reported yet. In yellow and olive baboons, males also tend to have intensive fights often resulting in serious injuries (yellow baboons: Drews 1996; olive baboons: MacCormick et al. 2012). In contrast to chacma baboons, however, subordinate males regularly form coalitions in which one of the coalition partners may take over the consort partner of a dominant male (Smuts 1985, Bercovitch 1988, Noe & Sluijter 1995, Henzi & Barrett 2003). These coalitions appear to be mainly formed opportunistically rather than constituting long-term bonds (Noe & Sluiter 1995; reviewed in van Hooff & van Schaik 1994). Consistent with this observation, males of both species do not show behavior typically associated with the occurrence of male bonds such as a high spatial tolerance or affiliation (olive baboons: e.g. Harding 1980, but see Sapolsky & Share 2004 for an exception; yellow baboons: S. Alberts, personal communication). The occurrence of coalitions may contribute to the lower mating skew observed in these two species compared to chacma baboons (Alberts 2012).

In hamadryas baboons, males have regular fights but these conflicts appear to be highly ritualized and often do not include intense body contact (Kummer 1995). While coalitions are apparently absent among males, they may nevertheless apply alternative strategies to directly challenge a leader male (Pines et al. 2011): some males form ‘initial units’ with immature females, or males opportunistically take over females from injured, old or weak males, or females that have been separated from their leader males during aggressive conflicts. Follower males may also ‘inherit’ a female of the OMU that they follow. Accordingly, male hamadryas baboons have possibilities to peacefully obtain mating opportunities. With regard to affiliation, solitary males sometimes groom each other (e.g. Abegglen 1984), but once a male becomes a leader, he ceases to affiliate with other males (e.g. Swedell 2006). Nevertheless, leader males may be tolerant towards each other (Kummer 1968), and they often show ‘greeting’ behaviors (formalized ‘notifying’ behavior;

Kummer 1968), which has been suggested to serve as a non-agonistic behavior to negotiate dominance relationships (Colmenares 1991).

In Guinea baboons, male aggressiveness is assumed to be low (Galat-Luong et al. 2006), and males form coalitions (e.g. Sharman 1981, Patzelt et al. in revision). Furthermore, they are described to be spatially tolerant and sometimes involved in grooming interactions (Galat-Luong et al. 2006, Patzelt et al. in revision), including males associated with females, thus reproductively active males (Sharman 1981, Patzelt, 2013). As the affiliation network and the coalition networks seem to be positively correlated (Patzelt et al. in revision), male Guinea baboons possibly form bonds, which would constitute a major difference to all other baboon species.

Life-histories of male baboons

Differences in social organization, mating system, and social structure are reflected in differences in male life histories of baboons. Male chacma baboons, with the most intense contest competition, rarely emigrate before they are fully grown (Cheney et al. 2004, Barrett & Henzi 2008, Henzi & Barrett 2003, Weingrill et al. 2003), while olive and yellow baboons sometimes emigrate during adolescence (Packer 1979a, Alberts & Altmann 1995, Charpentier et al. 2008). Following immigration, adult males usually begin to challenge resident males in an attempt to assume a high rank in the dominance hierarchy (Alberts & Altman 2001, Cheney & Seyfarth 2007); such challenges regularly escalate into fights resulting in injuries (chacma baboons: Kitchen et al. 2005; yellow baboons: Drews 1996; olive baboons MacCormick et al. 2012). Both, the intensity of aggression and the frequency of challenges to the dominance hierarchy are assumed to be higher in chacma than in yellow and olive baboons, but to my knowledge no published study has thus far systematically addressed this question. Rank changes among male chacma and yellow baboons occur often, and males rarely maintain the alpha position for longer than one year (chacma baboons: Cheney & Seyfarth 2007, Henzi et al. 2010; yellow baboons: Alberts et al. 2003). In yellow baboons, however, alpha males sometimes keep their position for up to two years (Alberts et al. 2003) and some male olive baboons retain the alpha position for three years or longer (Packer 1979b).

After immigration, male chacma baboons frequently commit infanticide (Palombit et al. 1997, Weingrill 2000, Palombit 2009, Henzi et al. 2010). By contrast, this rarely occurs in yellow and olive baboons (Henzi & Barrett 2003, Palombit 2003). A possible explanation for the high infanticide frequency in chacma baboons is the high reproductive skew and the short tenure length as an alpha male; within this short period of time males are forced to maximize their offspring production. Further supporting this view, male chacma baboons often form close, non-sexual bonds with lactating females (‘friendships’) in which they defend their friend’s infant -

which is often their own (Moscovice et al. 2010) – against infanticidal attacks by recent immigrant males (Palombit et al. 2001).

Young male hamadryas baboons normally leave their natal OMU at the age of 2-3 years to associate with other solitary subadult and adult males within the same band, or they become a follower male (Swedell 2006). As OMU leaders almost exclusively monopolize the reproduction of their females, non-leader males should have a strong motivation to found their own OMU. As mentioned above, males may adopt peaceful or aggressive strategies to become a leader. Leader males have a long tenure and females stay with one leader for an average of 26 months (Swedell et al. 2011). The association between a female and a leader male can even last up to seven years. Males show paternal behavior and protect their offspring as long as lactating females stay in their OMUs. After take-overs, infants usually die (Swedell 2006), in part due to infanticide (Swedell & Tesfaye 2003). Accordingly, males that have lost their OMU usually can no longer reproduce.

Life-history patterns of male Guinea baboons are still unknown. So far, genetic data indicate that males stay within their natal community. Some males may emigrate to other gangs, but it remains unclear at what age they leave. Assuming that the aggressiveness among males is relatively low and spatial tolerance high, and the short-term mating skew low, subordinate male Guinea baboons may have less incentive to challenge dominant males. Similar to hamadryas baboons, they may also apply peaceful strategies to associate with females, or, alternatively, form bonds with other males to obtain or defend mating opportunity. Accordingly, younger and older males with relatively low fighting abilities could still be able to obtain mating opportunities. Though associations between males and females seem to be rather permanent, they are spatially often loose which suggests that infanticide may not be perceived as a high risk in Guinea baboons. Further supporting this view, infanticide has not yet been observed in this species.

In sum, behavioral data collected during the last decades strongly suggest that a gradient in male dominance relationships exists along the historical dispersal pattern of the genus from southern to northern and western Africa (Henzi & Barrett 2003, Jolly 2007, Jolly 2009): male-male aggressiveness decreases while cooperation, tolerance and affiliation increases. Further, this gradient is correlated with (1) patterns of dispersal, including male philopatry and the age of emigration; (2) alpha male tenure length and the stability of male dominance hierarchies; (3) male mating skew and the number of mating opportunities for males with low fighting abilities (mainly younger and older males); and (4) the frequency of infanticide and the occurrence of ‘friendships’ with lactating females.

While hamadryas baboons in the North might represent a special case due to their exceptional social organization and mating system, chacma baboons in the South and Guinea baboons in the far West of Africa appear to represent opposite extremes along this continuum. This suggests that the adaptive value of intense male-male contest competition differs strikingly between the two species. This assumption is further supported by the observation that the relative canine length of males and sexual dimorphism – both thought to be indicators of the intensity of male-male competition – differ between both species: relative canine length is shorter in Guinea baboons than in chacma baboons (Guinea baboons: Patzelt 2013; chacma baboons: Thorén et al. 2006) and sexual dimorphism is more pronounced in chacma baboons (Guinea baboons: Patzelt 2013; chacma baboons: Thorén et al. 2006). These two species therefore provide an ideal opportunity to investigate the relation between male aggression, tolerance and parental behavior and other aspects of the social system in primates, but prior to my thesis studies comparing behavior between both species were missing.

Variation in testosterone levels in baboons

Supporting the view that testosterone secretion in male primates tracks their reproductive trajectory, levels of male chacma and yellow baboons increase during puberty, remain relatively high during several years of high mating effort, and decrease once a male ceases to reproduce (Beehner et al. 2006, Beehner et al. 2009). Testosterone levels of male chacma baboons quickly drop after maximum production while levels of male yellow baboons only decline gradually, which may be explained by ongoing mating activity of older, subordinate male yellow baboons (Alberts et al. 2006). Additionally, testosterone levels of male chacma and olive baboons increase during 'unstable periods' in which high ranks are contested (olive baboons: Sapolsky 1983, Sapolsky 1993; chacma baboons: Beehner et al. 2006). During such periods, aggressiveness in the group is generally higher (Sapolsky 1993 , Bergman et al. 2005) and individual testosterone levels correlate with individual aggression rates (Beehner et al. 2006), suggesting that testosterone in male baboon may promote aggressive behavior in the context of competition for mates. Moreover, testosterone levels in male chacma baboons appear to indicate competitive ability (Bergman et al. 2006) and are predictive of future rank changes (Beehner et al. 2006). Given the assumption about differences in male reproductive trajectories and aggressiveness between chacma and Guinea baboons, a comparison of testosterone patterns could provide further insights into the physiological regulation of male life histories in primates but studies on hormone variation in male Guinea baboons were missing.

Variation in glucocorticoid levels in baboons

Glucocorticoid levels are strongly affected by male dominance status in chacma (Bergman et al. 2005), yellow (Gesquiere et al. 2011), and olive baboons (Sapolsky 1983, Sapolsky 1993). Generally, glucocorticoid levels of adult males within a group increase during unstable periods in all three species. However, dominant chacma and olive baboons show higher levels than subordinate males during these periods, while subordinate males show higher levels during more stable periods. In yellow baboons, glucocorticoid levels of dominant males are always lower and levels of all males increase similarly during unstable periods. Only alpha males represent an exception to this pattern as they usually show much higher levels than beta males. This might be due to the frequent involvement of alpha males in consortships, which are known to result in an increase of glucocorticoid levels in male chacma baboons (Bergman et al. 2005). Given the assumption about variation in dominance relationships between chacma and Guinea baboons, a comparison of variation in glucocorticoid levels could reveal further insights into factors affecting allostatic load in primates. Before the beginning of my study, however, no data on glucocorticoid levels of male Guinea baboons were available.

Genetic foundation of variation in aggressiveness in baboons

As outlined above, an association of *5-HTTLPR* and *MAOALPR* genotypes and aggressiveness in primates has been suggested by several studies, but the functions of these loci, especially of *5-HTTLPR*, are still debated. Among macaques, these polymorphisms have been linked to variation in aggressiveness and tolerance between species (Wendland et al. 2006b, Chakraborty et al. 2010). Given the close phylogenetic relatedness between baboons and macaques (both belong to the tribe of Papionini), it is likely that baboons show similar polymorphism potentially associated with interspecific variation in aggressiveness, but no data about variation in these loci were available before the beginning of my thesis.

Global variation in *5-HTTLPR* in humans and non-human primates

During my thesis I participated in a review on the function of the *5-HTTLPR* in humans (Kalbitzer J. et al. 2013, presented in CHAPTER FIVE). Here, the *5-HTTLPR* has been commonly linked to anxiety-related traits and the development of depression in response to stressful life events, but more recent reviews suggested to consider this polymorphism rather as a ‘plasticity gene’ (Belsky et al. 2009, Homberg & Lesch 2011); in that view, specific alleles confer a higher susceptibility to environmental changes than other alleles. This can be adaptive but may also result in maladaptive responses to stress, such as exaggerated aggression or depression. Human populations show geographical variation in allele frequencies, and individuals at higher latitudes more often carry an allele conferring stronger fluctuation in available 5-HTT in the brain depending on number of daylight hours. We therefore suggested that the *5-HTTLPR* genotype in humans mediates a trade-off between a high behavioral flexibility to ecological variation, as represented by seasonal variation in daylight hours at higher latitudes, at the costs of increased vulnerability to stress. Coming back to non-human primates, macaques are widely distributed in Asia (see Thierry 2007, Box 1). A comparison of macaque alleles with alleles found in African papionin species, including baboons, could therefore reveal further indications whether a more global geographical pattern in the *5-HTTLPR* exists which may be related to climatic or ecological variability. Furthermore, such a comparison could offer further insight into the evolutionary history of this in primates widely distributed polymorphism.

Aims and Predictions

The general purpose of my thesis was to further investigate variation in male social relationships among baboon species by comparing behavioral, physiological, and genetic parameters. As outlined above, male chacma and Guinea baboons are assumed to represent opposite extremes in aggressiveness and tolerance. The first specific aim of my thesis was therefore to compare social relationships between male chacma baboons living in the Moremi Game Reserve in Botswana, and male Guinea baboons living in the Parc National de Niokolo Koba in Senegal. We predicted that male chacma baboons would show more frequent and more intense aggressive behaviors while male Guinea baboons would show a higher spatial tolerance towards other males. Furthermore, we predicted that male chacma baboons would have consistent dominance relationships and a linear and steep dominance hierarchy while Guinea baboons would show no or less rigid dominance relationships.

The second aim of my thesis was to further investigate the link between testosterone and dominance-related aggression by comparing testosterone patterns between male chacma and Guinea baboons in relation to age, aggression and dominance relationships. Given the assumption that male Guinea baboons show fewer age-related differences in mating effort and less rigid dominance relationships, we predicted that they would show less intra- and inter-individual variation in testosterone levels than chacma baboons.

The third aim of my thesis was to obtain more information about the effects of male social relationships on allostatic load by comparing variation in glucocorticoid levels in relation to dominance status between chacma and Guinea baboons. Given the assumption that male dominance relationships among Guinea baboons are relatively relaxed, we predicted that variation in allostatic load between males of different social status would be lower than in chacma baboons. The results for the first three aims are presented in CHAPTER TWO.

As endocrinological studies on wild primates are often conducted in remote areas, simple infrastructure and missing laboratory equipment at field stations is a common problem. Consequently, hormone levels cannot be assessed immediately and samples need to be stored for weeks or even months. During this time hormone metabolites may degrade which would affect assessed hormone levels. Another aim of my thesis was therefore to test several long-term storage methods for baboon hormone samples and results are presented in CHAPTER THREE (Kalbitzer & Heistermann 2013).

The fourth aim of my thesis was to investigate the genetic foundation of interspecific variation in male aggressiveness by comparing *5-HTTLPR* and *MAOALPR* alleles between five species of baboons. Given the assumption about variation in aggressiveness between species, and the involvement of the *5-HTTLPR* and *MAOALPR* genotypes in the regulation of aggressiveness in primates, we predicted that baboons of the different taxa show different sets of alleles in both polymorphisms. More precisely, we predicted that different baboon species carry different alleles or different species carry identical alleles but in different frequencies. In that case, we would predict a gradient from South to North in allele frequencies, reflecting the behavioral pattern described above. The results of this part of my thesis are presented in CHAPTER FOUR.

Following the idea about the role of *5-HTTLPR* in conferring a specific behavioral plasticity towards ecological variation, depending on the genotype (postulated in the review, Kalbitzer J et al. 2013, CHAPTER FIVE), another aim was to compare the *5-HTTLPR* among different species of papionins distributed in Africa and Asia. Therefore, we obtained DNA sequences from mandrills (*Mandrillus sphinx*), drills (*Mandrillus leucophaeus*), golden-bellied mangabeys (*Cercocebus chrysogaster*), and black mangabeys (*Lophocebus aterrimus*). We had no specific predictions concerning the variation among these species, but these data may help to further elucidate the global distribution and evolutionary history of this common polymorphism in primates. The results of this comparison are also included in CHAPTER FOUR.

With my thesis I want to contribute to the overall picture of variation in male social relationships in baboons which may ultimately help to better understand selection pressures acting on male behavior in primates. By shedding light on species differences concerning the relationships between levels of aggression and testosterone, glucocorticoids, and specific alleles, respectively, I believe that the comparative approach taken here will ultimately leading to a better understanding of the evolution of primate social systems.

CHAPTER TWO

Variation in aggressiveness and spatial tolerance between male chacma and Guinea baboons in relation to androgen and glucocorticoid levels

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Abstract

Male primates vary in aggressiveness depending on reproductive strategies. This variation has been linked to differences in testosterone profiles, which in turn are related to allostatic loads, reflected in glucocorticoid levels. Baboons constitute an intriguing model to examine the costs and benefits of male aggressiveness, as males of different baboon species (*Papio* spp.) differ in the intensity of contest competition. We focused on chacma baboons (*P. ursinus*) in Botswana and Guinea baboons (*P. papio*) in Senegal because they represent opposite extremes of male aggressiveness in this genus. We recorded male social and spatial behavior and assayed physiological correlates of dominance, specifically testosterone and glucocorticoids levels. Male chacma baboons were involved in agonistic interactions more frequently than Guinea baboons, while male Guinea baboons showed higher levels of male-male affiliative interactions and pronounced spatial tolerance. Notably, male chacma baboons were also more aggressive towards females, indicating an overall higher aggressiveness in this species. We found a linear dominance hierarchy in male chacma but not male Guinea baboons, although we observed some consistent dominance relationships between specific dyads in Guinea baboons. In contrast to our predictions, there was no relation between testosterone and age or rank of adult males in either species. In chacma baboons, however, we found a trend that testosterone correlates with aggression, while we did not find such a trend in Guinea baboons. Similarly, glucocorticoid levels were correlated with rank in chacma but not in Guinea baboons. Our results support the view that different social systems create differential selection pressures for male aggressiveness.

Introduction

In most mammalian species, male reproductive success is determined primarily by mating rather than parental effort (Trivers 1972). Males should therefore aim to compete intensely with other males over access to females (reviewed in Alberts 2012), but if males are not able to monopolize receptive females, competition may continue after copulation by sperm competition (reviewed in Birkhead & Kappeler 2004). The actual strategies may vary depending on the spatio-temporal distribution of receptive females (Emlen & Oring 1977, Altmann 1990), which in turn is related to food distribution, infanticide risk, and/or predation pressure ('socio-ecological models'; Wrangham 1980, van Schaik & van Hooff 1983, Sterck et al. 1997; reviewed in Koenig et al. 2013).

In most primate species, several females live cohesively together (Kappeler & van Schaik 2002). When female group size is small, a single male may be able to exclude other males from access to females through intense contest competition (e.g. in gorillas, *Gorilla gorilla*: Harcourt & Stewart 2007). Larger number of females, however, may prevent males from complete monopolization, resulting in multi-male groups in which males compete for mating opportunities within the group (e.g. *Macaca assamensis*: Ostner et al. 2011; *Papio ursinus*: Bulger et al. 1993). During receptive periods, males often engage in mate guarding (i.e. 'consortships'; e.g. *P. cynocephalus*: Alberts et al. 2003), though monopolization is often not complete (e.g. *M. sylvanus*: Brauch et al. 2008, Pfefferle et al. 2011). The number of males within a group further increases with estrous synchrony of females as the monopolization potential is reduced (e.g. Nunn 1999, Carnes et al. 2011).

Contest competition over access to receptive females appears to be the primary strategy among primate males (Alberts 2012) but physical aggression can be extremely costly. In many species where individuals regularly interact with each other, they establish dominance hierarchies based on differences in competitive abilities which avoids regular conflicts (e.g. Zinner & Wheeler 2012). In such hierarchies, the rank of a male often predicts the access to females (Altmann 1962). However, males may also circumvent 'one against one' competition for high ranks by employing alternative tactics, most importantly through coalitionary behaviors (Alberts et al. 2003, Alberts 2012). Coalitions can be formed opportunistically or be associated with long-lasting bonds, which are often expressed by high tolerance and affiliation (van Hooff & van Schaik 1994).

The availability of different reproductive strategies for males also has repercussions for the lifetime reproductive trajectories of males. In species with intense contest competition, males depend on a good physical condition, usually linked to age, to obtain high ranks (van Noordwijk & van Schaik 2004 , Clark et al. 2008). Accordingly, prime-aged males show a higher reproductive performance than younger or older ones (Alberts 2012). In species in which males can apply alternative tactics not (entirely) depending on their physical condition, they may reproduce during longer periods in life, after they have fallen in rank (e.g. Alberts et al. 2003, Beehner et al. 2009).

The reproductive trajectories of male primates are associated with the steroid hormone testosterone (reviewed in Muller & Emery Thompson 2012). Among other effects, testosterone affects traits related to competition and mating, including the stimulation of muscle tissue growth (e.g. Kemnitz et al. 1988), and the promotion of spermatogenesis (e.g. McLachlan et al. 1996). With regard to short-term fluctuation of testosterone, the ‘challenge hypothesis’ - originally postulated for birds (Wingfield et al. 1990) - predicts that elevated levels of testosterone enhance aggression in the context of competition for mating opportunities (Muller & Wrangham 2004). In accordance with that idea, testosterone levels have been observed to be higher during periods of intense mating competition and high aggression rates in primates (e.g. in *M. assamensis:* Ostner et al. 2011; *M. fascicularis*: Girard-Buttoz et al. 2009; *Pan troglodytes*: Muller & Wrangham 2004, Sobolowski et al. 2013). In species in which dominance ranks are related to mating success, testosterone levels are expected to be generally higher during periods of aggressive competition for rank (e.g. in *Mandrillus sphinx*: Setchell et al. 2008; *P. ursinus*: Beehner et al. 2006).

Variation in competition may also affect how individuals of different dominance positions may suffer from physiological costs, or allostatic load, which can be assessed by measuring glucocorticoid levels (Abbott et al. 2003 , Goymann & Wingfield 2004). Glucocorticoids are responsible for the mobilization of energy reserves and suppression of non-essential metabolic processes (reviewed in Sapolsky et al. 2000). As a result, high levels can be adaptive in response to acute stressors, but detrimental when sustained over long times (e.g. Sapolsky 2005). Allostatic load of dominant animals depends on how ranks are acquired and maintained, while in subordinate animals it depends on the degree of threat they have to suffer from dominants, the ability of avoiding these threats and the availability of resources or mating partners (Goymann & Wingfield 2004). In other words, the type and intensity of competition is reflected in differences in physiological costs between subordinate and dominant individuals.

Baboons constitute a suitable model to investigate the relation between male aggressiveness, tolerance and other aspects of a social system, to study the proximate mechanism regulating variation in aggressiveness, such as testosterone patterns, and to assess physiological costs of social status depending on the competitive regime. Males of different baboon species show a gradient in aggression, spatial tolerance, and cooperation (Henzi & Barrett 2003, Jolly 2007, Jolly 2009). Chacma baboons (*P. ursinus*) in southern Africa exhibit a high degree of direct male-male competition as intense fights are regularly observed, spatial tolerance is low, and coalitions are virtually absent (Bulger 1993 , Henzi & Barrett 2003 , Kitchen et al. 2003, Kitchen et al. 2005). Yellow baboons (*P. cynocephalus*), living in eastern Africa, and olive baboons (*P. anubis*), which are distributed from western to north-eastern Africa, are both described to engage in intensive male-male fights (e.g. MacCormick et al. 2012), and to exhibit low male-male spatial tolerance. Nevertheless, male coalitions are relatively common in these baboon species (e.g. Smuts 1985, Bercovitch 1988, Noe & Sluijter 1995), though they occur opportunistically and are not associated with long-term social bonds (Noe & Sluijter 1995). West African Guinea baboons (*P. papio*) do not adhere to this general pattern. In this species, several males and females form 'parties', which often aggregate into 'gangs' (Patzelt et al. in revision). Males, including reproductively active males, are spatially tolerant, sometimes groom each other, and form coalitions (Sharman 1981 , Galat-Luong et al. 2006 , Patzelt et al. in revision), while rates of aggression are low (e.g. Galat-Luong et al. 2006). Furthermore, the affiliation network is correlated with the support network (Patzelt et al. in revision), strongly suggesting that male Guinea baboons form bonds.

In chacma, yellow, and olive baboons, males form linear dominance hierarchies, in which rank position largely predicts mating activity, and presumably reproductive success (chacma baboons: Bulger 1993, Weingrill et al. 2000, Beehner et al. 2006 , yellow baboons: Alberts et al. 2006 , olive baboons: Packer 1979). Mating skew is probably higher in chacma baboons, as subordinate males of the other two species may form coalitions to increase their mating success (Bulger 1993, Henzi & Barrett 2003, Beehner et al. 2009). Dominance relationships among male Guinea baboons are less pronounced. A previous study failed to identify a clear dominance hierarchy, as numerous male dyads were never observed to engage in agonistic interactions (Patzelt 2013). Most adult males are associated with females (Patzelt 2013) suggesting that the short-term mating skew may be lower than in other baboon species.

Concerning the physiological foundation of reproductive trajectories and variation in aggression, data collected from yellow and chacma baboons support the idea that reproductive profiles are associated with long-term patterns of testosterone (Beehner et al. 2009). In male chacma baboons - with a very concise period of high mating activity - testosterone levels rapidly increase before individuals reach their maximum dominance position and sharply decline afterwards (Beehner et al. 2006, Beehner et al. 2009). By contrast, in yellow baboons, in which older males still produce a relatively large number of offspring (Alberts et al. 2006), testosterone levels only decline gradually (Beehner et al. 2009). With regard to short-term variation, testosterone levels of dominant male olive baboons increase during periods in which high ranks are contested (labelled as 'unstable' periods; Sapolsky 1983, Sapolsky 1993), and more specifically, testosterone levels are correlated with aggression rates during such periods in chacma baboons (Beehner et al.

2006). Additionally, high testosterone levels in chacma baboons are predictive of rises in dominance rank (Beehner et al. 2006, Bergmann et al. 2006). Comparative data on other baboon species are still missing but such data could be informative with regard to the general link of reproductive profile, competition, aggression, and testosterone in primates

Concerning allostatic load of social status, glucocorticoid levels in male chacma (Bergman et al. 2005, Cheney et al. in preparation), yellow (Gesquiere et al. 2011), and olive baboons (Sapolsky 1983, Sapolsky 1993) correlate with rank position and the stability of the hierarchy. Generally, glucocorticoid levels of all adult males increase during unstable periods. In chacma and in olive baboons, dominant males show higher glucocorticoid levels than subordinate males during these periods while subordinate males have higher levels during stable periods (Sapolsky 1983, Sapolsky 1993, Bergman et al. 2005, Cheney et al. in preparations). In yellow baboons, by contrast, dominant males always have lower levels irrespective of period (Gesquiere et al. 2011). Only alpha males represent an exception to this pattern as they usually show higher levels than beta males. This finding is potentially related to the frequent involvement of alpha males in consortships with receptive females, which are known to increase glucocorticoid levels in male chacma baboons (Bergman et al. 2005). As for testosterone, no data on glucocorticoid levels for males of other baboon species are available.

Despite this variation in male behavior among baboon species, direct comparative quantitative data are missing. Male chacma and male Guinea baboons appear to represent opposite extremes in aggressiveness and spatial tolerance related to variation in the employment of cooperative strategies. Thus, the first aim of this study was to compare aggressiveness, spatial tolerance, and dominance relationships between these two species. We predicted that male chacma baboons would show higher rates of agonistic behaviors than male Guinea baboons, while rates of affiliation and spatial tolerance, potentially associated with the formation and maintenance of bonds, would be higher in male Guinea baboons. To determine whether chacma baboon males are generally more aggressive we also analyzed male-female aggression. We predicted a higher linearity and steepness of hierarchies and a higher consistency of dominance relationships in chacma compared to Guinea baboons. Additionally, we expected more physical aggression to be involved in rank changes in chacma than in Guinea baboons.

The second aim of this study was to assess testosterone levels in chacma and Guinea baboons and to compare them with differences in age, rank and rank changes, and aggression. We predicted greater inter-individual variation among adult male chacma than among Guinea baboons, given the assumption that Guinea baboons have a more prolonged period of mating activity compared to chacma baboons. More specifically, we expected a pronounced effect of age on testosterone in chacma but only a slight effect in Guinea baboons. With regard to dominance rank, we predicted that testosterone levels, even when controlled for age, would be related to future rank changes in chacma but not in Guinea baboons as ranks were assumed to be less significant for reproductive success in the latter. Furthermore, we expected that testosterone levels would be generally unrelated to agonistic behaviors, but during unstable periods, testosterone levels would be correlated with rates of expressed aggression.

The third aim of our study was to compare the effect of rank and aggression on glucocorticoid levels in chacma and Guinea baboons, to deepen our understanding how variation in male competition affects variation in allostatic loads in different primate species. We predicted more inter-individual variation in glucocorticoid levels among male chacma than among male Guinea baboons. Specifically, we expected to replicate the finding that in chacma baboons dominant males have higher levels during rank instability but lower levels during stable periods (Bergman et al. 2005) while we expected no or only a weak effect of rank position in Guinea baboons. Furthermore, we evaluated in both species whether agonistic interactions had an effect on glucocorticoid levels.

Methods

Study sites and populations

Behavioral and hormonal data were collected from wild chacma baboons in the Moremi Game Reserve, Botswana, and wild Guinea baboons in the Niokolo Koba National Park in Senegal.

Data collection in Botswana took place between March and September 2011. The observed group (the so-called 'C-Troop') had been under continuous observation between 1978 and 2007 (described in Cheney et al. 2012). Despite the end of continuous observations in 2007, the group was still well habituated in January 2011. At that time, the group was composed of 10 adult males, 25 adult females and their immature offspring (Table 2.1). At the end of April, however, the group fissioned into two smaller groups, the 'Airstrip subgroup' (ASG) and the 'Hammerkop subgroup' (HSG). Five of the adult males and 13 of the adult females went into the ASG; two of these females disappeared during the remaining study period. The other five adult males went into the HSG with 12 females, and were immediately joined by a new male who took over the alpha position. One of the HSG males disappeared at the end of June and another male was found dead at the end of August 2011. After the fission, both subgroups stayed within the same territory and regularly encountered each other. We briefly describe the frequency and quality of these encounters.

The 11 adult male chacma baboons included in data collection were categorized into three broad age categories, estimated by tooth wear and other morphological characteristics (see Method S2.1, SI). Three adult males were categorized as 'young', five as 'prime-aged', and three as 'old'.

Table 2.1: Study groups, compositions, and periods of observation

Species	Group/ Gang	Party	Period of data collection	Number of males/focal males	Number of females	Focal hours
Chacma baboons	C-Troop	(before fission)	03.-04.2011	10/10	25	260h
	ASG	(after fission)	05.-09.2011	5/5	11-13	
	HSG		05.-09.2011	4-6/4-6	12	
Guinea baboons	Mare-gang	OSM	02.-07.2011	4/4	9-10	231h
		SNE	02.-07.2011	4/4	5-6	
		AND	-	2/0	0	
	Simenti-gang	JKY	03.-07.2011	7/6	11-12	
		MST	-	4/0	7-8	

Data collection in Senegal took place between February and July 2012 (the field site is described in Patzelt et al 2011). Guinea baboons live in a multi-level society in which several 'parties' form 'gangs' (Patzelt et al. in revision). While males of different gangs only rarely interact with each other, males within the same gang have regular interactions even if they belong to different parties. It therefore seems that Guinea baboon gangs are the social units most comparable to chacma baboon groups (see also Maciej et al. 2012). We therefore compared male behavior between chacma baboon groups and Guinea baboon gangs.

We collected data on two different gangs (Table 2.1). The 'Mare-gang' was composed of three different parties and we collected data on two of these, the 'OSM-party' (4 males and 9-10 females) and the 'SNE-party' (4 males and 5-6 females). The third party associated with the Mare-gang, the 'AND-party', was a bachelor group of two young adult males and 3-4 subadult males. We also collected data on one party of the 'Simenti-gang', the 'JKY-party'. This party represented the larger of two parties constituting this gang. Males of the 'MST-party', the second party of this gang, could not be included in data collection. The 14 males included in the Guinea baboon data set consisted of four young, seven prime-aged, and three old individuals.

Behavioral data collection

UK conducted focal observation on males of both species to make data as comparable as possible. Observations always took place between 6am and 1pm and were balanced over different times of the day for each individual. Focal subjects were chosen randomly whenever possible. Focal observations included observations of 20 and 30 minutes, respectively, depending on the availability of males (i.e. longer observations in small groups after the fission in chacma baboons, and when Guinea baboon parties were separated).

During focal observation, UK recorded all agonistic behaviors (i.e. fights, chases, chase-aways, threats and submissive behaviors; for definitions see Table S2.1, SI). He also noted all approaches and leaves within 10 cm (i.e. 'body-contact') and 1 m of the focal individual. When individuals were only briefly in close proximity (i.e. for less than 5 seconds) we labelled such interactions as either a supplant (when A approached B and B left); an 'In&out' (when A approached and immediately left B or A and B approached each other and both left), or a 'bump-in' (when A approached B and both left in different directions). During all these interactions we noted whether individuals exchanged 'greetings' (including all non-agonistic and non-affiliative physical contact; for a definition see Table S2.1, SI), as these have been associated with the formation of bonds (Whitham & Maestripieri 2003). During group movements we only recorded such interactions when proximity was clearly directed, meaning that one individual headed directly towards another; mere proximity while the group was walking 'in a row' was not included.

When one individual approached another one and both stayed in close proximity for longer than five seconds, this could potentially result in three different behaviors related to spatial tolerance or affiliation: '1 m proximity' (feeding, resting or standing within 1 m), 'contact sitting' (resting, feeding, or standing within 10 cm), or grooming. For all these behaviors we determined durations using recorded start and end times.

In addition to recordings during focal observations, we noted all agonistic interactions *ad libitum* to improve the assessment of dominance relationships. Further, we recorded whether fights resulted in injuries since we were interested in the intensity of fights. However, as fights are rarely observed, we also recorded each time a male had a fresh wound which could potentially resulted from a fight, including slashes, cuts, or punctures of the skin (see MacCormick et al. 2012).

Hormone data

For the non-invasive assessment of hormone levels, we collected fecal samples from focal individuals. Only samples uncontaminated with urine were collected immediately after defecation and only samples collected between 6.30am and 1pm were included to avoid diurnal effects on hormone levels (Heistermann 2010). For chacma baboons, we collected 258 samples in total, ranging between 13 and 29 per individual (mean± sd= 23.45±5.22; median = 26) and for Guinea baboons 269 samples, ranging between 10 and 27 per individual (mean ± sd= 19.2±7.8; median = 21.5). We analyzed at least one sample from each focal individual per analyzed period (see below).

Hormone metabolites were extracted from fecal samples as described in Method S2.2 (SI). The extracts were stored in a gas-refrigerator until transport to the German Primate Center (DPZ) for analysis. The maximum storage duration of extracts in the refrigerator was less than six months, which has been shown not to affect testosterone or glucocorticoid metabolite levels (Kalbitzer & Heistermann 2013, CHAPTER THREE). Once samples arrived in the DPZ they were immediately put into a freezer at -20°C and assayed within five months thereafter.

The extracts were assayed for immunoreactive testosterone (fT) and 11ß-hydroxyetiocholanolone (fGC), a major cortisol metabolite in the feces of primates, by using enzyme immunoassays (see Method S2.3, SI). For hormone measurements in samples collected from chacma baboons, inter-assay coefficients of variation (CVs) for the fT assay were 11.4% and 15.7% for high and low value quality controls, respectively, while for fGC-assays CV values were 7.7% and 16.5%. For samples collected from Guinea baboons, CVs for fT were 11.2% and 14.0% and for fGC 4.4% and 8.4%.

Data analysis

In a first step, we counted how often each focal male was involved in agonistic interactions with other individuals (i.e. individual rates of agonistic interactions). We then calculated rates of specific behaviors (fights, chases, chase-aways, threats, supplants, and submissive behaviors) for each individual (see Methods S2.4, SI).

In order to analyze dominance relationships, we included all directed dominance interactions in which the dominant and subordinate individual could be assigned (i.e. chases, chase-aways, supplants, and submissive behaviors). As we wanted to test if dominance relationships were less consistent in Guinea baboons, we also counted agonistic behavior which occurred in two directions within one bout; for example if a chase turned in direction, we included both chases. Such interactions would indicate that the dominance relationship between the two individuals involved was rather inconsistent at that time.

For chacma baboons, we analyzed dominance relationships in the C-troop before the group fissioned. We excluded the first week of focal data collection because a young male took over the alpha position one week after the start of observations, and we therefore had very little data from the time before this event occurred. After the group fission (7 weeks later), we analyzed data on both new groups, the ASG and the HSG separately until the end of the study period.

In Guinea baboons, we analyzed dominance relationships for five different constellations. First, we assessed dominance relationships for the two observed parties of the Mare-gang (OSM- and SNE-parties) separately. We then combined data from the two parties and included interactions with other males of this gang that were not part of focal observations (the two males of the AND-party). For the Simenti-gang, we assessed relationships within the JKY-party (including the young none-focal male) and then included data on interactions with males of the other party (the MST-party) which belonged to this gang but which was not included in focal observations.

In order to test hypotheses concerning the relationship between hormone levels and behavior in the two species, we combined results from hormone measurements and focal observation into discrete three-week time periods (Fig. S2.1, SI; only periods in the beginning of the study were slightly longer). We used between one and six hormone samples per individual for each time period (chacma baboons: range = 1-4, mean: 2.69±0.87; Guinea baboons: range=1-6, mean=2.69±1.00) and between 41 and 307 focal minutes (chacma baboons: range=48-307 minutes; mean=167±57 minutes; Guinea baboons: range=41-208 minutes; mean=139±32 minutes).

For hormone levels, we calculated mean values for each of these periods and then determined for each individual the deviation from this mean in percent. Accordingly, we used one value for each individual per period, which expressed individual hormone levels relative to the group´s mean for the given period. This procedure excluded all variation between periods – variation that might potentially have been caused by seasonal effects. For each period, we calculated rates of agonistic interactions per individual and the individual's dominance rank (see below).

Statistics

We compared rates of interactions between species using non-parametric Wilcoxon-Mann-Whitney-tests (function 'wilcox.test' in R 3.0.3; R Core Team, 2014). We compared rates of agonistic bouts and specific behaviors of males separately for each partner category. We used the same test to compare whether interactions occurred with or without greeting and whether male Guinea baboons spent more time engaged in behaviors indicating spatial tolerance and affiliation than chacma baboons.

To assess characteristics of the dominance relationships, we used MatMan 1.1 (Noldus, Wageningen, Netherlands; first described in de Vries et al. 1993) to calculate parameters describing the consistency of relationships (directional consistency index, DCI) and linearity of the hierarchy (Landau's linearity index h', corrected for unknown relationships). As the linearity is affected by the number of included individuals (by chance, smaller groups can have a higher linearity), we also extracted the expected value for h' under the assumption of no dominance bias and built the ratio between h'/expected h'. Furthermore, we calculated the steepness of hierarchies (de Vries et al. 2006). In order to make rank positions comparable for the analysis of the hormone-rank relationship, we used ranks calculated in MatMan (I&SI method) and scaled them from 0-1 with 0 for the lowest ranking individual and 1 for the highest ranking individual.

To test relations between hormone levels, age categories, dominance position, behavior, and species, we used general linear mixed models with respective predictor and response variables, and focal individual as a random effect. All models were calculated in R 3.0.3 (R Core Team, 2014; for further information see Methods S2.5, SI and GLMMs, SI).

Results

Rates of agonistic interactions

Chacma baboon males were involved in agonistic interactions with other males at higher rates than Guinea baboon males (Fig. 2.1a; for detailed values see Table S2.2, SI). The majority of agonistic interactions constituted of supplants, which also occurred at a higher rate in male chacma baboons (Fig. 2.1b). Additionally, chacma baboons showed a higher rate of submissive behaviors than Guinea baboons (Fig. 2.1c). Other, less frequent, agonistic behaviors were also more frequent in male chacma baboons (chases: Fig. 2.1d, chase-aways: Fig. 2.1e; threats: Fig. 2.1f).

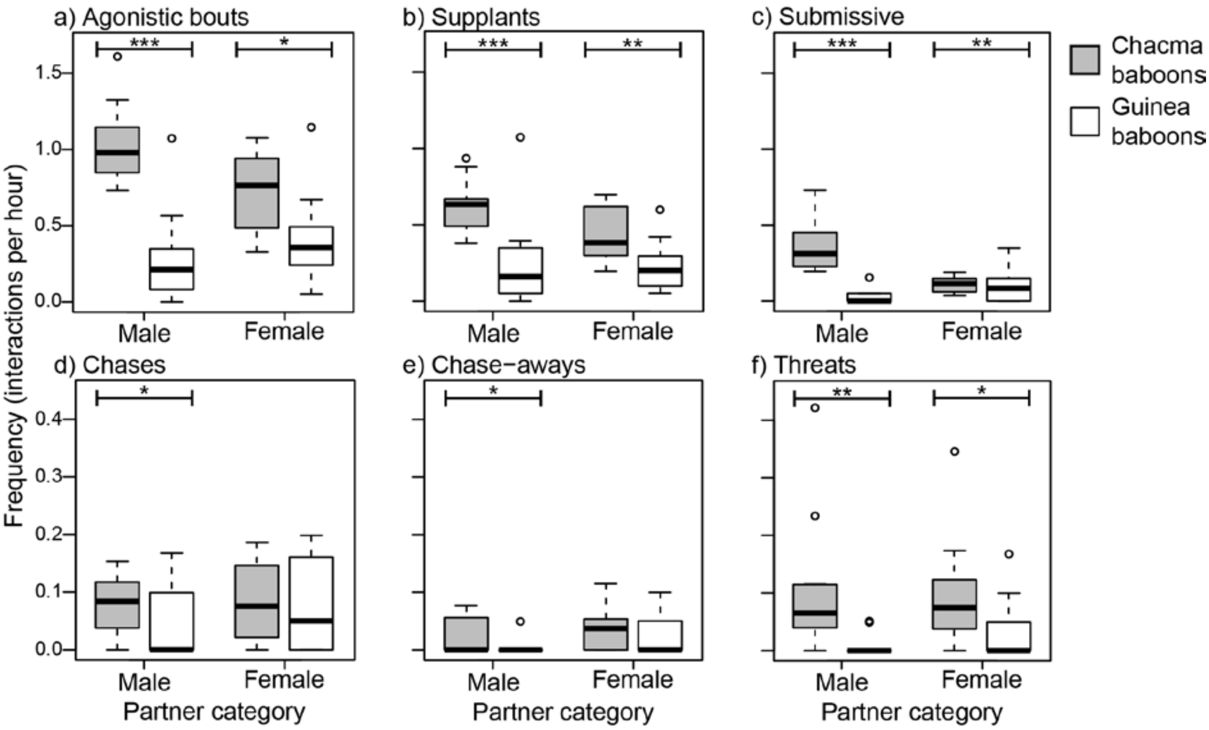

Fig. 2.1 Agonistic interactions of males categorized for interaction type and shown for males and females as partners separately. Stars indicate significant differences (Wilcoxon-Mann-Whitney tests) with *<0.05, **P<0.01, and ***P<0.001 (for more details see Table S2.2, SI)

Male chacma baboons were also involved in agonistic interactions with females at higher rates than were male Guinea baboons (Fig. 2.1a). More specifically, we detected significant differences between species in supplants and threats (Figs. 2.1b and 2.1f; rates in chacma baboons were higher in both cases). During focal observation we recorded three fights of male chacma baboons with females, and two fights of male Guinea baboons with females. With regard to the directionality of agonistic interactions between males and females, male chacma baboons could be clearly assigned as dominant in all interaction with the exception of 6.25% of supplants in which the male left after the approach of a female. In Guinea baboons, the male left after the approach of the female in 15.09% of supplants. Furthermore, in 12.50% of chases, the male was chased by the female, and in 16.65% of threats, the male was threatened by a female. In contrast, female chacma baboons were never observed to chase or threaten a male.

Fights and Wounds

Fights among males were extremely rare: we recorded only two fights in chacma baboons during all focal observations and six additional fights *ad libitum*. Five of these fights included bite attacks, but we could only observe injuries after one of these fights; both participants were injured, one had a deep cut in the leg and the other one was bleeding at the neck and the shoulder. Additionally, we observed 17 injuries in which we did not observe the wounding event, including 11 injuries to the face, 4 to the shoulder, one to the buttock, and one to the flank of a male. In Guinea baboons, we observed 9 fights *ad libitum*, but in none of these fights did we observe a bite-attack or an injury.

Interactions within close proximity and greeting rates

Guinea baboon males had more interactions within close-proximity than did chacma baboon males (Fig. 2.2a; Table S2.3, SI). As mentioned above, supplants were more common in chacma than in Guinea baboon males (Fig. 2.2b), but Guinea baboon males were more often involved in bump-ins (Fig. 2.2c) and in&outs (Fig. 2.2d). Interactions in male chacma baboons were more likely to occur without greetings, while interactions of male Guinea baboons typically included greetings (Fig. 2.2a). This generalization held for supplants, bump-ins, and in&outs (Figs. 2.2b, 2.2c, 2.2d).

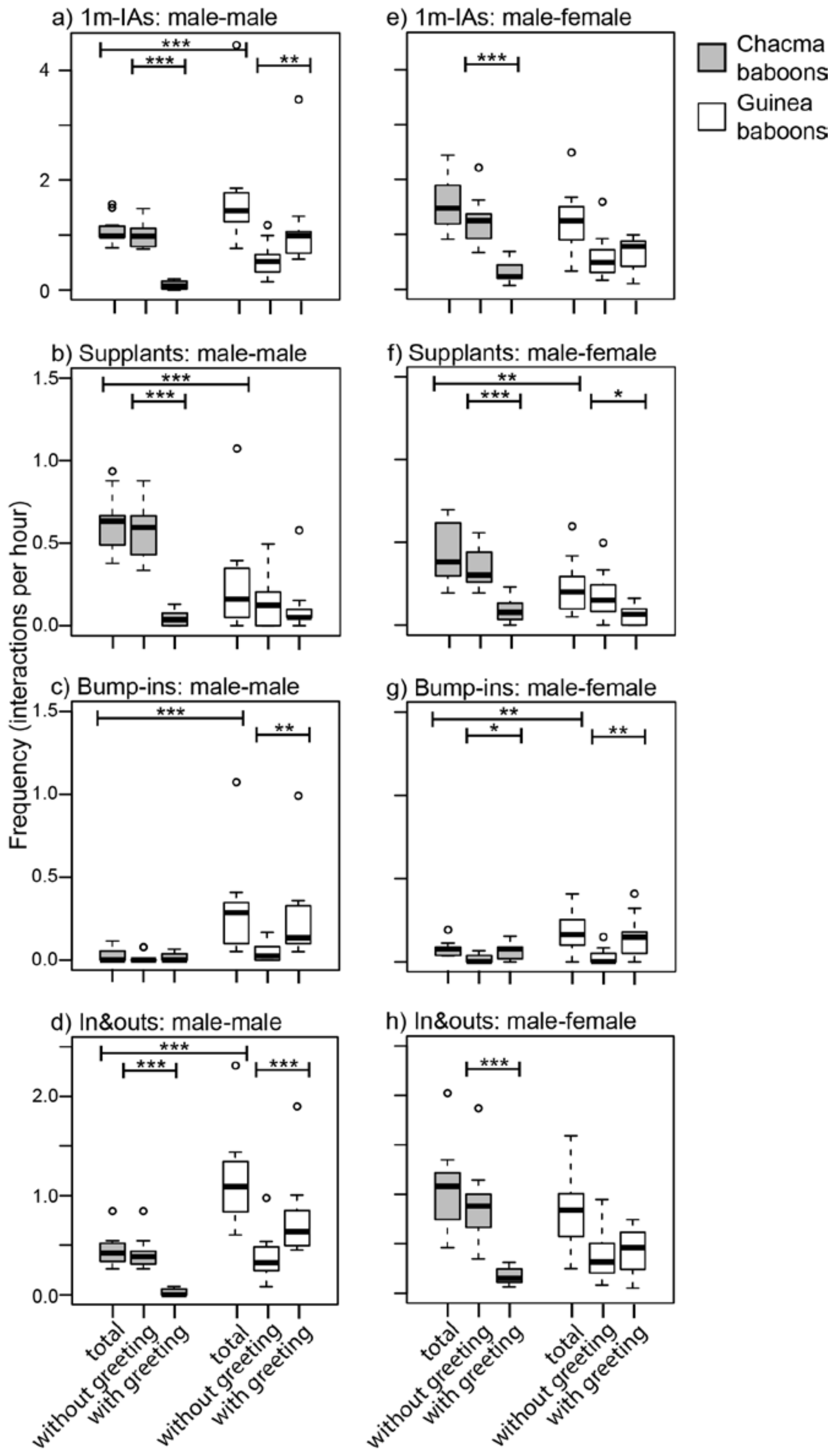

Fig.2.2: Rates of spatial interaction with and without greeting, separated by interactions with males or females. 1m-IAs = all interactions within 1 m (i.e. combined rates of supplants, bump-ins, and in&outs). Stars indicate significant differences (Wilcoxon-Mann-Whitney tests) with *<0.05, **P<0.01, and ***P<0.001 (see Table S2.3, SI for more details)

With respect to male-female interactions, there were the same differences in the rate of supplants (more in chacma baboons; Fig. 2.2f) and bump-ins (more in Guinea baboons; Fig. 2.2h). The pattern for the involvement of greetings in male-female interactions was similar as for male-

male interactions in chacma baboons (1m-interactions, supplants, and in&outs more often without than with greeting; Figs. 2.2e, 2.2f, 2.2h). In Guinea baboons, the majority of male-female supplants occurred without a greeting (Fig. 2.2f), while male-female bump-ins were slightly more often with than without greeting (Fig. 2.2g).

Spatial tolerance and affiliation

There were obvious differences between males of the two different species in the proportion of time spent in behaviors related to spatial tolerance and affiliation (Fig. 2.3). Male Guinea baboons regularly spent time resting, feeding or standing with at least one male within 1 m, while such behavior was extremely rare in chacma baboons (Fig. 2.3a). Contact-sitting occurred occasionally among male Guinea baboons but was never recorded for male chacma baboons (Fig. 2.3b). Male-male grooming followed a similar pattern (Fig. 2.3c). For male-female behavior, the direction of species differences was similar for proximity-1m (Fig. 2.3a) and contact-sitting (Fig. 2.3b; see Table S2.4, SI). Only in the context of male-female grooming did we not detect a difference between species (Fig. 2.3c). Interestingly, male Guinea baboons were often involved in grooming interactions with more than one partner simultaneously, while this was not observed in chacma baboons.

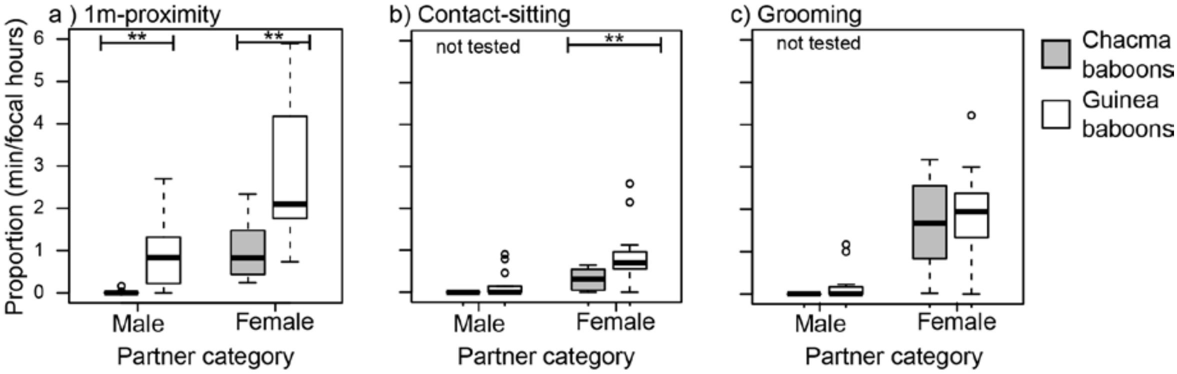

Fig. 2.3: Proportional durations of behaviors related to affiliation and spatial tolerance separated by interactions with males and females. Stars indicate significant differences (Wilcoxon-Mann-Whitney tests) with *<0.05, **P<0.01, and ***P<0.001 (see Table S2.3, SI for more details)

Dominance relationships

As agonistic interactions were much more frequent in chacma baboons, the number of interactions included to calculate characteristics of dominance relationships differed between species (Table 2.2). In chacma baboons, the linearity of dominance hierarchies (h’) within groups varied with a lower linearity before than after the fission, but both the C-troop and the HSG showed a significantly linear hierarchies (P <0.05; we could not test the linearity of the hierarchy for the ASG as only five males were in the group). Furthermore the ratio between h’ and expected h’ was larger than 2 for all groups.

Table 2.2: Characteristics of dominance relationships. Linearity h’ = Landau’s linearity index h’ of hierarchies, corrected for unknown relationships; Expected h’=linearity index h’ of hierarchies under the assumption of no dominance bias; DCI = directional consistency index. For details see Methods-section. [1]The number of males in the gangs is higher than the sum of males in the shown parties as we only calculated values for parties included in the focal observations.

	Chacma baboons			Guinea baboons				
	Before fission	After fission		Mare-Gang			Simenti-Gang	
	C-Troop	ASG	HSG	Gang[1]	OSM	SNE	Gang[1]	JKY
Males in group	10	5	6	10	4	4	11	7
Focal males	10	5	6	8	4	4	6	6
Interactions included	94	167	150	50	9	30	39	30
Focal hours included	41h	107h	105h	159h	80h	79h	72h	72h
Linearity h'	0.62	1.00	1.00	0.33	0.20	1.00	0.39	0.71
Expected h'	0.27	0.50	0.43	0.27	0.60	0.60	0.27	0.38
Ratio h'/expected h'	2.29	2.00	2.33	1.20	0.33	1.67	1.44	1.90
Significance of linearity (P)	0.021	NA	0.023	0.360	NA	NA	0.223	0.072
Consistency (DCI)	0.85	0.87	0.95	0.76	0.56	0.73	0.74	0.73
Steepness (S)	0.14	0.34	0.37	0.05	0.21	0.21	0.10	0.12

In Guinea baboons, linearity of hierarchies varied widely between gangs and parties (Table 2.2). Interestingly, the hierarchies of the two parties of the Mare gang (OSM- and SNE-parties) differed extremely in linearity. The ratio between h’ and expected h’ also varied strongly among parties, suggesting true differences in linearity of hierarchies among parties, but the ratio was always lower than in chacma baboons. None of the Guinea baboon hierarchies including at least six males (Mare-gang, Simenti-gang, Jky-party) had a significantly linear hierarchy even though there was a trend for linearity the JKY-party.

The consistency of dominance relationships (i.e. DCI) in chacma baboons was similar among groups, and was always higher than in Guinea baboons. In Guinea baboons, the DCI was similar for most gangs and parties, and only the males of the OSM-party showed a lower consistency in dominance relationships.

In chacma baboons before the fission, the steepness of the hierarchy was relatively low for the entire C-troop, but afterwards it was more than twice as large in the smaller groups. In Guinea baboons, the steepness was much lower for the entire Mare-gang, than for both parties separately. For the Simenti-gang, values were similar for the entire gang and for the JKY-party separately. For both smaller chacma baboon groups the steepness of hierarchy was higher than for any group of Guinea baboons, but in the C-troop the steepness was in the range of values for Guinea baboons.

Subgroup encounters in chacma baboon

Following the fission of the chacma C-troop, the two subgroups were not observed in proximity of each other during the first five weeks. During the remaining 16 weeks of the study period, the subgroups were seen within close proximity (i.e. within the range of vision) and responding to each other on 22 of 99 observations days (22%). The interval between encounters ranged between 0 and 19 days (mean = 4.1 days, median = 2 days). During all encounters, the HSG moved away from the ASG, and the ASG almost always followed the HSG, though we saw the ASG actively chasing the HSG on only three occasions. During the time after the fission, the flood in the Delta was relatively high and the baboon range consisted of several small islands (for a description of the habitat see Cheney & Seyfarth 2007). On 19 of the 22 days both groups were seen together, they were on the same island. On 11 of these occasions the HSG crossed at least once to another island, apparently to avoid the ASG, and the ASG followed on six occasions. For comparison, we observed only three encounters with other groups during that period.

Variation in testosterone levels (fT) among adult males

Inter-individual variation in fT levels was relatively similar in both species (average deviation from group mean: chacma baboons: 14.78±3.74%; Guinea baboons: 18.58±3.58%), but there was a trend that Guinea baboon males, contrary to our prediction, had a slightly higher variation (model 1-fT; species-effect: Chisq=3.2028, Df=1, P=0.074; all models and results are shown in GLMMs, SI).

Age category in interaction with species had no effect on fT values (model 2-fT; Chisq=0.817, Df=2, P=0.665), nor could we detect a main effect of age category on fT (Chisq=0.1736, Df=2, P=0.917; models calculated for each species separately also revealed p-values >0.7).

Initially, we planned to test if testosterone levels predicted future rank positions (e.g. Beehner et al. 2006), but during our study no resident males challenged higher ranking males. Using current rank as a variable (for Guinea baboons we used ranks assigned within parties, see above), we found no significant interaction between species and rank on fT levels (model 3-fT; Chisq: 1.8738, Df=1, P=0.171), nor was there a main effect of rank on fT (Chisq=0.0279, Df=1, P=0.867; models calculated for each species separately revealed P-values >0.25). To test whether rank was correlated with fT in interaction with stability, we used definitions applied previously (Beehner et al. 2006, Bergman et al. 2006) and labelled the weeks following rank changes in the two upper rank positions as unstable. This included two periods: the first period analyzed for the C-troop, and the first periods for both smaller groups (ASG and HSG) after the fission. However, we did not find a significant relation between rank in interaction with stability and fT (model 4-fT: Chisq=0.054577, Df=1, P=0.815)

Finally, we tested whether fT levels affected how often individuals in the two species expressed agonistic behaviors (i.e. a measure of individual agonistic tendency) and the model revealed a trend for an effect of fT depending on species (Fig. 2.4; Table 2.3; model 5-fT; Chisq=3.812, Df=1, P=0.051). More specifically, we did detect a trend that male chacma baboons showing higher fT levels also expressed more often agonistic behaviors (Fig. 2.4a; Table 2.4; Chisq=2.873, Df=1, P=0.090), but there was no effect in Guinea baboons (Fig. 2.4b; Table 2.4; Chisq=0.0787, Df=1, P=0.779).

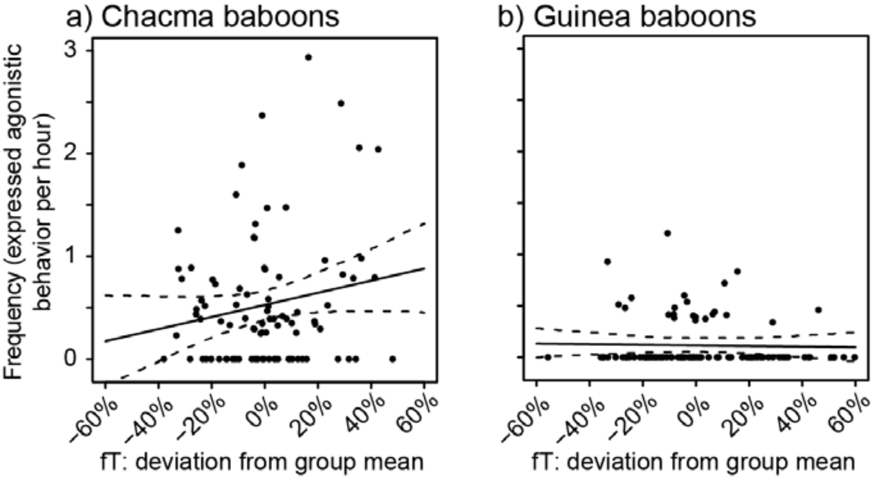

Fig. 2.4: Effect of relative testosterone levels on rates of expressed agonistic behaviors for a) chacma baboons, and b) Guinea baboons. Each point represents one value per individual per period (chacma baboons: N=11 individuals and 91 data points; Guinea baboons: N=14 individuals and 100 data points). The solid line depicts the model and dashed lines depict bootstrapped 95% confidence intervals.

Table 2.3 Results of the model testing the effect of testosterone levels (fT) on rates of expressed agonistic behaviors.. [1]Species was dummy coded with Guinea baboons as reference category.

Variable	Coefficient	SE	t	P
(Intercept)	0.116	0.053	2.185	
fT	-0.001	0.002	-0.261	
Species (Chacma)[1]	0.411	0.078	5.267	
fT:Species(Chacma)[1]	0.006	0.003	1.968	0.051

Table 2.4 Results of the model testing the effect of testosterone levels on rates of expressed agonistic behaviors in both species separately

	Variable	Coefficient	SE	t	P
Chacma baboons	(Intercept)	0.527	0.074	7.081	
	fT	0.006	0.003	1.710	0.090
Guinea baboons	(Intercept)	0.116	0.033	3.513	
	fT	-0.000	0.001	-0.284	0.779

Furthermore, in chacma baboons, we tested whether fT in interaction with hierarchy stability had an effect on rates of expressed agonistic behaviors, but did not find a significant effect (model 6-fT: Chisq=1.5079, Df=1, P=0.2195).

Variation in glucocorticoid levels (fGC) among adult males

Inter-individual variation in fGC levels was similar in both species (chacma baboons: 25.36±11.01%; Guinea baboons: 24.02±9.64%) and the model did not detect an effect of species (model 1-fGC; Chisq=0.11086, Df=1, P=0.739). We did detect, however, an effect of dominance position on fGC values depending on species (Fig. 2.5; Table 2.5; model 2-fGC: Chisq=5.8918, Df=1, P<0.05).

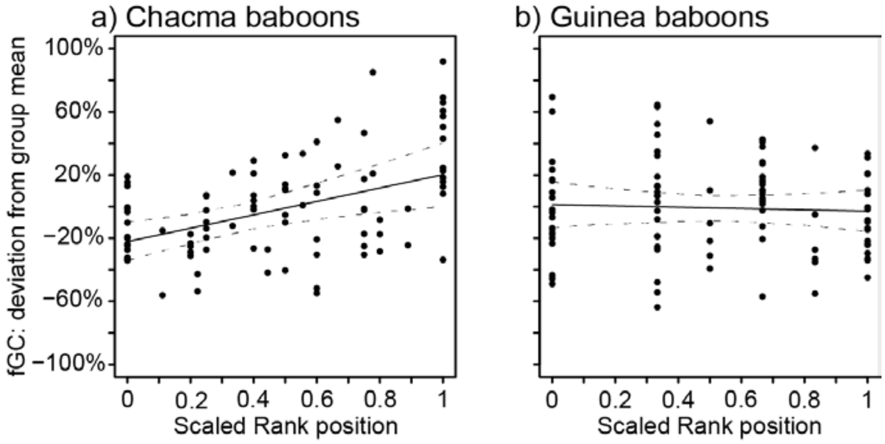

Fig.2.5: Effect of dominance position on relative glucocorticoid levels for a) chacma baboons, and b) Guinea baboons. Each point represents one value per individual per period (chacma baboons: N=11 individuals and 91 data points; Guinea baboons: N=14 individuals and 100 data points). The solid line depicts the model and dashed lines depict bootstrapped 95% confidence intervals.

Specifically, dominance position in chacma baboons was correlated with fGC in that higher ranking males showed higher concentrations of stress hormones (Fig. 2.5a; Table 2.6; model only for chacma baboons: Chisq=6.5142, Df=1, P=<0.05), while there was no effect in Guinea baboons (Fig. 2.5b, Table 2.6; model only for Guinea baboons; Chisq=0.13416, Df=1, P=0.714).

Hierarchy stability in interaction with rank had no effect on fGC levels (model 4-fGC: Chisq=0.0962, Df=1, P= 0.756), nor had stability a main effect (Chisq=0.014147, Df=1, P= 0.905). However, as we discuss later, group fissioning and the resulting disruptive interactions between the two sub-groups may have caused the entire study period to be characterized by uncertainty and instability.

Table 2.5: Results of the model testing the effect of rank and species on glucocorticoid metabolite (fGC) levels. [1]Species was dummy coded with Guinea baboons as reference category. [2]Not meaningful as the interaction of rank and species has a significant effect on fGC levels.

Variable	Coefficient	SE	t	P
(Intercept)	1.051	7.338	0.143	
Rank	-3.715	11.877	-0.313	(not meaningful)[2]
Species(Chacma)[1]	-24.644	10.786	-2.285	(not meaningful)[2]
Rank:Species(Chacma)[1]	50.287	17.723	2.837	$P<0.05$

Table 2.6: Results of the model testing the effect of rank on glucocorticoid metabolite levels in both species separately

	Variable	Coefficient	SE	t	P
Chacma baboons	(Intercept)	-22.183	6.596	-3.363	
	Rank	42.414	13.674	3.102	$P<0.05$
Guinea baboons	(Intercept)	1.343	7.266	0.185	
	Rank	-4.222	11.490	-0.368	0.448

Finally, we could not detect an effect of rate of agonistic interactions in interaction with species on fGC levels (model 4-fGC: Chisq=0.52097, Df= 1, P=0.470), nor when tested for both species separately (chacma baboons: Chisq=0.76705, Df= 1, P=0.381; Guinea baboons: Chisq=0.51172, Df= 1, P=0.474). The model with agonistic rates was potentially affected by many data points in which no agonistic interactions was measured (zero-inflated), but excluding all zero-values from the data-set did not reveal any significant results neither (all P-values > 0.6).

Discussion

We investigated several aspects of male-male competition in chacma and in Guinea baboons. Our data show that adult males of these two different species differed not only in their social system but also in agonistic rates, spatial tolerance, and affiliation. Furthermore, male chacma baboons exhibited rigid hierarchies, while male Guinea baboons did not, even though dominance relationships were not generally inconsistent. Dominance positions were correlated with glucocorticoid levels in chacma baboons in that higher ranking males showed higher levels of glucocorticoids, but there was no such relation in Guinea baboons. We did detect a trend that male chacma baboons with higher levels of testosterone more often expressed agonistic behaviors but we did not find any effect in Guinea baboons. Neither species, however, showed any relationship between testosterone and age or dominance position. Because we applied the same sampling protocols for both species, we can rule out methodological issues as a cause of the species differences. Although our systematic comparisons are restricted to one population from each species, we can place them in the broader context of several long-term studies on this genus, thus increasing our inferential strength.

Interactions among males

Male chacma baboons were more often involved in agonistic interactions than male Guinea baboons. This difference cannot be explained by an overall lower rate of male-male interactions in Guinea baboons, because Guinea baboons were more often involved in interactions within close proximity (i.e. 1 m) than male chacma baboons. Most of these interactions, however, consisted of bump-ins and in&outs and revealed little about the general quality of the relationship.

Fights represent the most intense type of agonistic interactions, but they occurred too rarely to conduct a statistical comparison between species. However, combining focal and *ad libitum* data showed that most fights observed in chacma baboons included serious bite-attacks, while fights in Guinea baboons appeared to be more benign. Although we observed only one fight between chacma males that resulted in injuries, we recorded many wounds to the face or shoulder in our demographic records, which have been described as the typical location for injuries after fights in chacma baboons (see also Kitchen et al. 2005). We cannot rule out that these injuries were the results of predator attacks, but this seems unlikely. In Guinea baboons, we never observed a fight resulting in a wound, nor have we observed injuries at all. Overall, these observations corroborate the assumption that male Guinea baboons are less aggressive than male chacma baboons in both the frequency and the intensity of aggression.

Male-male interactions often involved greetings among male Guinea but not among male chacma baboons. The function of such physical contact interactions, often including the manipulation of the other's genitals, is still debated. Some authors suggest that they serve as a non-aggressive strategy to negotiate social relationships (e.g. Colmenares 1991), to reduce tension (e.g. Dias et al. 2008), or in the formation and maintenance of bonds (Whitham & Maestripieri 2003 , Smuts & Watanabe 1990). These proposed functions are not mutually exclusive and could all explain reduced rates of overt aggression.

Male Guinea also showed a higher spatial tolerance than male chacma baboons. They even stayed within 'body contact' (<10 cm) of another male occasionally, which has often been interpreted as affiliative behavior (e.g. Swedell 2006), and sometimes groomed each other (see also Sharman 1981, Patzelt 2013). All of these behaviors were virtually absent in male chacma baboons, suggesting once more that in this species, male-male behavior is largely restricted to dominance interactions and males avoid spatial proximity.

Male-female behavior

Variation in behavior between males and females in the two species revealed similar, though less pronounced, differences between the two species. Male chacma baboon showed higher rates of agonistic interactions, supplants, submissive behaviors and threats with females than male Guinea baboons. Rates of male-female chases and chase-aways were relatively similar for both species, however. Importantly, in chacma baboons, all aggressive behaviors were directed by males toward females, whereas in Guinea baboon females sometimes chased or threatened a male. With regard to spatial tolerance and affiliation, male Guinea baboons spent more time within 1 m and within body contact of females than male chacma baboons, but males of both species spent a comparable amount of time grooming with females.

Taken together, males of the two species differed generally in aggressiveness and spatial tolerance, though these differences were more pronounced in male-male interactions. This suggests that selection pressures acted generally on male aggressiveness and tolerance in baboons but stronger with regard to male-male than to male-female behavior. In chacma baboons male-male aggression is most often associated with acquiring or maintaining high rank, and may enhance reproductive success, whereas this does not appear to be the case in Guinea baboons. High levels of male-female aggression, on the other hand, are not adaptive, because males must maintain some level of affiliative relations with females in order to mate, which may also explain the similar rates of male-female grooming in the two species.

Dominance relationships

Overall, male chacma baboons showed linear and steeper dominance hierarchies and more consistent dominance relationships than Guinea baboons. The relatively low steepness and linearity of the dominance hierarchy of the C-troop may be associated with the short period in which we could collect data for this group (only 7 weeks). In Guinea baboons, only the SNE-party exhibited a high linearity of the hierarchy. This party consisted of two males that were associated with females while the other two were apparently non-reproducing, older and subordinate males. In the other two parties, most males were associated with females (OSM-Party: 4 out of 4 males; JKY-Party: 5 out of 7 males) but even in the JKY-Party the two reproductively inactive males were subordinate to all others. In sum, it appears that, in contrast to chacma baboons, Guinea baboons do not form linear hierarchies, many males do not have clear dominance relationships, but some dyads may have relatively consistent, thus unidirectional, relationships (see also Patzelt et al. in revision). Such consistent relationships appear to occur mainly within parties, and there only between reproducing and apparently non-reproducing males.

Testosterone

We could not confirm our prediction that testosterone values vary more among male chacma than among male Guinea baboons. In contrast to our predictions there was even a trend that male chacma baboon show less inter-individual variation, though the variation and the difference between species was relatively low (14.78% vs. 18.58%) and therefore unlikely to explain differences between species. We could not detect an effect of age on testosterone levels resembling earlier studies in chacma baboons (Beehner et al. 2006, Beehner et al. 2009). As we had to use relatively broad age categories and small number of individuals per categories, future studies should integrate larger number of males, especially in Guinea baboons, to investigate whether age related patterns are less pronounced than in other species. We did, however, detect a trend that testosterone levels were correlated with rates of expressed agonistic behaviors in chacma but not in Guinea baboons. This effect has been previously found in male chacma baboon during unstable periods (Beehner et al. 2006). Technically, seven of the nine analyzed intervals were considered as stable, with no rank changes. However, given the previous group fission, and the multiple stressful inter-group encounters, the entire study period could be considered as unstable. In Guinea baboons, we did not observe a similar effect and in this species agonistic behaviors are apparently not as important to obtain mating opportunities as in chacma baboons. It remains to be investigated which factors determine the access to females in Guinea baboons, and whether variation in these factors is correlated to testosterone levels.

We did not detect a link between testosterone and dominance position. In former studies in chacma baboons such an effect has been detected (Beehner et al. 2006) though testosterone levels were much more strongly correlated with future rank position (Beehner et al. 2006, Bergman et al. 2005), which we could not test in our study. Correspondingly, it would be informative to assess testosterone levels of male Guinea baboons before they acquire or lose females, but such events occurred too rarely during the study period to conduct such a comparison (only two females changed to another male, one of them to a male that was not included in focal observations).

Glucocorticoids

The two species showed similar variation in glucocorticoid levels among individuals. We found, however, an effect of rank on glucocorticoid levels in chacma but not in Guinea baboons; high ranking male chacma baboons showed higher glucocorticoid levels than low-ranking males. Previously, such an effect was only observed during unstable periods (Bergman et al. 2005, Cheney et al, in preparation), supporting again the impression that the entire study period could be considered as unstable (see above). The lack of an effect of ranks on glucocorticoid levels in Guinea baboons indicates once again that dominance positions derived from agonistic interactions probably have less significance in this species. This contrasts with data from other baboon species for which the relationship between rank and glucocorticoids represents a very consistent finding (Sapolsky 1993, Gesquiere et al. 2011). Finally we could not detect an effect of the rate of agonistic interactions on glucocorticoid levels, which confirms former results for chacma baboons (Bergman et al. 2005) and also shows that agonistic interactions are not a predictor of allostatic load in Guinea baboons.

Why do the two species differ?

Why do male Guinea and chacma baboons differ in aggressiveness and spatial tolerance? A decrease in contest competition has been associated with lower potential to monopolize receptive females (e.g. van Hooff 2000), which is mainly determined by the spatio-temporal distribution of the latter (Emlen & Oring 1977, Altmann 1990). This hypothesis, however, cannot fully explain the observed variation in male-male competition between chacma and Guinea baboons. Females of both species show only a low degree of estrous synchrony (chacma baboons: e.g. Cheney & Seyfarth 2007; Guinea baboons: personal observation) and group size varies considerably in both chacma (Henzi & Barrett 2003) and Guinea baboons (Patzelt et al. 2011). Nevertheless, all former studies agreed that male Guinea baboons show a relatively low level of aggressiveness and high spatial tolerance towards other males (Sharman 1981, Galat-Luong et al. 2006, Patzelt et al. in revision), while male chacma baboons are generally described to compete intensely for females (Bulger 1993, Weingrill et al. 2000, Kitchen et al. 2003, Kitchen et al. 2005, Clark et al. 2008,).

The variation in aggressiveness and spatial tolerance appears to be linked to variation in male-male cooperation. The lack of coalitions among male chacma baboons has been suggested to represent a phylogenetic constraint (Henzi & Barrett 2003). According to this hypothesis, the historical ecology of chacma baboon habitats only allowed for small groups and the most appropriate reproductive strategy of males was to exclude other males from their group entirely. Today, male chacma baboons still follow this single-male strategy, wherein males compete to achieve high dominance status. This hypothesis, however, does not explain why chacma males do not currently form coalitions like those observed in olive and yellow baboons (Noe & Sluijter 1995). According to Clifford Jolly, the transition to a baboon society with males forming bonds occurred due to demographic effects during the range expansion of the genus (Jolly 2007, Jolly 2009). In his so-called 'frontier hypothesis', he suggested that baboons rapidly expanded into baboon-free territories which favored philopatric and more tolerant males, facilitating the formation of male bonds (discussed in Patzelt et al. in revision). As alternative – cooperative - reproductive tactics became possible, the need for aggressive contest competition became less important, leading to the variation observed today in baboons.

Summary and Conclusion

By collecting data from chacma and Guinea baboons using identical methods and recorded by the same observer, we could confirm the assumed differences in male aggressiveness and spatial tolerance between both species. Furthermore, our data on male-female interactions indicates that male chacma baboons are generally more aggressive and less tolerant than male Guinea baboons. Concerning dominance relationships, male Guinea baboons, in contrast to chacma baboons, show no rigid hierarchies. We did not find any variation in testosterone levels related to age or rank. However, we did observe a trend that testosterone correlated with expressed agonistic behaviors in chacma baboons, replicating previous finding, but we did not detect such a relationship in Guinea baboons. This may be linked to the assumption that access to mating partners in Guinea baboons is not (primarily) regulated by agonistic behaviors. Furthermore, we did find a relation between rank and glucocorticoids in chacma but not in Guinea baboon ranks, confirming previous results on chacma baboons and indicating that allostatic load in Guinea baboons is not affected by dominance position. Forthcoming studies on Guinea baboons should assess how the access to females is negotiated among males and the role of bonds on this 'negotiation'. Furthermore, the assessment of reproductive profiles in relation to testosterone and glucocorticoid levels would help to further investigate the causes and mechanism of behavioral variation among baboons and, more generally, among primates.

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Supporting Information

Supporting Information - Tables

Table S2.1: Definitions of behavior

Agonistic interactions	
Threat	Raised eyebrows, slaps on the ground, lunges. Also interactions with body contact like slaps and pushes which do not represent a fight. Threats were not recorded separately during chase-aways, chases, or fights.
Chase-away	A jumps towards B or quickly pursues B for less than 5m while B runs away.
Chase	A pursues B for more than 5m without physically fighting
Fight	Fights with physical contacts
Submissive behaviors	Fear-barks, fear grimaces (displaying bare-teeth), lean-aways (animal glances at other animal and extends body away from other animal). We also included when an individual quickly moved away (while looking back) in response to a threat or ran away in response to a (slow) approach. Submissive behaviors were not noted separately during fights, chases, or chase-aways.
Spatial Interactions	
In&Out	A approaches B (10cm/1m) and then leaves B within 5 seconds OR both approach and both leave each other OR both approach and only one individual leaves.
Supplant	A approaches B (10cm/1m), B leaves A within 5 seconds OR A approaches B (1-5m), B leaves and A takes immediately former place of B.
BumpIn	A approaches B (10cm/1m), both leave each other within 5 sec
Greetings	
Greeting	Non-agonistic and non-affiliative interactions with contact: interactions in which hands are involved (but not grooming and no aggression) like genital touches, embraces, touch or pull legs, and also mounts and soft-bites
Spatial tolerance behavior	
Grooming	Grooming
Contact sitting	A and B feed/sit/stand within 10cm for > 5 seconds
1 m proximity	A and B feed/sit/stand within 1m for > 5 seconds

Table S2.2: Rates of agonistic interactions of male baboons for different partner categories in comparison between chacma and Guinea baboons

Type of interaction	Species	Partner category	Rates (per hour)		P
			Median	Mean±sd	
Agonistic interactions	Chacma baboon	Male	0.979	1.04±0.262	**0.000**
	Guinea baboon		0.212	0.282±0.29	
	Chacma baboon	Female	0.763	0.709±0.281	**0.011**
	Guinea baboon		0.356	0.406±0.272	
	Chacma baboon	Immature	0.447	0.436±0.169	**0.015**
	Guinea baboon		0.166	0.249±0.187	
Supplants	Chacma baboon	Male	0.634	0.62±0.177	**0.000**
	Guinea baboon		0.161	0.23±0.274	
	Chacma baboon	Female	0.382	0.435±0.18	**0.005**
	Guinea baboon		0.201	0.23±0.158	
	Chacma baboon	Immature	0.186	0.192±0.087	**0.025**
	Guinea baboon		0.070	0.108±0.111	
Submissive behaviors	Chacma baboon	Male	0.312	0.358±0.159	**0.000**
	Guinea baboon		**0.000**	0.022±0.043	
	Chacma baboon	Female	0.115	0.11±0.055	0.309
	Guinea baboon		0.083	0.089±0.097	
	Chacma baboon	Immature	0.139	0.115±0.053	**0.005**
	Guinea baboon		**0.000**	0.038±0.063	
Chases	Chacma baboon	Male	0.084	0.079±0.055	**0.045**
	Guinea baboon		**0.000**	0.034±0.058	
	Chacma baboon	Female	0.076	0.084±0.07	0.761
	Guinea baboon		0.050	0.074±0.071	
	Chacma baboon	Immature	0.078	0.073±0.069	0.234
	Guinea baboon		**0.000**	0.044±0.061	
Chase-aways	Chacma baboon	Male	**0.000**	0.027±0.034	**0.031**
	Guinea baboon		**0.000**	0.004±0.013	
	Chacma baboon	Female	0.037	0.034±0.039	0.338
	Guinea baboon		**0.000**	0.02±0.035	
	Chacma baboon	Immature	**0.000**	0.03±0.036	0.356
	Guinea baboon		**0.000**	0.017±0.029	
Threats	Chacma baboon	Male	0.065	0.104±0.124	**0.003**
	Guinea baboon		**0.000**	0.011±0.021	
	Chacma baboon	Female	0.074	0.094±0.1	**0.022**
	Guinea baboon		**0.000**	0.026±0.051	
	Chacma baboon	Immature	0.074	0.082±0.086	0.433
	Guinea baboon		**0.000**	0.063±0.087	

Table S2.3 Spatial Interactions

Type of Interaction	Species	Partner category	Greeting	Rates (per hour) Median/h	Rates (per hour) Mean±sd	P (greeting)	P (species)
Spatial Interactions	Chacma baboons	Male	Total	0.979	1.094±0.241		**0.000**
			Without	0.977	1.006±0.268	**0.000**	
			With	0.076	0.088±0.076		
	Guinea baboons		Total	1.444	1.621±0.881		
			Without	0.517	0.545±0.294	**0.001**	
			With	0.989	1.077±0.726		
	Chacma baboons	Female	Total	1.477	1.568±0.481		0.149
			Without	1.250	1.246±0.428	**0.000**	
			With	0.229	0.322±0.183		
	Guinea baboons		Total	1.248	1.214±0.544		
			Without	0.491	0.572±0.369	0.475	
			With	0.781	0.642±0.304		
	Chacma baboons	Immature	Total	1.037	1.104±0.448		0.979
			Without	0.932	0.968±0.442	**0.000**	
			With	0.149	0.136±0.096		
	Guinea baboons		Total	0.947	1.1±0.528		
			Without	0.345	0.392±0.248	**0.047**	
			With	0.690	0.708±0.346		
Supplant	Chacma baboons	Male	Total	0.634	0.62±0.177		**0.000**
			Without	0.596	0.577±0.186	**0.000**	
			With	0.037	0.043±0.049		
	Guinea baboons		Total	0.161	0.23±0.274		
			Without	0.125	0.131±0.149	0.624	
			With	0.051	0.099±0.146		
	Chacma baboons	Female	Total	0.382	0.435±0.18		**0.005**
			Without	0.303	0.345±0.132	**0.000**	
			With	0.078	0.09±0.073		
	Guinea baboons		Total	0.201	0.23±0.158		
			Without	0.150	0.168±0.132	**0.016**	
			With	0.065	0.062±0.05		
	Chacma baboons	Immature	Total	0.186	0.192±0.087		**0.025**
			Without	0.186	0.189±0.088	**0.000**	
			With	**0.000**	0.003±0.011		
	Guinea baboons		Total	0.070	0.108±0.111		
			Without	0.050	0.066±0.088	0.343	
			With	0.000	0.043±0.075		

Bump-ins	Chacma baboons	Male	Total	0.000	0.031±0.041		**0.000**
			Without	0.000	0.014±0.031	0.587	
			With	0.000	0.017±0.024		
	Guinea baboons		Total	0.286	0.281±0.263		
			Without	0.025	0.047±0.058	**0.001**	
			With	0.134	0.233±0.246		
	Chacma baboons	Female	Total	0.077	0.077±0.046		**0.015**
			Without	0.000	0.016±0.024	**0.042**	
			With	0.077	0.061±0.051		
	Guinea baboons		Total	0.164	0.176±0.12		
			Without	0.000	0.031±0.045	**0.002**	
			With	0.149	0.145±0.114		
	Chacma baboons	Immature	Total	0.000	0.024±0.034		**0.007**
			Without	0.000	0.017±0.03	0.502	
			With	0.000	0.007±0.015		
	Guinea baboons		Total	0.083	0.12±0.106		
			Without	0.000	0.007±0.026	**0.000**	
			With	0.083	0.112±0.104		
In&Outs	Chacma baboons	Male	Total	0.423	0.443±0.166		**0.000**
			Without	0.384	0.415±0.166	**0.000**	
			With	0.000	0.028±0.035		
	Guinea baboons		Total	1.090	1.11±0.434		
			Without	0.323	0.367±0.227	**0.000**	
			With	0.636	0.744±0.376		
	Chacma baboons	Female	Total	1.081	1.055±0.424		0.149
			Without	0.881	0.884±0.408	**0.000**	
			With	0.149	0.171±0.091		
	Guinea baboons		Total	0.839	0.808±0.369		
			Without	0.315	0.373±0.23	0.370	
			With	0.461	0.435±0.222		
	Chacma baboons	Immature	Total	0.766	0.889±0.392		0.979
			Without	0.746	0.763±0.397	**0.000**	
			With	0.131	0.126±0.086		
	Guinea baboons		Total	0.829	0.872±0.388		
			Without	0.317	0.319±0.209	**0.017**	
			With	0.574	0.553±0.239		

Table S2.4: Proportion of time spent in spatial tolerance behavior

			min/focal hour		
Behavior	**Species**	**Partner category**	**Median**	**Mean±sd**	**P**
1 m proximity	Guinea baboon	Males	0.833	0.931±0.851	**0.001**
	Chacma baboon		0.000	0.019±0.049	
	Guinea baboon	Females	2.103	2.878±1.693	**0.001**
	Chacma baboon		0.824	1.003±0.687	
	Guinea baboon	Immatures	2.853	2.725±1.148	**0.003**
	Chacma baboon		0.195	0.984±1.322	
Contact-sitting	Guinea baboon	Males	0.006	0.179±0.31	Not tested
	Chacma baboon		0.000	0±0	
	Guinea baboon	Females	0.706	0.868±0.702	**0.007**
	Chacma baboon		0.316	0.304±0.253	
	Guinea baboon	Immatures	0.626	0.748±0.521	**0.030**
	Chacma baboon		0.018	0.34±0.411	
Grooming	Guinea baboon	Males	0.000	0.189±0.388	Not tested
	Chacma baboon		0.000	0±0	
	Guinea baboon	Females	1.939	1.926±1.003	0.809
	Chacma baboon		1.668	1.635±1.111	
	Guinea baboon	Immatures	0.593	0.725±0.681	0.056
	Chacma baboon		0.106	0.251±0.54	

Supporting Information - Methods

Method S2.1: Age estimation

In chacma baboons, males were estimated by tooth wear (see Kitchen et al. 2003). Males with relatively white and sharp canines were categorized as 'young' (4-5 on the scale) while males with canines with extensive discoloration and one or both canines missing or extremely worn (1-2 on the scale) were categorized as 'old'. All other males with tooth wear falling between these two categories were categorized as 'prime-aged'. In Guinea baboons, males which were still subadult in the year before were categorized as 'young'. 'Old' males were identified by their haggard appearance and their brown and extensively worn or missing canines. Again, all males falling between these categories were classified as 'prime-aged'.

Method S2.2: Hormone metabolite extraction

To extract hormone metabolites from fecal samples, we homogenized the sample using a wooden spatula. Then, ~0.5g were placed into a 15mL polypropylene tube which was filled with 4mL EtoH (80% in water). The tube was then shaken by hand for two minutes to produce a fecal suspension for hormone extraction. Back at the field station, the sample was mixed with a battery powered hand-mixer (Hecht Assistant, Germany) for 1 minute. The tube was then centrifuged at maximum speed for 2 minutes using a manually operated hand-centrifuge (Hettich, Germany) and the supernatant (i.e. the hormone extract) aliquoted into 2mL tubes. The tubes were tightly closed, wrapped with parafilm for storage. The remaining extract was discarded and the fecal matter was sun-dried in a metallic box in order to determine fecal dry weight.

Method S2.3: Assay procedures and validation of the assay in baboons

Details of the assay procedures are described elsewhere (fT: Palme & Moestl 1994, Moehle et al. 2002, fGC: Ganswindt et al. 2003). Prior to each assay, extracts were diluted with assay buffer (phosphate buffered saline, pH 7.2) to bring hormone concentrations into the working range of the assay. We ran each sample in duplicate and calculated mass steroid metabolite per mass fecal dried weight in ng/g.

Both steroid metabolites have been validated for monitoring androgen and glucocorticoid output in various primate species (Moehle et al. 2002, Girad-Buttoz et al. 2009, Ostner et al. 2008, Heistermann et al. 2006). For the use in baboons, we validated the fT-assay with fecal extracts from chacma baboons collected in 2011: 43 samples from 11 adult males and 43 samples from 10 juvenile males were measured and metabolite levels compared between age classes. As predicted, fT levels were significantly higher in adult males compared to juvenile males (t-test: F[1, 19]=7.3492, P<0.05), indicating that the fT measure provides a reliable estimate of male androgen status (see also Beehner et al. 2009). The fGC–assay was previously validated for olive baboons using an ACTH challenge (A. Daspre, M. Heistermann, L. Rosetta and P.C. Lee, unpublished data) and was biologically validated in Guinea baboons in 2013 by comparing fGC responses to the stressful event of trapping. As expected, fGC levels increased significantly in response to trapping, indicating the validity of the fGC measure in reflecting adrenocortical acitivity (A. Goffe, M. Heistermann, unpublished data).

Method S2.4: Definition of Bouts

An agonistic bout included all agonistic interactions until participants engaged in non-agonistic activities, such as resting or feeding, for at least 30 seconds. Agonistic bouts and specific agonistic behaviors were analyzed with respect to partner categories (males, females, immatures). Each bout was counted once per partner category. For example, agonistic behaviors by a male directed towards a male and two females at the same time were counted once for male-male and once for male-female interactions. Within each bout, specific behaviors were counted once per partner category. For example, if a male chased two females, then another male, and finally had a fight with that male; such a sequence would be counted as one male-female chase, one male-male chase, and one male-male fight.

Method S2.5, SI: General linear mixed models

To calculate general linear mixed models, we used the function ‚lmer‘ from the R-package ‚lme4‘ (Bates et al. 2014) in R 3.0.3 (R Core Team, 2014). Whenever necessary (i.e. when one individual was measured in different conditions), we included random slopes to keep type I error rates at the nominal level of 5% (Schielzeth & Forstmeier 2009, Barr et al. 2013). All variables were checked visually for distribution and transformed when necessary (see GLMMs, SI). We also checked whether the assumptions of normally distributed and homogeneous residuals were fulfilled by visually inspecting a qqplot and the residuals plotted against fitted values. Furthermore, model stability was controlled by excluding subjects one at a time from the data and comparing variation in coefficient estimates (function kindly provided by R. Mundry). Significance levels for individual variables or interactions of variables were tested based on comparisons of full and null models (not including the tested variable or interaction but all other terms), and established using likelihood ratio tests (function ‘anova’ with argument ‘test = Chisq’). To achieve more reliable P-values we fitted the models using Maximum Likelihood (rather than Restricted Maximum Likelihood; Bolker et al. 2009).

Supporting Information - Figures

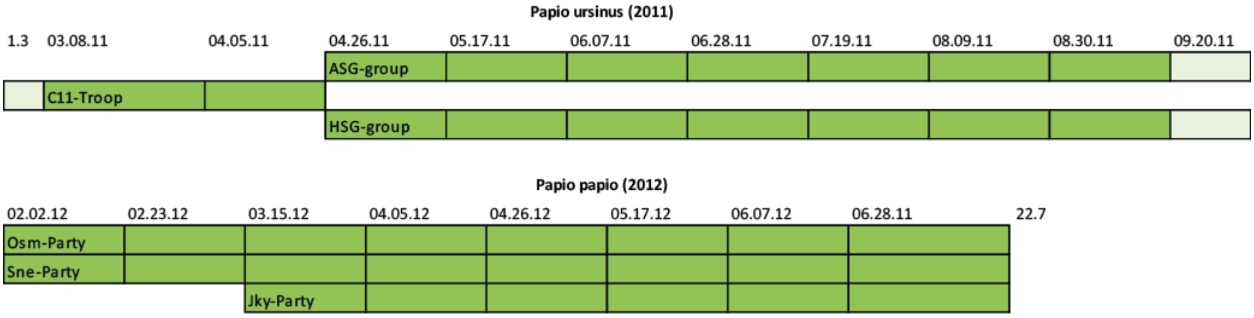

Fig. S2.1: Combined time periods for hormone-behavior analysis for each group. Light green indicates periods excluded from these analyses

Supporting Information - GLMMs

Model 1-fT - Effect of species on variation

Values aggregated for subjects before calculation of mean

Species	Mean±sd
Chacma baboons	14.78±3.74%
Guinea baboons	18.58±3.58%

Model: fT[abs%] ~ Species + (1|subject)

Transformation: fT values were square-rooted prior to running the model.

Variable	Coefficient	SE	t	P
(intercept)	3.900	0.1743	22.381	
Species (Chacma)	-0.454	0.2525	-1.797	0.074

Full-null model comparison (species effect): Chisq: 3.2028, Df = 1, P = 0.07351

Model 2-fT: Effect of Age

Species	Young	Established	Old
Chacma baboons	3.30±14.10	-1.33±8.92	-3.33±12.65
Guinea baboons	-1.85±8.89	-2.40±13.07	2.51±17.66

Model: fT ~ Age: Species + Age + Species + (1|subject)

Variable	Coefficient	SE	t	P
(Intercept)	-1.361	5.520	-0.246	
Age (Prime-aged)	-0.520	6.908	-0.075	
Age (Old)	4.538	8.381	0.542	
Species(Chacma)	4.571	8.251	0.554	
Age (Prime-aged):Species(Chacma)	-3.483	10.403	-0.335	0.6648
Age (Old):Species(Chacma)	-10.772	12.060	-0.893	0.6648

Full-null model comparison (effect of interaction age:species): Chisq: 0.8165, Df=2, P=0.6648

Full-null model comparison (effect of age category): Chisq=0.1736, Df=2, P=0.9169

Only in chacma baboons: (effect of age category): Chisq=0.63089, Df=2, P=0.7295

Only in Guinea baboons: (effect of age category): Chisq=0.41152, Df=2, P=0.814

Model 3-fT: Effect of Rank

Model: fT~ Rank:Species + Rank + Species + (1|subject) + (0 + Rank|subject)

Variable	Coefficient	SE	t	P
(Intercept)	2.876	5.081	0.566	
Rank	-6.678	8.035	-0.831	
Species (Chacma)	-8.482	7.460	-1.137	
Rank:Species(Chacma)	17.266	12.002	1.438	0.171

Full-null model comparison (effect of interaction rank:species): Chisq: 1.8738, Df=1, P=0.171

Full-null model comparison (effect of rank): Chisq : 0.0279, Df=1, P =0.8673

Only in chacma baboons: (effect of rank): Chisq=1.1229; Df=1; P=0.2893

Only in Guinea baboons: (effect of rank): Chisq=0.57507; Df = 1; P= 0.4483

Model 4-fT: Effect of rank:stability in chacma baboons

Model: fT ~Rank: Stability + Rank + Stability + (1|subject) + (0+Rank|subject) + (0 +Stability|subject)

Variable	Coefficient	SE	t	P
(Intercept)	-5.314	5.116	-1.039	
Rank	9.694	8.460	1.146	
Stability	-1.064	7.766	-0.137	
Rank:Stability	3.077	12.951	0.238	0.815

Full-null model comparison (effect of interaction rank:stability): Chisq= 0.054577, Df=1, P=0.8153

Full-null model comparison (effect of stability): Chisq=0.025647 , Df=1, P=0.8728

Model 5-fT: Effect on expressed agonism

Model: agonism.active.period.hour ~ T.pcdev.mean:Species + T.pcdev.mean + Species + (1 | focalID)

Variable	Coefficient	SE	t	P
(Intercept)	0.116	0.053	2.185	
fT	-0.001	0.002	-0.261	
Species (Chacma)	0.411	0.078	5.267	
fT:Species(Chacma)	0.006	0.003	1.968	0.051

Full-null model comparison (effect of interaction fT:species): Chisq=3.812, Df=1, P=0.05089

Only in chacma baboons:

Variable	Coefficient	SE	t	P
(Intercept)	0.527	0.074	7.081	
fT	0.006	0.003	1.710	0.090

Full-null model comparison (effect of fT): Chisq=2.873, Df=1, P=0.09008

Only in Guinea baboons:

Variable	Coefficient	SE	t	P
(Intercept)	0.116	0.033	3.513	
fT	-0.000	0.001	-0.284	0.7791

Full-null model comparison (effect of fT): Chisq=0.078655, Df=1, P=0.7791

Model 6-fT: Effect of fT:Stability on expressed agonism in chacma baboons

Model: agonism.active.period.hour ~ T.pcdev.mean:Stability + T.pcdev.mean + Stability + (1 | focalID)

Variable	Coefficient	SE	t	P
(Intercept)	0.517	0.081	6.346	
fT	0.003	0.004	0.888	
Stability (Unstable)	0.042	0.149	0.286	
fT:Stability(Unstable)	0.010	0.008	1.233	0.2195

Full-null model comparison (effect of interaction fT:stability): Chisq=1.5079, Df=1, P=0.2195

Model 1-fGC: Effect of species on variation

Values aggregated for subjects before calculation of mean

Species	Mean±sd
Chacma baboons	25.36±11.01%
Guinea baboons	24.02±9.64%

Model: fGC[absolut %] ~ Species + (1|subject)

Transformation: fGC values were square-rooted prior to running the model.

Variable	Coefficient	SE	t	P
(Intercept)	4.5061	0.2630	17.132	
Species(Chacma)	0.1301	0.3899	0.334	0.739

Full-null model comparison (effect of species): Chisq=0.11086 , Df=1, P=0.7392

Model 2-fGC: Effect of rank

Model: fGC ~ Rank:Species + Rank + Species + (1|subject) + (0 + Rank|subject)

Variable	Coefficient	SE	t	P
(Intercept)	1.051	7.338	0.143	
Rank	-3.715	11.877	-0.313	
Species (Chacma)	-24.644	10.786	-2.285	
Rank:Species (Chacma)	50.287	17.723	2.837	0.015

Full-null model comparison (effect of interaction rank:species): Chisq=5.8918, Df=1, P=0.01521

<u>Only in chacma baboons:</u>

Variable	Coefficient	SE	t	P
(Intercept)	-22.183	6.596	-3.363	
Rank	42.414	13.674	3.102	0.0107

Full-null model comparison (effect of rank): Chisq=6.5142, Df=1, P=0.0107

<u>Only in Guinea baboons:</u>

Variable	Coefficient	SE	T	P
(Intercept)	1.343	7.266	0.185	
Rank	-4.222	11.490	-0.368	0.448

Full-null model comparison (effect of rank): Chisq=0.57507 , Df=1, P=0.4483

Model 3-fGC: Effect of rank:stability in chacma baboons

Model: fGC ~ Rank:Stability + Rank + Stability + (1|subject) + (0 +Rank|subject) + (0 + Stability|subject)

Variable	Coefficient	SE	t	P
Intercept)	-22.166	6.675	-3.321	
Rank	41.799	13.214	3.163	
Stability	1.022	13.324	0.077	
Rank:Stability	2.604	21.855	0.119	0.9053

Full-null model comparison (effect of rank:stability): Chisq=0.014147, Df=1, P= 0.9053

Full-null model comparison (effect of stability):Chisq=0.0962, Df=1, P= 0.756458

Model 4-fGC: Effect of agonistic Interactions

Model: fGC ~Agonistic interactions (per hour): Species + Agonistic interactions (per hour) + Species + (1|subject) + (0 + Agonistic interactions (per hour)|subject)

Variable	Coefficient	SE	t	P
(Intercept)	-1.444	5.055	-0.286	
Agonism	2.862	7.018	0.408	
Species(Chacma)	4.236	7.927	0.534	
Agonism:Species(Chacma)	-5.922	7.979	-0.742	0.470

Full-null model comparison (effect of agonism:species): Chisq=0.52097, Df= 1, P=0.4704

Only in chacma baboons: (effect of agonism): Chisq=0.76705, Df= 1, P= 0.3811

Only in Guinea baboons: (effect of agonism): Chisq=0.51172, Df= 1, P=0.4744

Excluding zeros from agonistic rates:

Both species (interaction agonism:species): Chisq=0.0037735, Df= 1, P=0.951

Chacma baboons: (effect of agonism): Chisq=0.21156, Df= 1, P=0.6456

Guinea baboons: (effect of agonism): Chisq=0.062841, Df= 1, P=0.8021

CHAPTER THREE

Long-term storage effects in steroid metabolite extracts from baboon (*Papio* sp.) faeces – a comparison of three commonly applied storage methods

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Abstract

1. The measurement of steroid hormone metabolites from faeces in wild animal populations is a powerful, non-invasive tool in behavioural endocrinology of all major vertebrate taxa. However, because such research is often done in remote areas with limited infrastructure, storage of samples for hormone analysis over long periods at high temperature is a critical issue in field endocrinology. Previous studies have indicated that storage of alcoholic faecal extracts is more reliable than storage of unprocessed faeces if no freezer is available, but a standard method has not been established yet.
2. We tested the validity of three commonly applied storage conditions - liquid extracts, dried extracts, and extracts placed on solid phase extraction (SPE)-cartridges - to preserve concentrations of glucocorticoid and androgen metabolites from faecal extracts of olive baboons (*Papio anubis*) at high temperature over one year.
3. Temporal variation in concentrations was detected for all metabolites and all storage conditions, including values measured from the control condition, i.e. extracts stored at -20°C. This suggested that most variation was due to inter-assay variability, corroborated by comparisons of variation in ‘quality controls’ and samples.
4. Compared to frozen control samples, liquid extracts were stable for up to 24 weeks, extracts on SPE-cartridges were stable for up to 50 weeks, while steroid metabolite concentrations in dried extracts decreased slightly over time.
5. If steroid samples have to be stored at ambient temperature, we suggest storage of liquid extracts for up to 24 weeks in a dark and cool place. For longer periods, SPE-cartridges should be applied as evaporation, a potential confound arising with long-term storage of liquid extracts at higher temperatures, is not a problem in this storage condition. Storage of dried extracts is more cost-effective, but may result in small time-dependent changes in steroid concentrations.

CHAPTER FOUR

Length-polymorphisms in the promoter regions of serotonin-related genes (*5-HTTLPR* and *MAOALPR*) and interspecific variation in aggressiveness in adult male baboons (*Papio* spp.)

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Prepared for submission

Abstract

Aggressive behaviors are an integral part of competitive interactions with considerable variation in aggressiveness among individuals, but also among species. Aggressiveness is considered to be a quantitative trait that is highly heritable. In modern humans and macaques, variation in aggressiveness among individuals has been linked to polymorphisms in the serotonergic (5-HT) neurotransmitter system. To investigate the genetics underlying interspecific variation in male aggressiveness from a broader comparative perspective, we screened 123 individuals from five baboon species (*Papio papio*, *P. hamadryas*, *P. anubis*, *P. cynocephalus*, and *P. ursinus*) for two polymorphisms in promoter regions of genes relevant for the 5-HT system (*5-HTTLPR* and *MAOALPR*). Surprisingly, despite considerable interspecific variation in aggressiveness, baboons are monomorphic in *5-HTTLPR*, except for *P. hamadryas*, which carries one additional allele. Accordingly, this locus cannot be linked to behavioral variation among species. A comparison among 19 papionin species, including Asian macaques, shows that the most common baboon allele is similar to the one described for Barbary macaques (*Macaca sylvanus*), probably representing the ancestral allele in this tribe. Baboons are, however, polymorphic in *MAOALPR*, the so-called ’warrior gene’, and variation in allele frequencies broadly maps onto interspecific variation in aggressiveness. This study provides another indication that *5-HTTLPR* may not be linked to aggressiveness in primates *per se*, but may have been under differential selective pressures among species and potentially among regions. For the regulation of male aggressiveness in baboons, genes affecting the metabolism of several monoamine neurotransmitters, such as *MAOA*, may be more important.

Introduction

In order to maximize their fitness, individuals compete for resources and mating opportunities. In this context, aggressive behaviors, which are commonly defined as physical attacks and the threat of such attacks (Zinner & Wheeler 2012) play a key role. Escalated aggression may incur high costs such as fatal injuries. Therefore intermediate levels of aggressiveness should be favored, and thus aggressiveness under stabilizing selection (Anholt & Mackay 2012). Nevertheless, variation in the tendency to show aggression can be observed. In addition to short-term variation within individuals, for example in relation to context, there are also relatively stable long-term differences among individuals (i.e. personality differences; e.g. Yeh et al. 2010) and also among species (e.g. Thierry 2000)

Within many species, including modern humans (*Homo sapiens*; e.g. Yeh et al. 2010) and non-human primates (e.g. Fairbanks et al. 2004), heritability estimates for differences in aggressiveness are generally high (Anholt & Mackay 2012). The strong genetic component has been demonstrated by experiments in which highly aggressive or docile individuals have been successfully bred within a few generations (mice, *Mus musculus*: e.g. van Oortmerssen & Bakker 1981; silver foxes, *Vulpes vulpes*: Belyaev 1979). Aggressiveness thereby constitutes a quantitative trait affected by multiple genes, but the specific combination of genes involved in aggressiveness is not clear (Anholt & Mackay 2012).

Several hormone and neurotransmitter systems are assumed to affect aggressiveness and the corresponding genes may therefore be involved in the regulation of associated behaviors (Craig & Halton 2009, Popova 2006). One neurotransmitter system that has been linked to aggressiveness and impulsiveness in mammals is the brain serotonin (5-HT) system (reviews: Nelson & Chiavegatto 2001, Yanowitch & Coccaro 2013). Research on rhesus macaques (*Macaca mulatta*) indicates that individual differences in 5-HT activity are heritable (Clarke et al. 1995, Rogers et al. 2004) and stable over time (Higley et al. 1992, Higley et al. 1996, Howell et al. 2007). This makes the 5-HT system a good candidate to be associated with genetic-based stable differences among individuals or among species in aggressiveness.

The 5-HT transporter (5-HTT) and monoamine oxidase A (MAOA) are two important proteins regulating the 5-HT system. 5-HTT is responsible for the reuptake of 5-HT from the synaptic cleft while MAOA oxidizes 5-HT to its metabolite 5-hydroxyindoleacetic acid (5-HIAA). Accordingly, variants of genes encoding for these proteins may affect variation in aggressiveness. Regulatory regions (i.e. promoters) are of particular interest as they determine the transcription profile of a gene (Wray et al. 2003). While mutations in coding regions can affect the functionality of a gene product, including complete inactivation, mutations in promoter regions can only affect transcriptional activity. Hence, promoter regions appear to be especially suitable targets for natural selection acting on quantitative traits (Wray et al. 2003), such as aggressiveness.

For the *5-HTT* gene (*SLC6A4*), a functional length-polymorphism in the promoter region, the *5-HTT*-linked polymorphic region (*5-HTTLPR*), is well documented in humans (Heils et al. 1996) and several species of apes and old world monkeys (Lesch et al. 1997, Trefilov et al. 2000). The length variation is caused by a variable number of 21-23 base pairs (bp)-repeat elements. Humans and apes vary at polymorphic locus 1 (PL1), while macaques (*Macaca* spp.) vary at polymorphic locus 2 (PL2; Lesch et al. 1997). The *5-HTTLPR* genotype appears to affect the in-vitro transcription rate (humans: Heils et al. 1996; *M. mulatta*: Bennett et al. 2002), and various behaviors (humans: e.g. Lesch et al. 1996, Canli & Lesch 2007; *M. mulatta*: Barr et al. 2003, Schwandt et al. 2010). As aggression is thought to be linked to 5-HT activity, an effect of the *5-HTTLPR* genotype on aggressiveness has been investigated (e.g. Schwandt et al. 2010). The results, however, are inconsistent and a recent meta-analysis indicated no general effect of the genotype (Vassos et al. 2014). As such, the involvement of this polymorphism remains disputed.

Likewise, the *MAOA* gene has been intensively studied. In 1993, Brunner et al. (1993) reported on a Dutch family carrying a nonsense mutation in the *MAOA* gene. This resulted in an abnormal behavioral phenotype in males including “impulsive aggression, arson, attempted rape, and exhibitionism” (Brunner et al. 1993, p. 578). Importantly, the gene is located on the X-chromosome; males only possess one copy whose disruption leads to a complete inactivation of MAOA. The behavioral consequences of this disruption were confirmed by ‘knock-out’ experiments in mice which resulted in a similar increase in male aggressiveness (Cases et al. 1995, Popova et al. 2001, Scott et al. 2008). These observations indicate the importance of the *MAOA* gene for the regulation of aggression, but genetic variants must be more common than such rare (and disruptive) non-sense mutations in order to be linked to common variation in behavior.

The *MAOALPR* (or *MAOA-uVNTR*) represents such a common and important polymorphism in primates (Sabol et al. 1998, Newman et al. 2005, Wendland et al. 2006a). Similar to *5-HTTLPR,* this polymorphism consist of a variable number of repeats within the promoter region of the *MAOA* gene. The consensus sequence varies among species (18-30 bp), and the number of repeats differs both among, and within many species (Wendland et al. 2006a, Wendland et al. 2006b). In humans (Sabol et al. 1998) and in *M. mulatta* (Newman et al. 2005), different alleles affect the in-vitro transcription rate and appear to have an impact on individual variation in aggressiveness and impulsiveness (humans: Caspi et al. 2002; *M. mulatta*: Newman et al. 2005, Karere et al. 2009; review: Manuck et al. 2000; meta-analysis: Vassos et al. 2014). These observations gave rise to the nickname 'warrior gene' for the *MAOA* gene (e.g. McDermott et al. 2009).

Interspecific behavioral variation in macaques in relation to 5-HTTLPR and MAOALPR genotypes

At the individual level, the effects of *5-HTTLPR* and *MAOALPR* genotypes on aggressiveness do not appear to be simple additive genetic effects. Instead, both the *5-HTTLPR* genotype (Schwandt et al. 2010) and the *MAOALPR* genotype (Caspi et al. 2002, Newman et al. 2005) affect variation in aggressiveness depending on early experiences (i.e. G×E interaction). At the species level, in contrast, variation in aggressiveness may be more generally linked to different genotypes in these loci. This is suggested for different species of macaques, which vary in their degree of tolerance (Thierry 2000), possibly related to the distribution of different alleles in *5-HTTLPR* and *MAOALPR* genotypes (Suomi 2006, Wendland et al. 2006b, Chakraborty et al. 2010). It should be noted that most samples used in these studies came from captive colonies (Wendland et al. 2006b), whose genetic composition may not reflect a natural population, and sample sizes ranged from two to several hundred individuals per species.

Interspecific behavioral variation among male baboons

Baboons (*Papio* spp.) are closely related to macaques (both belong to the tribe Papionini of the Cercopithecidae). The genus is thought to have originated in southern Africa and then dispersed over large parts of Africa during the Pleistocene (Zinner et al. 2013b). Nowadays, the genus inhabits much parts of sub-Saharan Africa and a small part of Arabia (Fig. 4.3a). Behavioral observations suggest that adult males of different baboon species vary in their competitive strategies. While some species show a high degree of direct male-male competition, other species show more frequent male-male cooperative behavior, such as coalitions (Henzi & Barrett 2003).

Male chacma baboons (*P. ursinus*) in southern Africa appear to be the most aggressive and uncooperative baboon males as they do not form coalitions with other males (Bulger 1993, Henzi & Barrett 2003), show no affiliative behaviors (e.g. grooming) among males, possess a very low spatial male-male tolerance, and often inflict severe wounds on other males during heavy fights (Kitchen et al. 2005). In contrast, males of the more northern yellow (*P. cynocephalus*) and olive baboons (*P. anubis*) form coalitions (e.g. Smuts 1985, Noe & Sluijter 1995) and spatial tolerance appears to be higher. They, however, very rarely show affiliative behaviors (Sapolsky & Share 2004) and fights regularly result in serious wounds (MacCormick et al. 2012). In the north-eastern hamadryas baboons (*P. hamadryas*), bachelor males only rarely form coalitions to challenge harem leader males (i.e. males associated with females; Pines et al. 2011), and males, foremost bachelor males, exchange affiliative behaviors (Abegglen 1984, Swedell 2006). While spatial tolerance is often high among bachelor males, once a male becomes a leader it is less tolerant, especially towards bachelor males (Kummer 1968, Swedell 2006). Fights among males are highly ritualized and rarely result in injuries (Kummer 1968). Finally, males of the north-western Guinea baboons (*P. papio*) often form coalitions, regularly exchange affiliative behaviors, and show high spatial tolerance as well as low intensity of fights (Patzelt et al. submitted; Kalbitzer et al. in preparation, see CHAPTER TWO). As behavioral variation among species is assumed to have a genetic component (Henzi & Barrett 2003, Jolly et al. 2009), this genus represents a promising model for further investigating the genetics underlying such interspecific variation in primates.

Aims of this study

We investigated the *5-HTTLPR* and *MAOALPR* genotypes in baboons to test whether interspecific differences in allele frequencies are linked to behavioral variation in male aggressiveness and tolerance. It appears that males of different species vary quantitatively rather than qualitatively in behavior, not excluding variation within one species. Therefore, we predicted that: 1) different species carry the same alleles but in different frequencies and 2) *P. papio* and *P. ursinus* are the most distinct species concerning their genotypes as they seem to represent opposite extremes in male aggressive behavior. As we are interested in the distribution of alleles in different species, and since, in this case, alleles are inherited independently of sex, we included samples from males and females in this study. Finally, we wanted to compare the *5-HTTLPR* and *MAOALPR* genotypes of baboons with those of other papionin species to obtain further insights into the evolution of these well-known promoter polymorphisms. To do so, we used published sequence information from other species, and, in the case of *5-HTTLPR*, we analyzed additional samples from other papionin species.

Materials and Methods

Animals

We analyzed five species of baboons for *5-HTTLPR* and *MAOALPR*. In total, we screened 123 wild baboons (Table S4.1, Supporting information), including 31 *P. papio* (15 females, 16 males) from Senegal, Guinea, and Mali; 32 *P. hamadryas* (11 females, 21 males) from Eritrea, Ethiopia, and Saudi Arabia; 21 *P. anubis* (8 females, 13 males) from Lake Manyara National Park in Tanzania (Knauf et al. 2011) and Gashaka-Gumti National Park in Nigeria; 22 *P. cynocephalus* (8 females, 13 males) from throughout Tanzania (Keller et al. 2010); 18 *P. ursinus* (3 females, 15 males) from Moremi Game Reserve in Botswana, and from the Cape region and around Drakensberg in South Africa. Samples included blood, tissue, and feces. We determined the genotypes of all samples for *5-HTTLPR* while we could only assess *MAOALPR* for 98 samples. Additionally, we analyzed samples for *5-HTTLPR* from one mandrill (*Mandrillus sphinx*), one drill (*Mandrillus leucophaeus*), one golden-bellied mangabey (*Cercocebus chrysogaster*), and one black mangabey (*Lophocebus aterrimus*) originating from zoos in Germany.

Genotyping

All samples that were not provided as DNA were extracted from feces and tissue using the Gen-ial all-tissue DNA-kit (GEN-IAL, Troisdorf, Germany) following the standard protocol with some modifications (Method SM4.1, Supporting information).

In a first step for *5-HTTLPR* genotyping, we amplified high-quality (i.e. tissue or blood) samples using primers described to amplify this locus in other Papionini (stpr5, 5'-GGCGTTGCCGCTCTGAATGC; stpr3, 5'-GAGGGACTGAGCTGGACAACCAC; amplicon size ~700 bp; Lesch et al. 1997). After obtaining sequences for baboons, we designed new primers using AmplifX ver. 1.6.3 (by Nicolas Jullien; CNRS, Aix-Marseille Université, France, http://crn2m.univ-mrs.fr/pub/amplifx-dist). These primers (p*5-HTTLPR*f, 5'-CTCTGAATGCCAGCACCTAACC; p*5-HTTLPR*r, 5'-AGGGGAGATAATGAGGGTGCAA) amplify shorter fragments of 255/277 bp, including the entire PL2. This enabled us to genotype low-quality (i.e. fecal) samples.

For *MAOALPR* genotyping, we also started by using primers formerly described to work in other Papionini (*MAOA*-jrwF2, 5'-AGAAGGGCTGCGGGAAGC; *MAOA*-jrwR, 5'-GTGCTCCACTGGGAACTGG; Wendland et al. 2006a; amplicon sizes 423/441/459 bp in baboons) and then designed primers amplifying shorter fragments of 377/395/413 bp in baboons (p*MAOALPR*f, 5'-GGCTGCGGGAAGCAGAACA; p*MAOALPR*r, CCACTCAGAACGGATGCTCCATT). We were not able to design primers amplifying shorter fragments, as primers within the repeat region would bind at more than one position. This explains the dropout of several samples for this genotype as the amplification of nuclear DNA fragments of ~400bp from fecal DNA is sometimes not possible due to degradation processes (e.g. Buchan et al. 2005). PCR-conditions and thermo cycler settings for all primers are given in the supporting information (Method SM4.2).

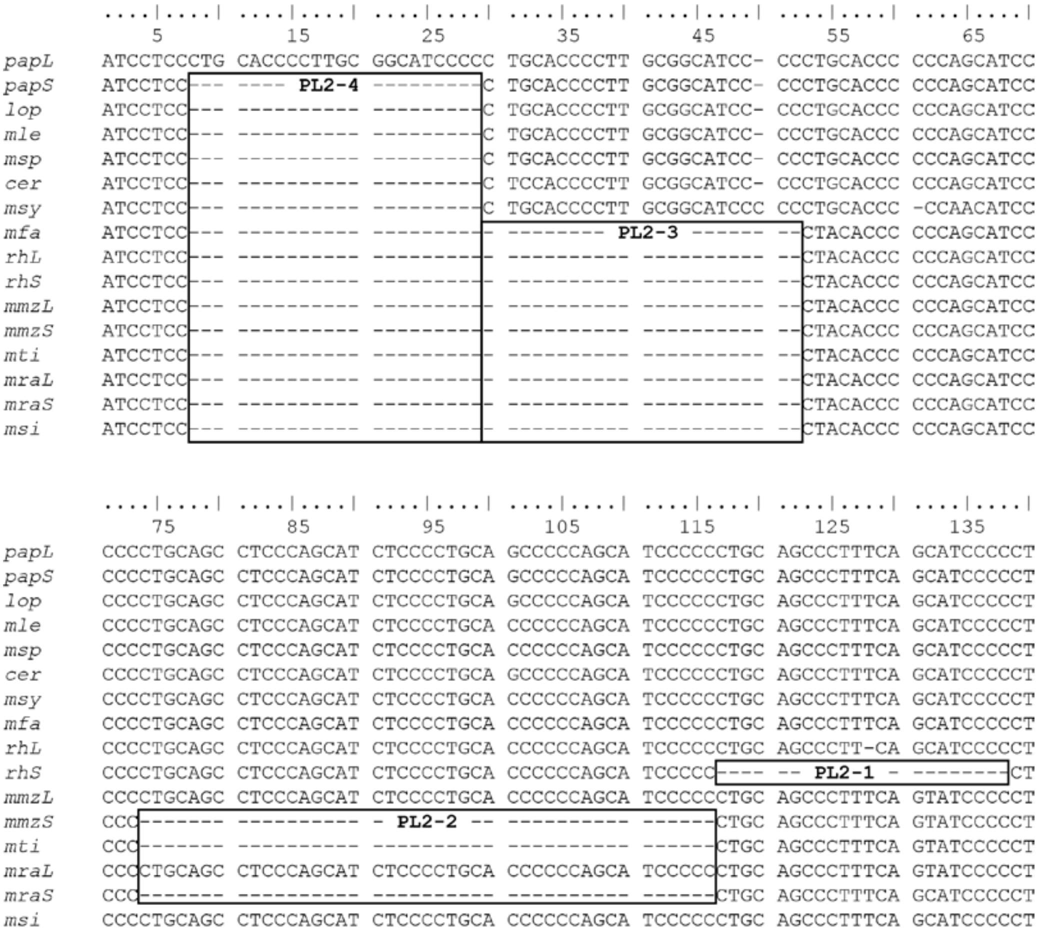
To obtain sequences, we excised PCR products from 1-2.5% agarose gels, purified them with the Qiagen Gel Extraction Kit (Qiagen, Germany), and analyzed them on an ABI3130xL sequencer using the BigDye Terminator Cycle Sequencing Kit (Applied Biosystems, Germany). Sequences were checked, edited and aligned in Bioedit ver. 7.2.3 (Hall, 1999). To compare loci among species, we used Tandem Repeats Finder ver. 4.07b (Benson, 1999) to identify core sequences and number of tandem repeats.

Genotypes of non-sequenced samples were determined by comparing the size of PCR-products with fragments of known length on 2-3% agarose gels. Genotyping was repeated once for *5-HTTLPR* as most baboon species were monomorphic; only samples from (polymorphic) African *P. hamadryas* were repeated twice to avoid allelic dropout (Miller et al. 2002). Similarly for *MAOALPR*, genotyping was repeated twice for all samples. As males only possess one copy the X-chromosomal *MAOA* gene, we report only allele frequencies instead of genotype frequencies for all loci (for all genotypes see Table S4.1, Supporting information). For samples derived from individuals of unknown sex, we determined the sex by a gonosomal PCR-based sexing method (C. Roos, unpublished). Sex determination was repeated once for each sample.

Results

5-HTTLPR

The 5-HTTLPR genotype in baboons consists of multiple repeats with the core sequence 5’-CTGCACCCCTCCCAGCATCTCCC-3’. There is, however, considerable variation between consecutive repeats (Fig. S4.1, Supporting information). We detected a short allele (*papS*) with 24.2 repeats, and a long allele (*papL*) with one additional repeat in the PL2-4 (Fig. 4.1). The sequence of this additional repeat is identical to the adjacent repeat, which is remarkable given the variation between other repeats. The papL-allele is only carried by African *P. hamadryas*. Within this population, the allele frequency is lower than for the short allele (Table 4.1; *papL*: 25%; *papS*: 75%). All other screened baboon populations, including Arabian *P. hamadryas*, are monomorphic, carrying only the *papS*-allele.



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         ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
             5         15         25         35         45         55         65
papL     ATCCTCCCTG CACCCCTTGC GGCATCCCCC TGCACCCCTT GCGGCATCC- CCCTGCACCC CCCAGCATCC
papS     ATCCTCC--- ---- PL2-4 ---------C TGCACCCCTT GCGGCATCC- CCCTGCACCC CCCAGCATCC
lop      ATCCTCC--- ---------- ---------C TGCACCCCTT GCGGCATCC- CCCTGCACCC CCCAGCATCC
mle      ATCCTCC--- ---------- ---------C TGCACCCCTT GCGGCATCC- CCCTGCACCC CCCAGCATCC
msp      ATCCTCC--- ---------- ---------C TGCACCCCTT GCGGCATCC- CCCTGCACCC CCCAGCATCC
cer      ATCCTCC--- ---------- ---------C TCCACCCCTT GCGGCATCC- CCCTGCACCC CCCAGCATCC
msy      ATCCTCC--- ---------- ---------C TGCACCCCTT GCGGCATCCC CCCTGCACCC -CCAACATCC
mfa      ATCCTCC--- ---------- ---------- -------- PL2-3 ------ --CTACACCC CCCAGCATCC
rhL      ATCCTCC--- ---------- ---------- ---------- ---------- --CTACACCC CCCAGCATCC
rhS      ATCCTCC--- ---------- ---------- ---------- ---------- --CTACACCC CCCAGCATCC
mmzL     ATCCTCC--- ---------- ---------- ---------- ---------- --CTACACCC CCCAGCATCC
mmzS     ATCCTCC--- ---------- ---------- ---------- ---------- --CTACACCC CCCAGCATCC
mti      ATCCTCC--- ---------- ---------- ---------- ---------- --CTACACCC CCCAGCATCC
mraL     ATCCTCC--- ---------- ---------- ---------- ---------- --CTACACCC CCCAGCATCC
mraS     ATCCTCC--- ---------- ---------- ---------- ---------- --CTACACCC CCCAGCATCC
msi      ATCCTCC--- ---------- ---------- ---------- ---------- --CTACACCC CCCAGCATCC

         ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
             75        85         95         105        115        125        135
papL     CCCCTGCAGC CTCCCAGCAT CTCCCCTGCA GCCCCCAGCA TCCCCCCTGC AGCCCTTTCA GCATCCCCCT
papS     CCCCTGCAGC CTCCCAGCAT CTCCCCTGCA GCCCCCAGCA TCCCCCCTGC AGCCCTTTCA GCATCCCCCT
lop      CCCCTGCAGC CTCCCAGCAT CTCCCCTGCA GCCCCCAGCA TCCCCCCTGC AGCCCTTTCA GCATCCCCCT
mle      CCCCTGCAGC CTCCCAGCAT CTCCCCTGCA CCCCCCAGCA TCCCCCCTGC AGCCCTTTCA GCATCCCCCT
msp      CCCCTGCAGC CTCCCAGCAT CTCCCCTGCA CCCCCCAGCA TCCCCCCTGC AGCCCTTTCA GCATCCCCCT
cer      CCCCTGCAGC CTCCCAGCAT CTCCCCTGCA GCCCCCAGCA TCCCCCCTGC AGCCCTTTCA GCATCCCCCT
msy      CCCCTGCAGC CTCCCAGCAT CTCCCCTGCA CCCCCCAGCA TCCCCCCTGC AGCCCTTTCA GCATCCCCCT
mfa      CCCCTGCAGC CTCCCAGCAT CTCCCCTGCA CCCCCCAGCA TCCCCCCTGC AGCCCTTTCA GCATCCCCCT
rhL      CCCCTGCAGC CTCCCAGCAT CTCCCCTGCA CCCCCCAGCA TCCCCCCTGC AGCCCTT-CA GCATCCCCCT
rhS      CCCCTGCAGC CTCCCAGCAT CTCCCCTGCA CCCCCCAGCA TCCCCC---- -- PL2-1 - --------CT
mmzL     CCCCTGCAGC CTCCCAGCAT CTCCCCTGCA CCCCCCAGCA TCCCCCCTGC AGCCCTTTCA GTATCCCCCT
mmzS     CCC------- ---------- - PL2-2 -- ---------- ------CTGC AGCCCTTTCA GTATCCCCCT
mti      CCC------- ---------- ---------- ---------- ------CTGC AGCCCTTTCA GTATCCCCCT
mraL     CCCCTGCAGC CTCCCAGCAT CTCCCCTGCA CCCCCCAGCA TCCCCCCTGC AGCCCTTTCA GTATCCCCCT
mraS     CCC------- ---------- ---------- ---------- ------CTGC AGCCCTTTCA GCATCCCCCT
msi      CCCCTGCAGC CTCCCAGCAT CTCCCCTGCA CCCCCCAGCA TCCCCCCTGC AGCCCTTTCA GCATCCCCCT
```

Fig. 4.1: Sequence alignment of the polymorphic locus 2 (PL2) in Papionini. This study: *papL* = long allele in *P. hamadryas*; *papS* = short allele in baboons; *lop* = allele in *L. aterrimus*; *mle* = allele in *Mandrillus leucophaeus*; *msp* = allele in *Mandrillus sphinx*; *cer* = allele in *C. chrysogaster*. Former studies: *msy* = allele in *Macaca sylvanus*; *mfa* = allele in *M. fascicularis*; *rhL, rhS* = long and short alleles in *M. mulatta*; *mmzL* and *mmzS*= long and short alleles in *M. munzala*; *mti* = allele in *M. thibetana*; *mraL* and *mraS* = long and short alleles in *M. radiata; msi* = allele in *M. silenus*. For the complete alignment and GenBank accession numbers see supporting information (Fig. S4.1).

Table 4.1: Frequencies of *5-HTTLPR* alleles in baboons (*Papio* spp.). In case where different populations were sampled within a species, values are given for each population.

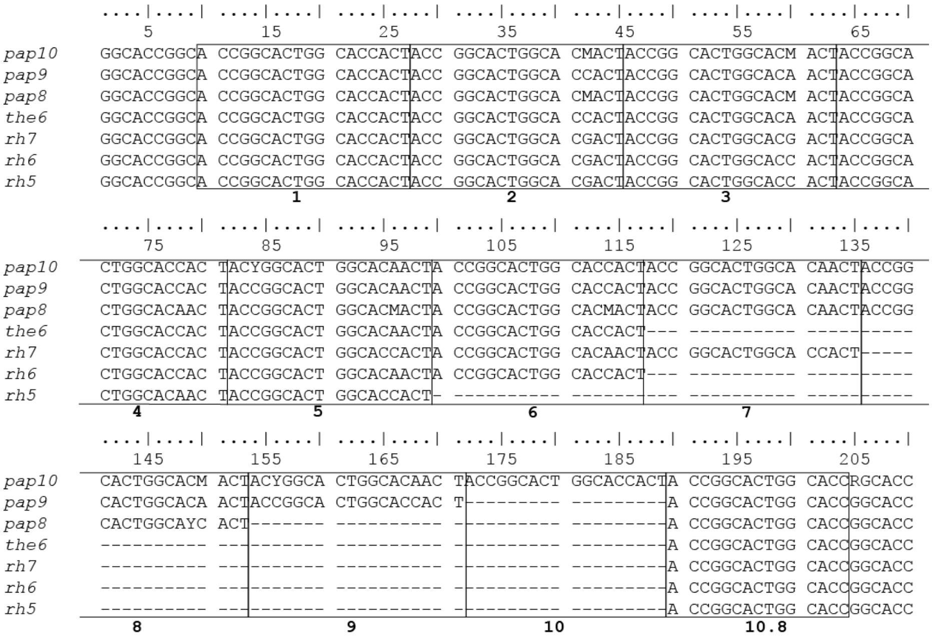
		Number of individuals			Number of alleles	Allele frequencies			
						papL		*papS*	
Species	Population	N	Females	Males		N	Freq.	N	Freq.
Guinea baboons (*P. papio*)	Total	31	15	16	62	0	0.0%	62	100.0%
Hamadryas baboons (*P. hamadryas*)	Total	32	11	21	64	10	15.6%	54	84.4%
	African	20	7	13	40	10	25.0%	30	75.0%
	Arabian	12	4	8	24			24	100.0%
Olive baboons (*P. anubis*)	Total	21	8	13	42	0	0.0%	42	100.0%
	West African	11	2	9	22			22	100.0%
	East African	10	6	4	20			20	100.0%
Yellow baboons (*P. cynocephalus*)	Total	21	8	13	42	0	0.0%	42	100.0%
Chacma baboons (*P. ursinus*)	Total	18	3	15	36	0	0.0%	36	100.0%
	South Africa	5	2	3	10			10	100.0%
	Moremi	13	1	12	26			26	100.0%
Total		123	45	78	246	10	4.1%	236	95.9%

Despite the considerable sequence variation between different repeats of the same allele, all Papionini exhibit a high similarity in the locus (Fig. 4.1; Fig. S4.1, Supporting information). Differences in the core sequence (5'-CTGCACCCCTCCCAGCATCTCCC-3' compared to 5'–CCCCCCCAGCATCCCCCCTGCA-3' in macaques; sequence from Trefilov et al. 2000; differences underlined) are due to the method chosen to determine the repeat sequence (see Materials and Methods). Nevertheless, there are several length differences among taxa. The *papL* allele is the longest allele described so far in Papionini and we only detected this variant in African *P. hamadryas*. The other four papionin species assessed in this study (*Mandrillus sphinx*, *Mandrillus leucophaeus*, *C. chrysogaster, and L. aterrimus*) carry an allele similar to the *papS*-allele and the allele described for Barbary macaques (*Macaca sylvanus*; *msy*-allele; Wendland et al. 2006b).

5-HTTLPR in all other macaque species lacks a 23bp-repeat at PL2-3 (Fig. 4.1), resulting in shorter alleles. *Macaca mulatta* carry two alleles, one lacking only the repeat in PL2-3 (*rhL)*, and a shorter allele which, additionally, lacks a repeat of 21/23 bp at PL2-1 (*rhS*; Lesch et al. 1997). The *rhS*-allele has, so far, only been detected in *M. mulatta*, but several other macaque species carry an allele similar to *rhL* (Wendland et al. 2006b, Chakraborty et al. 2010): Crab-eating macaque (*M. fascicularis*; *mfa*), stump-tailed macaque (*M. arctoides*; not shown), Arunachal macaque (*M. munzala*; *mmzL*), bonnet macaque (*M. radiata*; *mraL*), Tonkean macaque (*M. tonkeana*; not shown), pig-tailed macaque (*M. nemestrina*; not shown*)*, and lion-tailed macaque (*M. Silenus*; *msi*). *Macaca radiata* and *M. munzala*, additionally, carry an allele which lacks two repeats comprising 43 bp at PL2-2 (*mraS* and *mmzS*). Finally, the only allele found in Tibetan macaque (*M. thibetana*; *mti*) is similar to these two alleles. As sample sizes for *M. thibetana* and *M. arctoides* were small (three and two individuals, respectively; Wendland et al. 2006b) it is possible that other alleles exist in these species. Taken together, papionins differ at four sites within PL2; baboons vary only at one site, while macaques show considerable length variation and vary at three sites.

MAOALPR

MAOALPR in baboons consists of a variable number of repeats with the core sequence 5'-ACYGGCACTGGCAYVACT-3'. We detected alleles with 8.8 (*pap8*), 9.8 (*pap9*), and 10.8 (*pap10*) repeats (Fig. 4.2). In contrast to *5-HTTLPR*, there is little variation in nucleotide composition between consecutive repeats but baboons differ in the frequency of alleles (Fig. 4.3b; Table 4.2): *P. papio* only carry the *pap9*-allele. *Papio hamadryas* carry mainly the *pap9*-allele (84.4%) but some individuals also carry the *pap8*-allele (15.6%). *Papio anubis* carry the *pap8*- and *pap9*-allele in similar frequencies (46.2% and 42.3%, respectively), while the *pap10*-allele is uncommon (11.5%). We observed considerable differences, however, between populations. West African *P. anubis* baboons only carry the *pap9*-allele, while East African *P. anubis* mainly carry the *pap8*-allele (75.0%), and relatively few carry the *pap9*- (6.3%) or *pap10*-allele (18.8%). *Papio cynocephalus* mainly carry the *pap8*-allele (52.9%) and equal frequencies of the *pap9*- and *pap10*-alleles (23.5% each). *Papio ursinus* show the highest frequency of the *pap8*-allele (65%) and low frequency of the *pap9*-allele (35%). Again, populations differ considerably; Botswana *P. ursinus griseipes* exclusively carry the shorter allele, while South African *P. ursinus ursinus* exclusively carry the *pap9*-allele.



```
          ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
              5         15         25         35         45         55         65
pap10     GGCACCGGCA CCGGCACTGG CACCACTACC GGCACTGGCA CMACTACCGG CACTGGCACM ACTACCGGCA
pap9      GGCACCGGCA CCGGCACTGG CACCACTACC GGCACTGGCA CCACTACCGG CACTGGCACA ACTACCGGCA
pap8      GGCACCGGCA CCGGCACTGG CACCACTACC GGCACTGGCA CMACTACCGG CACTGGCACM ACTACCGGCA
the6      GGCACCGGCA CCGGCACTGG CACCACTACC GGCACTGGCA CCACTACCGG CACTGGCACA ACTACCGGCA
rh7       GGCACCGGCA CCGGCACTGG CACCACTACC GGCACTGGCA CGACTACCGG CACTGGCACG ACTACCGGCA
rh6       GGCACCGGCA CCGGCACTGG CACCACTACC GGCACTGGCA CGACTACCGG CACTGGCACC ACTACCGGCA
rh5       GGCACCGGCA CCGGCACTGG CACCACTACC GGCACTGGCA CGACTACCGG CACTGGCACC ACTACCGGCA
                          1                     2                     3

          ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
             75         85         95        105        115        125        135
pap10     CTGGCACCAC TACYGGCACT GGCACAACTA CCGGCACTGG CACCACTACC GGCACTGGCA CAACTACCGG
pap9      CTGGCACCAC TACCGGCACT GGCACAACTA CCGGCACTGG CACCACTACC GGCACTGGCA CAACTACCGG
pap8      CTGGCACAAC TACCGGCACT GGCACMACTA CCGGCACTGG CACMACTACC GGCACTGGCA CAACTACCGG
the6      CTGGCACCAC TACCGGCACT GGCACAACTA CCGGCACTGG CACCACT--- ---------- ----------
rh7       CTGGCACCAC TACCGGCACT GGCACCACTA CCGGCACTGG CACAACTACC GGCACTGGCA CCACT-----
rh6       CTGGCACCAC TACCGGCACT GGCACAACTA CCGGCACTGG CACCACT--- ---------- ----------
rh5       CTGGCACAAC TACCGGCACT GGCACCACT- ---------- ---------- ---------- ----------
             4                  5                     6                    7

          ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
            145        155        165        175        185        195        205
pap10     CACTGGCACM ACTACYGGCA CTGGCACAAC TACCGGCACT GGCACCACTA CCGGCACTGG CACCRGCACC
pap9      CACTGGCACA ACTACCGGCA CTGGCACCAC T--------- ---------A CCGGCACTGG CACCGGCACC
pap8      CACTGGCAYC ACT------- ---------- ---------- ---------A CCGGCACTGG CACCGGCACC
the6      ---------- ---------- ---------- ---------- ---------A CCGGCACTGG CACCGGCACC
rh7       ---------- ---------- ---------- ---------- ---------A CCGGCACTGG CACCGGCACC
rh6       ---------- ---------- ---------- ---------- ---------A CCGGCACTGG CACCGGCACC
rh5       ---------- ---------- ---------- ---------- ---------A CCGGCACTGG CACCGGCACC
             8                   9                    10                10.8
```

Fig. 4.2 Sequence alignment of *MAOALPR* in Papionini. Number of repeats indicated below. This study: *pap10* = 10.8-repeat allele (*P. cynocephalus*: KJ494409; *P. anubis*: KJ494408); *pap9 =* 9.8-repeat allele (*P. ursinus*: KJ494410; *P. cynocephalus*: KJ494411, *P. anubis*: KJ494412, *P. hamadryas*: KJ494413; *P. papio*: KJ494414); *pap8 =* 8.8-repeat allele (*P. ursinus*: KJ494415; *P. cynocephalus*: KJ494416; *P. anubis*: KJ494417; *P. hamadryas*: KJ494418). Former studies: *the6* = 6.8-repeat allele in *T. gelada* (AY615803.1); *rh5*, *rh6*, *rh7* = 5.8- (JN207466.1) 6.8- (JN207467.1) and 7.8-repeat (JN207468.1) alleles in *M. mulatta*.

Table 4.2: Frequencies of *MAOALPR* alleles in baboons (*Papio* spp.). In case where different populations were sampled within a species, values are given for each population.

		Number of individuals			Number of alleles*	Allele frequencies					
						pap8		*pap9*		*pap10*	
Species	Population	N	females	males		N	freq.	N	freq.	N	freq.
Guinea baboons (*P. papio*)	Total	26	13	13	39			39	100.0%		
Hamadryas baboons (*P. hamadryas*)	Total	24	8	16	32	5	15.6%	27	84.4%		
	African	12	4	8	16	5	31.3%	11	68.8%		
	Arabian	12	4	8	16			16	100.0%		
Olive baboons (*P. anubis*)	Total	18	8	10	26	12	46.2%	11	42.3%	3	11.5%
	West African	8	2	6	10			10	100.0%		
	East African	10	6	4	16	12	75.0%	1	6.3%	3	18.8%
Yellow baboons (*P. cynocephalus*)	Total	13	4	9	17	9	52.9%	4	23.5%	4	23.5%
Chacma baboons (*P. ursinus*)	Total	17	3	14	20	13	65.0%	7	35.0%		
	South Africa	5	2	3	7			7	100.0%		
	Moremi	12	1	11	13	13	100.0%				
Total		98	36	62	134	39	29.1%	88	65.7%	7	5.2%

***MAOA* is located on the X-chromosome.**

Compared with available data from other papionins, the *MAOALPR* of baboons shows the same core sequence (Fig. 4.2). Notably, alleles of baboons are longer than those of other papionin species: macaques carry only five (*rh5*), six (*rh6*) or seven (*rh7*) repeats. *Macaca mulatta* carry all three of these alleles, *M. fascicularis*, *M. nemestrina* and *M. tonkeana* carry the *rh6*- and *rh7*-alleles, *M. thibetana* and *M. arctoides* only the *rh7*-allele, and *M. sylvanus* only the *rh6*-allele (Wendland et al. 2006b). Geladas (*Theropithecus gelada*), which are more closely related to baboons than to macaques (Fig. 4.4), carry alleles with six repeats, which is more similar to macaques.

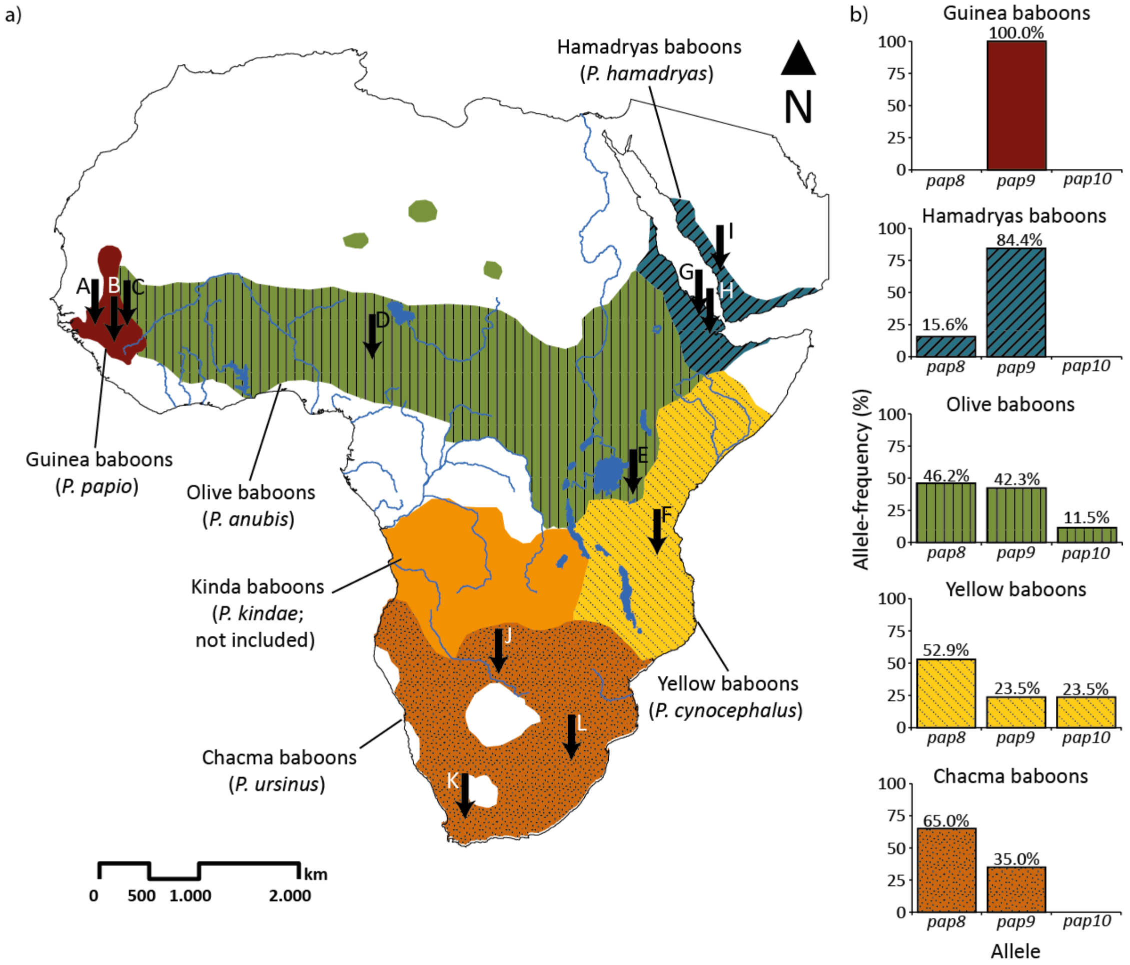


Figure 4.3 Geographical distribution of baboon species (*Papio* spp.) and *MAOALPR* allele frequencies: a) distribution map of baboons (adapted from Zinner et al. 2013b). Arrows with letters indicate sample locations (Table S4.1, Supporting information). Kinda baboon (*P. kindae*), which is often recognized as a subspecies of *P. cynocephalus*, was not included in this study; b) frequencies of *pap8*, *pap9*, and *pap10*-alleles.

Discussion

We analyzed variation in *5-HTTLPR* and *MAOALPR* genotypes in five species of baboons which exhibit pronounced differences in aggressiveness and tolerance among adult males. The results indicate that *5-HTTLPR* cannot be linked to interspecific variation in behavior. In contrast, the interspecific distribution of *MAOALPR* alleles is mostly consistent with behavioral variation related to male competitive strategies among species.

5-HTTLPR

Four out of five baboon species are monomorphic in *5-HTTLPR*. Only some African (but not Arabian) *P. hamadryas* carry a second allele. Accordingly, the genotype of this locus cannot be associated with interspecific behavioral variation. Nevertheless, in comparison with previous studies, our results give some insights into evolutionary changes at PL2. Given the existence and supposed functionality of *5-HTTLPR* in many primates, such comparisons may help to better understand the evolution of promoter regions.

Wendland et. al (2006b) suggested that the *msy*-allele found in *M. sylvanus* represents the ancestral allele in macaques. Our data confirm this assumption. Comparing alleles of 19 papionin species with respect to the evolutionary history of this tribe (Perelman et al. 2011), we suggest that *msy*-/*papS*-allele even represents the ancestral state of the locus for all Papionini. To date, this is the most parsimonious explanation as it only assumes four changes during the last 8 million years (Fig. 4.4):

1) As mentioned above, sequences of tandem repeats in this region are highly variable (Fig. S4.1, Supporting information) but the additional repeat at PL2-4 in the longest allele in Papionini, *papL*, is identical in sequence to the adjacent repeat. This points towards a recent insertion of this repeat. Thus the allele probably emerged recently in some African *P. hamadryas*.

2) After the split of *M. sylvanus*, other macaque species lost the repeat at PL2-3, resulting in the *rhL*-allele. Interestingly, the other macaque species all occur in Asia, while *M. sylvanus* and all other Papionini (with the exception some *P. hamadryas* in Arabia) live in Africa where the tribe is thought to have its origin (Zinner et al. 2013a). Thus, Asian macaques probably lost the repeat at PL2-3 during dispersal from Africa to Asia.

3) The *rhS*-allele only occurs in *M. mulatta*. Thus, the partial loss of the repeat at PL2-1 probably occurred after the split from other macaque species.

4) Finally, *mti*-like alleles only occur in *M. munzala*, *M. thibetana*, and *M. radiata*, which all belong to the *Sinica*-Group of macaques (Chakraborty et al. 2007). Thus, the deletion of two repeats at the PL2-2 probably occurred in the common ancestors of these three species.

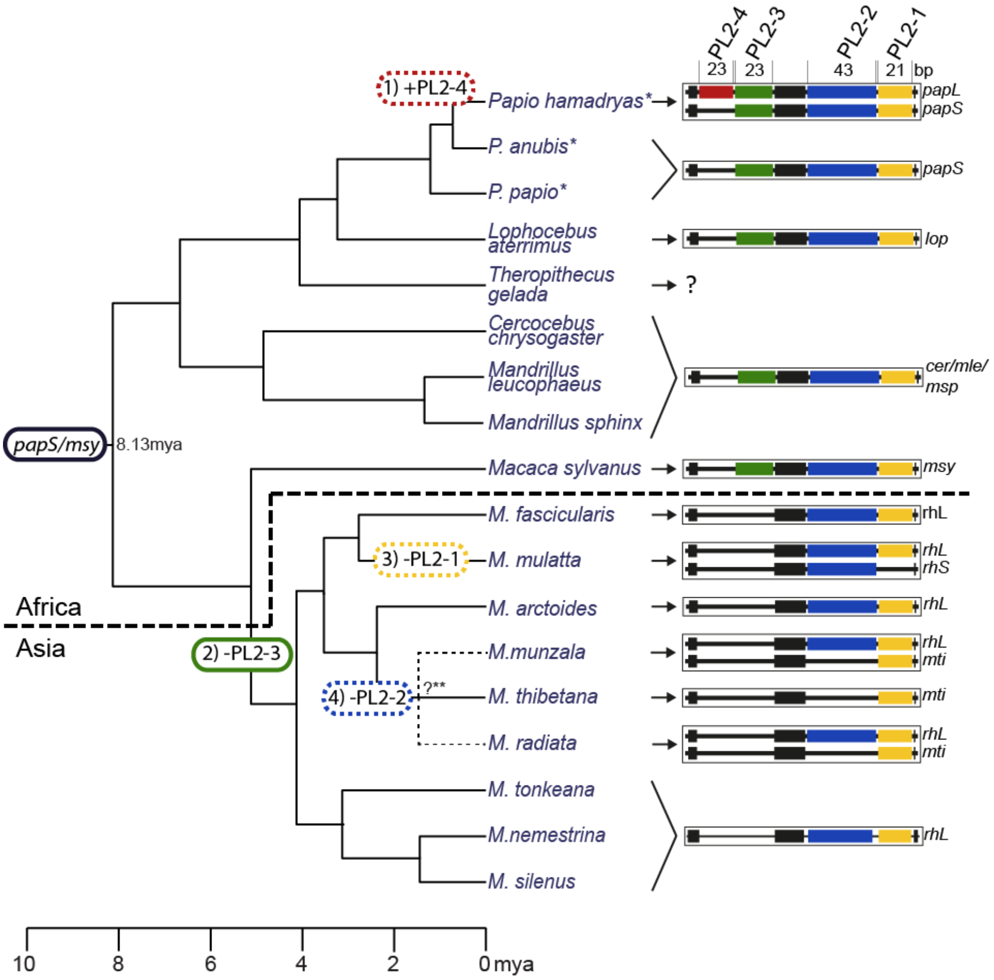


Figure 4.4: Distribution and evolutionary history of alleles in *5-HTTLPR* in Papionini. Shown are hypothesized positions of insertions/deletions (indels) of repeats within the polymorphic locus 2 (PL2) in the phylogenetic tree for Papionini. Partial indels are encircled by dashed lines and complete indels by solid lines. For further explanation see Discussion. Phylogenetic tree and divergence ages adapted from Perelman et al. 2011. *Nuclear DNA data for the position of other baboon species in the phylogeny are not yet available; **comparable date for *M. munzala* and *M. radiata* are lacking but both species belong, together with *M. thibetana*, to the *Sinica*-Group of macaques (Chakraborty et al. 2007).

Overall, this could indicate that selective pressures acting on this locus may differ between Asian and African populations of papionins. Interestingly, the short allele in humans (which differs at PL1) also seems to be the derived version of the allele (Claw et al. 2010). Furthermore, frequencies of the short allele vary among populations. This variation cannot be solely explained by demographic factors, rather selective pressures need to be considered (Claw et al. 2010). Geographical allele distribution in humans (Esau et al. 2008), hereby, superficially resembles the distribution in papionin species; shorter alleles have a lower frequency in African (~15-30%) than in Asian populations (~70-80%), while European populations show intermediate frequencies (~40-

50%). If the short allele confers an advantage requires further investigations (see Kalbitzer J. et al. 2013, CHAPTER FIVE). In macaques, the advantage of having several alleles in this genotype has been suggested to be advantageous in highly variable habitats (Suomi 2006, Chakraborty et al 2010). To our knowledge, however, this hypothesis has not been properly tested and comparisons of variation in ecological conditions among Asian and African Papionin habitats are not available. The question in which way range expansions in papionin species into new and potentially highly variable territories create specific selective pressures and evolutionary dynamics may provide a fruitful avenue for further research.

Alternatively, the distribution of *5-HTTLPR* alleles could also be a result of random processes (i.e. genetic drift). Testing for selection signals, as commonly done in coding regions, is unfortunately much more complicated in promoter regions (Wray et al. 2003). Due to the (nearly) universal genetic code, synonymous and non-synonymous mutations in coding regions are easily inferred from the sequence, while comparative information on promoter properties (e.g. transcription factor binding sites) must be assessed experimentally.

MAOALPR

The overall distribution of different alleles of *MAOALPR* in baboons suggests a link between this locus and interspecific variation in behavior of adult males. *Papio papio*, apparently the most tolerant and cooperative species regarding male-male relationships, exclusively carry the *pap9*-allele. *Papio hamadryas*, in which males seem to be (at least temporarily) tolerant and fights are more ritualized, also have a high frequency of the *pap9*-allele (84.4%). In contrast, *P. ursinus*, as the most aggressive and uncooperative species, only 35% of the individuals carry this allele but 65% the *pap8*-allele. *Papio anubis* and *P. cynocephalus* show intermediate levels of aggressiveness and cooperation, and both taxa show intermediate frequencies of these two alleles (*P. anubis*: *pap8/pap9*: 46.2%/42.3%; *P. cynocephalus*: *pap8/pap9*: 52.6%/26.3%), and, additionally, carry the *pap10*-allele (11.5% and 23.5%, respectively).

Variation in genotypes between populations within *P. ursinus* and within *P. anubis* is, however, considerable. All *P. ursinus* from the Moremi Game Reserve in Botswana carry the *pap8*-allele, while all *P. ursinus* from South Africa carry the *pap9*-allele. Similarly, East African *P. anubis* show a high frequency of the *pap8*-allele (75%), while West African *P. anubis* exclusively carry the *pap9*-allele. This suggests that population differences instead of species differences are more important in baboons and should be considered in behavioral and genetic comparisons. To date, behavioral data on male-male relationships are not published for all populations (e.g. West-African olive baboons) and it would be necessary to investigate genetic differences in other populations more thoroughly for which behavioral data are available (e.g. chacma baboons from Drakensberg region; samples PU-1386 and PU-1419, Table S1, Supporting information). Consequently, more data is needed to draw further conclusions about the link between male aggressiveness and *MAOALPR* genotype among different baboon populations.

Another important question is the functionality of the *MAOALPR* in baboons. Although several studies on humans and macaques indicate that variation in the *MAOALPR* genotype has an effect on transcriptional activity (Sabol et al. 1998, Newman et al. 2005), corresponding studies for baboons are still lacking. Importantly, MAOA is involved in other monoamine neurotransmitter systems in addition to 5-HT while 5-HT transporter activity only affects the 5-HT system. For example, MAOA also metabolizes noradrenalin (NA) and dopamine (DA) and both of these monoamines appear to play an important role in the expression of aggression (e.g. Eichelman et al. 1972; reviews in Nelson & Trainor 2007, Yanowitch & Coccaro 2013). Noradrenalin, in combination with adrenalin, is closely linked to the fight-or-flight reflex (e.g. Haller et al. 1998), and NA levels appear to be correlated with aggressiveness in *M. mulatta* (Higley et al. 1992). The brain DA system appears to be involved in the initiation and execution of aggressive behaviors in rodents and humans (Miczek et al. 2002, Miczek & Fish 2005). Effects of neurotransmitters are, however, very complex due to the numerous receptor types, differences in action depending on the brain area, and interactions with other substances and the environment. Results are, therefore, sometimes inconsistent (e.g. Yanowitch & Coccaro 2013) and, thus, predictions on directionality of effects are difficult.

Despite these limitations, we believe that comparative data on monoamine neurotransmitter levels from different baboon populations would be informative with respect to the link between differential MAOA activity and behavior. So far, such data are only available for some *P. hamadryas* and *P. anubis* from Ethiopia (Jolly et al. 2008, Jolly et al. 2013). The authors measured cerebrospinal fluid (CSF) levels of 5-HIAA (the metabolite of 5-HT), homovanillic acid (HVA; the metabolite of DA), and 3-methoxy-4-hydroxyphenylglycol (MHPG; the metabolite of NA). While they could not detect a significant difference in 5-HIAA levels, adult male *P. hamadryas* show higher levels of HVA and MHPG than adult male *P. anubis*. Therefore, behavioral variation in baboons could be associated with differential activity of other monoamine neurotransmitters than 5-HT, potentially regulated by differences in MAOA availability as a result of a given *MAOALPR* genotype.

Conclusion

Our results indicate that there is no corresponding variation in male behavior and *5-HTTLPR* in baboons. Nevertheless, comparisons of alleles among 19 papionin species indicate differences between African and Asian species potentially linked to geographic differences in selective pressures on this locus. *MAOALPR*, on the other hand, shows considerable variation in allele frequencies among populations that might be partly linked to behavioral differences. The genotype of this so-called ’warrior gene’ may play a role in behavioral variation through differential activity of MAOA. To further examine this relationship, future studies should investigate the effect of different alleles on transcription profiles, protein levels, neurotransmitter levels, and behavior in polymorphic populations of baboons. While this explorative study represents a first step to investigate the genetics underlying behavioral variation among baboon populations, future studies should examine sequence variation in coding and non-coding regions of those genes encoding for other proteins involved in neurotransmitter systems.

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Data Accessibility

DNA sequences: GenBank accession numbers: KJ494398-KJ494418

Supporting Information

Supporting Information - Methods

SM4.1: DNA Extraction

DNA was extracted using the 'Gen-ial all-tissue DNA-kit' (GEN-IAL, Troisdorf, Germany) following the standard protocol with three modifications: 1) 10µL of 1M DTT were added before the first incubation, 2) samples were incubated on a thermo block at 65°C/600rpm for 60min followed by overnight incubation at 37°C/300rpm, and 3) on the next day after the first centrifugation step, a maximum of 1000µL of the supernatant was transferred into a new tube and 80%Vol. chloroform was added, shortly mixed by hand, centrifuged for 10min at 13,000rpm, and the upper phase was transferred into a new tube in which 75%Vol. of Lyse 3 was added.

SM4.2: PCR conditions and thermo cycler settings

All PCR reactions were conducted in a 30µL PCR-mix [1x reaction buffer, 0.16mM for each dNTP, 0.33µM for each primer, 1 U BiothermTaq 5000 (Genecraft, Germany), and 0.6 mg/ml BSA]. We used ~50ng of DNA per reaction for tissue and blood samples. As the determination of target-species-DNA concentration in extracts from fecal samples is very labor-intensive (Perry et al. 2010), we started here with 1µL of extract and increased incremental to 2µL and 4µL in case the initial amplification was without success.

Thermo cycler setting: For **stpr**-primers: 1. initial denaturation step at 94°C for 2min followed by 2) 35 cycles of 94°C-60°C-72°C, each step for 60sec and 3) a final elongation at 72°C for 5min. For **p*5-HTTLPR***-primers: 1. initial denaturation step at 94°C for 2min followed by 2) 35-45 cycles (depending on sample quality) of 94°C–62°C–72°C, each step for 30sec, and 3) a final elongation at 72°C for 5min. For **jrw**-primers: 1) an initial denaturation step at 94°C for 2min followed by 2) 35 cycles of 94°C–65°C–72°C, each step 60sec followed by 3) a final elongation at 72°C for 5min. For **p*MAOALPR*-**primers: 1) an initial denaturation step at 94°C for 2min followed by 2) 40-50 cycles of 94°C–70°C-72°C, each step 60sec followed by 3) a final elongation at 72°C for 5min.

Supporting Information – Tables

Table S4.1: Sample information and genotypes of all tested samples

Species	Country	Population	Location	Letter on map	*MAOA-LPR*	*5HTT-LPR*	Sex	Internal_ID
Papio anubis	Nigeria	West African	Gashaka	D	9	ps/ps	Male	PA-EY16
P. anubis	Nigeria	West African	Gashaka	D	9	ps/ps	Male	PA-EY17
P. anubis	Nigeria	West African	Gashaka	D	9/9	ps/ps	Female	PA-EY18
P. anubis	Nigeria	West African	Gashaka	D	9	ps/ps	Male	PA-EY19
P. anubis	Nigeria	West African	Gashaka	D	no	ps/ps	Male	PA-EY21
P. anubis	Nigeria	West African	Gashaka	D	9	ps/ps	Male	PA-EY23
P. anubis	Nigeria	West African	Gashaka	D	no	ps/ps	Male	PA-EY24
P. anubis	Nigeria	West African	Gashaka	D	9	ps/ps	Male	PA-EY25
P. anubis	Nigeria	West African	Gashaka	D	no	ps/ps	Male	PA-EY26
P. anubis	Nigeria	West African	Gashaka	D	9	ps/ps	Male	PA-EY27
P. anubis	Nigeria	West African	Gashaka	D	9/9	ps/ps	Female	PA-EY28
P. anubis	Tanzania	East African	Lake Manyara	E	9	ps/ps	Male	PA-S03
P. anubis	Tanzania	East African	Lake Manyara	E	10/10	ps/ps	Female	PA-S04
P. anubis	Tanzania	East African	Lake Manyara	E	8	ps/ps	Male	PA-S05
P. anubis	Tanzania	East African	Lake Manyara	E	8/10	ps/ps	Female	PA-S06
P. anubis	Tanzania	East African	Lake Manyara	E	8/8	ps/ps	Female	PA-S07
P. anubis	Tanzania	East African	Lake Manyara	E	8	ps/ps	Male	PA-S08
P. anubis	Tanzania	East African	Lake Manyara	E	8	ps/ps	Male	PA-S09
P. anubis	Tanzania	East African	Lake Manyara	E	8/8	ps/ps	Female	PA-S10
P. anubis	Tanzania	East African	Lake Manyara	E	8/8	ps/ps	Female	PA-S11
P. anubis	Tanzania	East African	Lake Manyara	E	8/8	ps/ps	Female	PA-S12
P. cynocephalus	Tanzania	East African	Mikumi	F	8	ps/ps	Male	PC-0951
P. cynocephalus	Tanzania	East African	Mikumi	F	9	ps/ps	Male	PC-0954
P. cynocephalus	Tanzania	East African	North of Morogoro	F	8	ps/ps	Male	PC-0961
P. cynocephalus	Tanzania	East African	North of Morogoro	F	8/8	ps/ps	Female	PC-0962
P. cynocephalus	Tanzania	East African	North of Morogoro	F	no	ps/ps	Female	PC-0963
P. cynocephalus	Tanzania	East African	Dodoma-->Iringa	F	8	ps/ps	Male	PC-0978
P. cynocephalus	Tanzania	East African	Dodoma-->Iringa	F	8/8	ps/ps	Female	PC-0981
P. cynocephalus	Tanzania	East African	Dodoma-->Iringa	F	9/10	ps/ps	Female	PC-0983
P. cynocephalus	Tanzania	East African	Kilewa->Kibiti	F	9	ps/ps	Male	PC-0985
P. cynocephalus	Tanzania	East African	Dodoma-->Iringa	F	8	ps/ps	Male	PC-0988
P. cynocephalus	Tanzania	East African	Iringa-->Makambaku	F	8	ps/ps	Male	PC-0991
P. cynocephalus	Tanzania	East African	100km North of Songea	F	10	ps/ps	Male	PC-1002
P. cynocephalus	Tanzania	East African	North of Namtumbo	F	no	ps/ps	Male	PC-1017
P.	Tanzania	East African	Kilimansela	F	no	ps/ps	Male	PC-1024

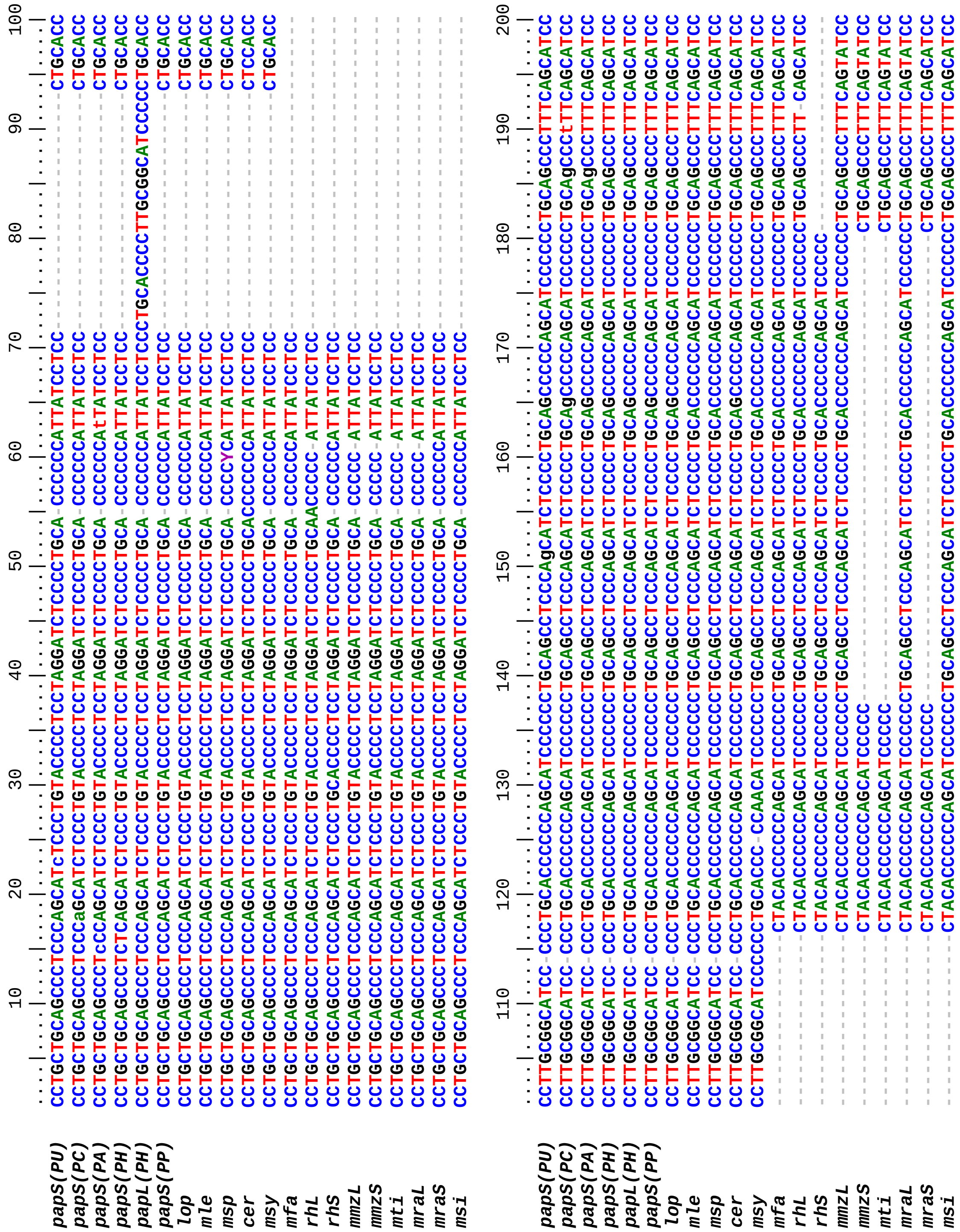
Species	Country	Population	Location	Letter on map	*MAOA-LPR*	*5HTT-LPR*	Sex	Internal_ID
cynocephalus								
P. cynocephalus	Tanzania	East African	Chem-Chem	F	no	ps/ps	Female	PC-1027
P. cynocephalus	Tanzania	East African	Chem-Chem	F	no	ps/ps	Male	PC-1028
P. cynocephalus	Tanzania	East African	Tunduru->Masasi	F	no	ps/ps	Female	PC-1042
P. cynocephalus	Tanzania	East African	Tunduru->Masasi	F	no	ps/ps	Male	PC-1045
P. cynocephalus	Tanzania	East African	West of Masasi	F	10/10	ps/ps	Female	PC-1057
P. cynocephalus	Tanzania	East African	Chiwata	F	no	ps/ps	Female	PC-1063
P. cynocephalus	Tanzania	East African	Nanguruwe	F	9	ps/ps	Male	PC-1073
P. hamadryas	Saudi Arabia	Arabian	Abha	I	9/9	ps/ps	Female	PH-A01
P. hamadryas	Saudi Arabia	Arabian	Abha	I	9/9	ps/ps	Female	PH-A02
P. hamadryas	Saudi Arabia	Arabian	Baha	I	9	ps/ps	Male	PH-A03
P. hamadryas	Saudi Arabia	Arabian	Al Akhal	I	9	ps/ps	Male	PH-A04
P. hamadryas	Saudi Arabia	Arabian	Taif	I	9	ps/ps	Male	PH-A05
P. hamadryas	Saudi Arabia	Arabian	Taif	I	9	ps/ps	Male	PH-A06
P. hamadryas	Saudi Arabia	Arabian	Abha	I	9	ps/ps	Male	PH-A07
P. hamadryas	Saudi Arabia	Arabian	Abha	I	9/9	ps/ps	Female	PH-A08
P. hamadryas	Saudi Arabia	Arabian	Baha	I	9/9	ps/ps	Female	PH-A09
P. hamadryas	Saudi Arabia	Arabian	Baha	I	9	ps/ps	Male	PH-A10
P. hamadryas	Saudi Arabia	Arabian	Al Akhal	I	9	ps/ps	Male	PH-A11
P. hamadryas	Saudi Arabia	Arabian	Al Akhal	I	9	ps/ps	Male	PH-A12
P. hamadryas	Eritrea	African	Af Himbol	G	no	ps/ps	Male	PH-E205
P. hamadryas	Eritrea	African	Af Himbol	G	9/9	ps/ps	Female	PH-E206
P. hamadryas	Eritrea	African	Af Himbol	G	no	ps/ps	Female	PH-E207
P. hamadryas	Eritrea	African	Af Himbol	G	no	ps/ps	Male	PH-E208
P. hamadryas	Eritrea	African	Af Himbol	G	9	ps/ps	Male	PH-E209
P. hamadryas	Eritrea	African	Filfil Bridge	G	9/9	ps/ps	Female	PH-E236
P. hamadryas	Eritrea	African	Filfil Bridge	G	no	ps/ps	Male	PH-E237
P. hamadryas	Eritrea	African	Filfil Bridge	G	no	ps/pl	Female	PH-E238
P. hamadryas	Eritrea	African	Durfo	G	no	ps/ps	Female	PH-E240
P. hamadryas	Eritrea	African	Durfo	G	no	ps/pl	Male	PH-E241
P. hamadryas	Eritrea	African	Durfo	G	9/9	ps/pl	Female	PH-E243
P. hamadryas	Ethiopia	African	Gerba Luku	H	9	ps/pl	Male	PH-E310
P. hamadryas	Ethiopia	African	Gerba Luku	H	8	ps/pl	Male	PH-E311
P. hamadryas	Ethiopia	African	Gerba Luku	H	8	pl/pl	Male	PH-E312
P. hamadryas	Ethiopia	African	Gerba Luku	H	9	ps/ps	Male	PH-E313

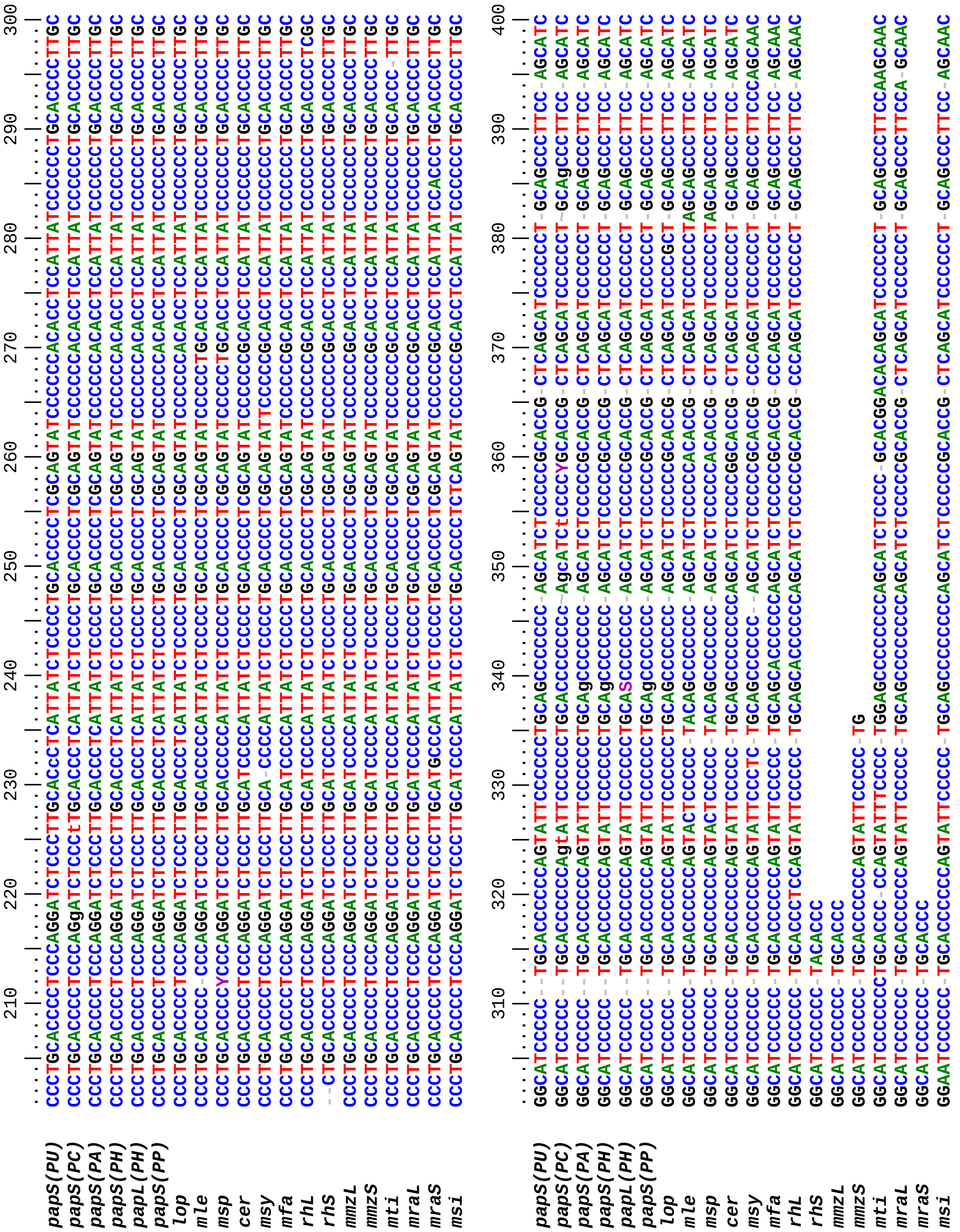
Species	Country	Population	Location	Letter on map	*MAOA-LPR*	*5HTT-LPR*	Sex	Internal_ID
P. hamadryas	Ethiopia	African	Gerba Luku	H	no	ps/pl	Male	PH-E314
P. hamadryas	Ethiopia	African	Gerba Luku	H	8	ps/ps	Male	PH-E315
P. hamadryas	Ethiopia	African	Gerba Luku	H	8	ps/pl	Male	PH-E316
P. hamadryas	Ethiopia	African	Gerba Luku	H	9/9	ps/ps	Female	PH-E318
P. hamadryas	Ethiopia	African	Gerba Luku	H	8	ps/pl	Male	PH-E319
P. papio	Senegal	West African	Niokolo Koba	A	9	ps/ps	Male	PP-001
P. papio	Senegal	West African	Niokolo Koba	A	9	ps/ps	Male	PP-002
P. papio	Senegal	West African	Niokolo Koba	A	9	ps/ps	Male	PP-005
P. papio	Senegal	West African	Niokolo Koba	A	9	ps/ps	Male	PP-007
P. papio	Senegal	West African	Niokolo Koba	A	9/9	ps/ps	Female	PP-009
P. papio	Senegal	West African	Niokolo Koba	A	9/9	ps/ps	Female	PP-011
P. papio	Senegal	West African	Niokolo Koba	A	9	ps/ps	Male	PP-015
P. papio	Senegal	West African	Niokolo Koba	A	9	ps/ps	Male	PP-027
P. papio	Senegal	West African	Niokolo Koba	A	9/9	ps/ps	Female	PP-029
P. papio	Senegal	West African	Niokolo Koba	A	9/9	ps/ps	Female	PP-034
P. papio	Senegal	West African	Niokolo Koba	A	9/9	ps/ps	Female	PP-045
P. papio	Senegal	West African	Niokolo Koba	A	9/9	ps/ps	Female	PP-056
P. papio	Mali	West African	Boucle du Baoué	C	9/9	ps/ps	Female	PP-187
P. papio	Mali	West African	Boucle du Baoué	C	9/9	ps/ps	Female	PP-188
P. papio	Mali	West African	Boucle du Baoué	C	9/9	ps/ps	Female	PP-189
P. papio	Mali	West African	Boucle du Baoué	C	9	ps/ps	Male	PP-190
P. papio	Mali	West African	Boucle du Baoué	C	no	ps/ps	Female	PP-205
P. papio	Mali	West African	Boucle du Baoué	C	9	ps/ps	Male	PP-206
P. papio	Mali	West African	Boucle du Baoué	C	9	ps/ps	Male	PP-207
P. papio	Senegal	West African	Niokolo Koba	A	9	ps/ps	Male	PP-246
P. papio	Guinea	West African	Fouta Djallon	B	9/9	ps/ps	Female	PP-248
P. papio	Guinea	West African	Fouta Djallon	B	no	ps/ps	Male	PP-249
P. papio	Guinea	West African	Fouta Djallon	B	no	ps/ps	Male	PP-254
P. papio	Guinea	West African	Fouta Djallon	B	no	ps/ps	Female	PP-255
P. papio	Guinea	West African	Fouta Djallon	B	no	ps/ps	Male	PP-269
P. papio	Guinea	West African	Fouta Djallon	B	9	ps/ps	Male	PP-279
P. papio	Guinea	West African	Fouta Djallon	B	9	ps/ps	Male	PP-281
P. papio	Guinea	West African	Kankan	B	9/9	ps/ps	Female	PP-283
P. papio	Guinea	West African	Fouta Djallon	B	9	ps/ps	Male	PP-291
P. papio	Guinea	West African	Fouta Djallon	B	9/9	ps/ps	Female	PP-292
P. papio	Guinea	West African	Boké	B	9/9	ps/ps	Female	PP-293
P. ursinus	Botswana	Moremi	Moremi Game Reserve	J	8	ps/ps	Male	PU-0024
P. ursinus	Botswana	Moremi	Moremi Game Reserve	J	8	ps/ps	Male	PU-0025
P. ursinus	Botswana	Moremi	Moremi Game Reserve	J	8	ps/ps	Male	PU-0026

Species	Country	Population	Location	Letter on map	*MAOA-LPR*	*5HTT-LPR*	Sex	Internal_ID
P. ursinus	Botswana	Moremi	Moremi Game Reserve	J	8	ps/ps	Male	PU-0028
P. ursinus	Botswana	Moremi	Moremi Game Reserve	J	8	ps/ps	Male	PU-0029
P. ursinus	Botswana	Moremi	Moremi Game Reserve	J	8	ps/ps	Male	PU-0050
P. ursinus	Botswana	Moremi	Moremi Game Reserve	J	8	ps/ps	Male	PU-0067
P. ursinus	Botswana	Moremi	Moremi Game Reserve	J	8	ps/ps	Male	PU-0069
P. ursinus	Botswana	Moremi	Moremi Game Reserve	J	no	ps/ps	Male	PU-0074
P. ursinus	Botswana	Moremi	Moremi Game Reserve	J	8	ps/ps	Male	PU-0075
P. ursinus	Botswana	Moremi	Moremi Game Reserve	J	8/8	ps/ps	Female	PU-0079
P. ursinus	Botswana	Moremi	Moremi Game Reserve	J	8	ps/ps	Male	PU-0114
P. ursinus	Botswana	Moremi	Moremi Game Reserve	J	8	ps/ps	Male	PU-0120
P. ursinus	South Africa	South African	Newcastle/ Drakensberg Region	L	9	ps/ps	Male	PU-1386
P. ursinus	South Africa	South African	Mt. Currie/ Drakensberg Region	L	9	ps/ps	Male	PU-1419
P. ursinus	South Africa	South African	Olifantskop/ Cape Region	K	9	ps/ps	Male	PU-1441
P. ursinus	South Africa	South African	Cape Town/ Cape Region	K	9/9	ps/ps	Female	PU-U04
P. ursinus	South Africa	South African	Cape Town/ Cape Region	K	9/9	ps/ps	Female	PU-U11

Supporting informations – Figures

Fig. S4.1 - Complete alignment of 5-HTTLPR in Papionini

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papS(PU)
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papS(PP)
lop
mle
msp
cer
msy
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rhL
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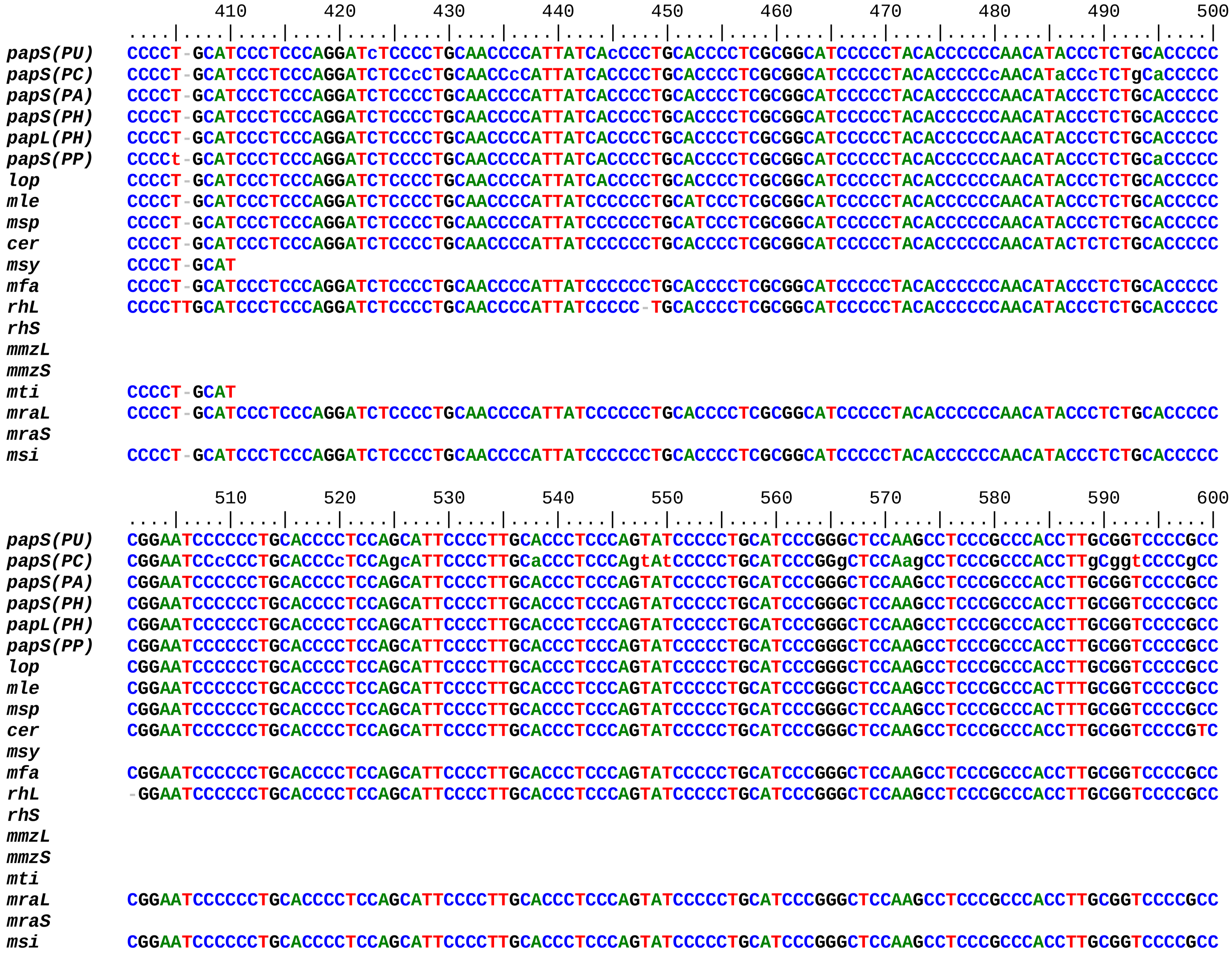

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papS(PC)      CCCCT-GCATCCCTCCCAGGATCTCCcCTGCAACCcCATTATCACCCCTGCACCCCTCGCGGCATCCCCCTACACCCCCcAACATaCCcTCTgCaCCCCC
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papS(PH)      CCCCT-GCATCCCTCCCAGGATCTCCCCTGCAACCCCATTATCACCCCTGCACCCCTCGCGGCATCCCCCTACACCCCCCAACATACCCTCTGCACCCCC
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papS(PP)      CCCCt-GCATCCCTCCCAGGATCTCCCCTGCAACCCCATTATCACCCCTGCACCCCTCGCGGCATCCCCCTACACCCCCCAACATACCCTCTGCaCCCCC
lop           CCCCT-GCATCCCTCCCAGGATCTCCCCTGCAACCCCATTATCACCCCTGCACCCCTCGCGGCATCCCCCTACACCCCCCAACATACCCTCTGCACCCCC
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msp           CCCCT-GCATCCCTCCCAGGATCTCCCCTGCAACCCCATTATCCCCCCTGCATCCCTCGCGGCATCCCCCTACACCCCCCAACATACCCTCTGCACCCCC
cer           CCCCT-GCATCCCTCCCAGGATCTCCCCTGCAACCCCATTATCCCCCCTGCACCCCTCGCGGCATCCCCCTACACCCCCCAACATACTCTCTGCACCCCC
msy           CCCCT-GCAT
mfa           CCCCT-GCATCCCTCCCAGGATCTCCCCTGCAACCCCATTATCCCCCCTGCACCCCTCGCGGCATCCCCCTACACCCCCCAACATACCCTCTGCACCCCC
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rhS
mmzL
mmzS
mti           CCCCT-GCAT
mraL          CCCCT-GCATCCCTCCCAGGATCTCCCCTGCAACCCCATTATCCCCCCTGCACCCCTCGCGGCATCCCCCTACACCCCCCAACATACCCTCTGCACCCCC
mraS
msi           CCCCT-GCATCCCTCCCAGGATCTCCCCTGCAACCCCATTATCCCCCCTGCACCCCTCGCGGCATCCCCCTACACCCCCCAACATACCCTCTGCACCCCC

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papL(PH)      CGGAATCCCCCCTGCACCCCTCCAGCATTCCCCTTGCACCCTCCCAGTATCCCCCTGCATCCCGGGCTCCAAGCCTCCCGCCCACCTTGCGGTCCCCGCC
papS(PP)      CGGAATCCCCCCTGCACCCCTCCAGCATTCCCCTTGCACCCTCCCAGTATCCCCCTGCATCCCGGGCTCCAAGCCTCCCGCCCACCTTGCGGTCCCCGCC
lop           CGGAATCCCCCCTGCACCCCTCCAGCATTCCCCTTGCACCCTCCCAGTATCCCCCTGCATCCCGGGCTCCAAGCCTCCCGCCCACCTTGCGGTCCCCGCC
mle           CGGAATCCCCCCTGCACCCCTCCAGCATTCCCCTTGCACCCTCCCAGTATCCCCCTGCATCCCGGGCTCCAAGCCTCCCGCCCACTTTGCGGTCCCCGCC
msp           CGGAATCCCCCCTGCACCCCTCCAGCATTCCCCTTGCACCCTCCCAGTATCCCCCTGCATCCCGGGCTCCAAGCCTCCCGCCCACTTTGCGGTCCCCGCC
cer           CGGAATCCCCCCTGCACCCCTCCAGCATTCCCCTTGCACCCTCCCAGTATCCCCCTGCATCCCGGGCTCCAAGCCTCCCGCCCACCTTGCGGTCCCCGTC
msy
mfa           CGGAATCCCCCCTGCACCCCTCCAGCATTCCCCTTGCACCCTCCCAGTATCCCCCTGCATCCCGGGCTCCAAGCCTCCCGCCCACCTTGCGGTCCCCGCC
rhL           -GGAATCCCCCCTGCACCCCTCCAGCATTCCCCTTGCACCCTCCCAGTATCCCCCTGCATCCCGGGCTCCAAGCCTCCCGCCCACCTTGCGGTCCCCGCC
rhS
mmzL
mmzS
mti
mraL          CGGAATCCCCCCTGCACCCCTCCAGCATTCCCCTTGCACCCTCCCAGTATCCCCCTGCATCCCGGGCTCCAAGCCTCCCGCCCACCTTGCGGTCCCCGCC
mraS
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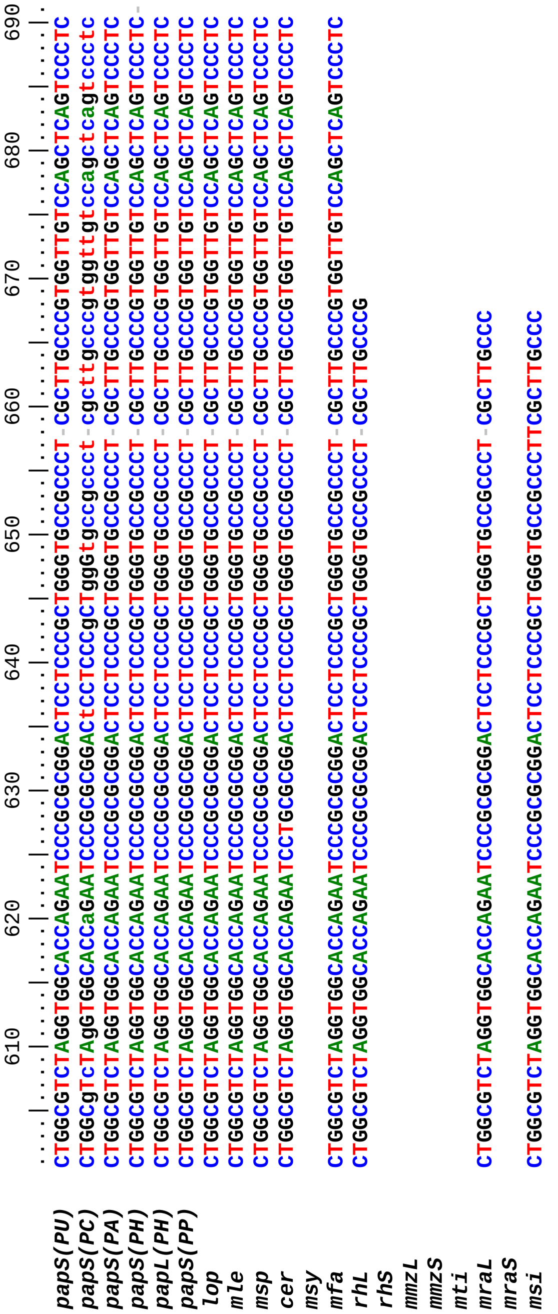

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papS(PP)    CTGGCGTCTAGGTGGCACCAGAATCCCGCGCGGACTCCTCCCGCTGGGTGCCGCCCT-CGCTTGCCCGTGGTTGTCCAGCTCAGTCCCTC
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msp         CTGGCGTCTAGGTGGCACCAGAATCCCGCGCGGACTCCTCCCGCTGGGTGCCGCCCT-CGCTTGCCCGTGGTTGTCCAGCTCAGTCCCTC
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msy
mfa         CTGGCGTCTAGGTGGCACCAGAATCCCGCGCGGACTCCTCCCGCTGGGTGCCGCCCT-CGCTTGCCCGTGGTTGTCCAGCTCAGTCCCTC
rhL         CTGGCGTCTAGGTGGCACCAGAATCCCGCGCGGACTCCTCCCGCTGGGTGCCGCCCT-CGCTTGCCCG
rhS
mmzL
mmzS
mti
mraL        CTGGCGTCTAGGTGGCACCAGAATCCCGCGCGGACTCCTCCCGCTGGGTGCCGCCCT-CGCTTGCCC
mraS
msi         CTGGCGTCTAGGTGGCACCAGAATCCCGCGCGGACTCCTCCCGCTGGGTGCCGCCCTTCGCTTGCCC
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Fig. S4.1: Complete alignment of *5-HTTLPR* in Papionini. Sequences from this study (with GenBank-Accession numbers): *papS(PU)* = short allele in *P. ursinus* (KJ494398); *papS(PC)* = short allele in *P. cynocephalus (*KJ494399); *papS(PA)* = short allele in *P. anubis (*KJ494400); *papS(PH)* = short allele in *P. hamadryas* (KJ494401); *papL(PH)* = long allele in *P. hamadryas* (KJ494402); *papS(PP)* = short allele in *P. papio (*KJ494403); *lop* = allele from *Lophocebus aterrimus* (KJ494404); *mle* = allele from *Mandrillus leucophaeus* (KJ494405); *msp* = allele from *Mandrillus sphinx* (KJ494406); *cer* = allele from *Cercocebus chrysogaster* (KJ494407).

Sequences described for *Macaca* spp. originating from other studies: *msy* = allele *M. sylvanus* (AY897212.1); *mfa* = allele in *M. fascicularis (*EF126284.1*)*; *rhL, rhS* = long (AF191557.1) and short (Lesch et al. 1997; Wendland et al. 2006) alleles in *M. mulatta*; *mmzL* and *mmzS*= long (HM114278.1) and short (HM114279.1) alleles in *M. munzala*; *mti* = allele in *M. thibetana* (AY897213.1); *mraL* and *mraS* = long (HM114280.1) and short (HM114281.1) alleles in *M. radiata; msi* = allele in *M. silenus* (HM114282.1).

CHAPTER FIVE

How the cerebral serotonin homeostasis predicts environmental changes: A model to explain seasonal changes of brain 5-HTT as intermediate phenotype of the 5-HTTLPR

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Abstract

Molecular imaging studies with positron emission tomography have revealed that the availability of the serotonin transporter (5-HTT) in human brain fluctuates over the course of the year. This effect is most pronounced in carriers of the short allele of the 5-HTT promoter region (5-HTTLPR), which has in several previous studies been linked to an increased risk to develop mood disorders. We argue that long-lasting fluctuations in the cerebral serotonin transmission, which is regulated via the 5-HTT, are responsible for mediating responses to environmental changes based on an assessment of the expected "safety" of the environment; this response is obtained in part through serotonergic modulation of the hypothalamic-pituitary-adrenal (HPA) axis.

We posit that the intermediate phenotype of the s-allele may properly be understood as mediating a trade-off, wherein increased responsiveness of cerebral serotonin transmission to seasonal and other forms of environmental change imparts greater behavioral flexibility, at the expense of increased vulnerability to stress. This model may explain the somewhat higher prevalence of the s-allele in some human populations dwelling at geographic latitudes with pronounced seasonal climatic changes, while this hypothesis does not rule out that genetic drift plays an additional or even exclusive role. We argue that s-allele manifests as an intermediate phenotype in terms of an increased responsiveness of the 5-HTT expression to number of daylight hours, which may serve as a stable surrogate marker of other environmental factors, such as availability of food and safety of the environment in populations who live closer to the geographic poles.

CHAPTER SIX - General Discussion

In most primate species, males compete intensely for the access to receptive females and relationships among males are therefore commonly characterized by aggressive interactions and intolerance. There is, however, considerable variation among species and some males even cooperate with each other, which is often accompanied by reduced aggressiveness and increased tolerance. Baboons constitute a well suited model to investigate the causes and consequences of such variation as closely related species show variation in different aspects of their social systems, including the intensity of male contest competition and cooperation.

One aim of my thesis was therefore to collect and analyze quantitative and comparable behavioral data from chacma and Guinea baboons, the two species which are considered to be most distinct in male aggressiveness, tolerance, and cooperation (CHAPTER TWO). Another aim was to investigate whether variation in testosterone could be linked to variation in dominance relationships, and whether the distribution of allostatic load of social status, assessed by glucocorticoid levels, differs between species (CHAPTER TWO). Finally, a comparison of genetic polymorphisms, *5-HTTLPR* and *MAOALPR*, among several species of baboons was utilized to investigate the genetic foundation of the behavioral variation (CHAPTER FOUR). These polymorphisms have been previously linked to variation in aggressiveness in other primate species.

Variation in male social relationships between chacma and Guinea baboons

Variation in aggressiveness and spatial tolerance could be confirmed by comparing behavior of male chacma baboons recorded in the Moremi Game Reserve, Botswana, with behavior of male Guinea baboons recorded in the Niokolo Koba National Park in Senegal (CHAPTER TWO). Male chacma baboons were more often involved in agonistic interactions than male Guinea baboons, while male Guinea baboons showed a higher spatial tolerance towards other males and sometimes even exchanged affiliative behaviors. Furthermore, male chacma baboons formed linear hierarchies with highly consistent dominance relationships, while in male Guinea baboons the linearity of hierarchies was generally low. Although in one small party the hierarchy showed a high linearity and some consistent dominance relationships among males were observed.

The observations made during this study are consistent with former reports of the same population of chacma baboons, in which male-male relationships consisted of regular agonistic interactions (e.g. Kitchen et al. 2005, Bergman et al. 2005) and males formed highly linear hierarchies with consistent dominance relationships (e.g. Bulger 1993, Beehner et al. 2006, Bergman et al. 2006). In addition to the Moremi population, several other populations of chacma baboons have been studied during the last decades, for example in the Drakensberg mountains (e.g. Weingrill et al. 2003), in the De Hoop Nature Reserve (e.g. Clark et al. 2008) and on the Cape peninsula in South Africa, or at Tsaobis in Namibia (e.g. Cowlishaw 1995). The most striking observation is that male-male coalitions are apparently absent in all populations of chacma baboons despite considerable variation in habitat, group size, and number of males in a group, and infanticide is a common phenomenon (Henzi & Barrett 2003; for one possible exception with regard to coalitions see Saayman 1971). In addition to data from Moremi, the most comprehensive data on male behavior are available from the Drakensberg Mountains and De Hoop Nature Reserve. Males from both populations have been described as similar to baboons in Moremi concerning male-male competition (e.g. Weingrill et al. 2000, Weingrill et al. 2003, Clark et al. 2008): immigrant males often aggressively challenge alpha males and male-male affiliation is apparently absent. Furthermore, hierarchies seem to be linear and dominance positions unambiguous (though linearity- or consistency-indices are rarely explicitly mentioned). Rank is highly predictive for access to mating partners in all populations of chacma baboons (e.g. Bulger 1993, Weingrill et al. 2000, Beehner et al. 2006), further supporting the view of intense contest competition.

With regard to behavior of male Guinea baboons, data from wild baboons at two different locations within the Niokolo Koba National Park, namely Simenti and Mt. Assirik, have been reported. Data assessed for this study in the Simenti area resembles previous reports from the same study site with regard to male aggressiveness, spatial tolerance, and affiliation (Galat-Luong et al. 2006, Patzelt et al. in revision). Concerning dominance relationships, one previous study at Simenti (Patzelt et al. in revision) indicated, similar to the present study, that male Guinea baboons do not form linear hierarchies, and only some dyads show consistent dominance relationships. Importantly, the present study suggests that consistent relationships were mainly found between reproductively active and non-active males, and the latter were always subordinate (see discussion CHAPTER TWO). Data from Mt. Assirik, about 60 km away from Simenti, also resemble the data of this study, as male-male tolerance was high, and adult males were observed to groom each other (Sharman 1981). With the exception of one study (Patzelt et al. in revision), all of the older data were not derived from focal observations and detailed comparisons are not feasible, but it appears that the population of Guinea baboons in the Niokolo Koba area shows a typical pattern of male-male behavior. Data on male-male behavior observed in the Brookfield Zoo in Chicago (Whitham & Maestripieri 2003) revealed an extremely similar pattern with regard to rates of agonistic interactions, spatial tolerance, and affiliation, though the grooming time among males was much higher (2.5% vs. 0.3% this study). However, the zoo population only consisted of 15 adult males and 25 adult females without any immature individuals. The authors also constructed a dominance hierarchy but they stated that “*If the dominance relationships between two or more males could not be determined unequivocally, these individuals were assigned an average ranking (e.g., the top four males were all ranked as 2.5)*” (Whitham & Maestripieri 2003, p. 850), which strongly suggests a similar pattern with regard to dominance relationships as found at Simenti.

Taken together, the data collected for this study and published data suggest that both species show different patterns of male behavior. It appears that direct contest competition among male chacma baboons is more important than among male Guinea baboons, while behaviors traditionally linked to social bonding only occur among male Guinea baboons.

Proximate mechanisms of behavioral variation

In primates, birds and other vertebrates, levels of the steroid hormone testosterone are associated with male reproductive trajectories, as levels increase during breeding seasons, or, in non-seasonal breeders, during the period of highest mating activity in life (Wingfield et al. 1990, Beehner et al. 2009). The ‘challenge hypothesis’ predicts that during mating or rank competition among males a further increase of testosterone levels promotes aggressive behaviors (birds: Wingfield et al. 1990; primates: e.g. Muller & Wrangham 2004, Beehner et al. 2006). As male reproductive trajectories are assumed to differ between chacma and Guinea baboons, and males of both species vary with regard to aggressiveness, one approach taken here in order to investigate proximate mechanisms underlying behavioral variation was to test the relation between testosterone and age, dominance status, and aggressiveness, respectively (CHAPTER TWO).

By using relative values of testosterone levels for each species in this study, a trend for an interaction between testosterone and species on agonistic rates was observed. This interaction was most likely due to a trend for an effect of testosterone on agonistic rates in chacma baboons while there was no effect in Guinea baboons. The results for chacma baboons replicate previous observations (Beehner et al. 2006) in which testosterone levels were correlated with aggression rates during periods of unstable hierarchies in which aggressive behaviors are important to obtain or defend high ranks. Though the study period for chacma baboons was considered stable using definitions applied previously (e.g. Beehner et 2006), the recent fission of the groups may have had the same effect (see discussion CHAPTER TWO). For Guinea baboons, agonistic behaviors apparently play no obvious role in the competition for mates, which may explain the lack of a correlation between testosterone and expressed agonistic behaviors.

Despite previous results in chacma and yellow baboons showing that testosterone levels of adult males were correlated with age (Beehner et al. 2009), no such correlation in chacma or Guinea baboons could be detected in the present study. Furthermore, correlations between testosterone and dominance status were found in none of the two study species. Previous studies indicated that testosterone levels of male chacma baboons are predictive for the future rank rather than current rank position (Beehner et al. 2006, Bergman et al. 2006). During my data collection period, however, too few rank changes occurred to test this relation. For Guinea baboons, instead of changes in rank positions, changes in the number of females associated with a male may be linked to testosterone levels, though it was not possible to test this statistically as only a few females changed their partners.

Length variability in the genetic polymorphisms *5-HTTLPR* and *MAOALPR* has been previously linked to variation in primate aggressiveness. Therefore, the second approach taken here in order to study proximate mechanisms regulating behavioral variation was to compare these polymorphisms among baboon species (CHAPTER FOUR). Here, genetic samples not only from chacma and Guinea baboons, but from all baboon species with the exception of Kinda baboons were used. Most species were monomorphic and carried the same allele in *5-HTTLPR*, and consequently this polymorphism could not be linked to behavioral variation between species. However, a comparison of *5-HTTLPR* alleles among 19 papionine species (of which 9 were genotyped for this study) revealed interesting insights into the evolution of this polymorphism in Papionini, and variation may be linked to environmental variability (see discussion CHAPTER FOUR, CHAPTER FIVE).

By contrast, *MAOALPR*, the investigated region in the promoter region in the MAOA gene (the so called 'warrior gene'; e.g. McDermott et al. 2009), was highly variable and the distribution of different alleles broadly mapped onto behavioral variation among baboon species. There were, however, some contradictory results from West-African olive baboons and chacma baboons from the Drakensberg area in South Africa making conclusions about the role of this polymorphism in behavioral variation between species premature. Nevertheless, the variability in nucleotide composition found in baboons suggests that further investigations of this locus could be worthwhile.

The MAOA enzyme is not only involved in the 5-HT system, but is also responsible for the metabolization of several other monoamine neurotransmitters, such as noradrenalin or dopamine. Activity of these two neurotransmitter systems has been linked to the expression of aggression in several mammals (e.g. Eichelman et al. 1972, Higley et al. 1992; reviewed e.g. in Haller et al. 1997, Miczek & Fish 2005, Nelson & Trainor 2007). Studies conducted on wild baboons in the Awash National Park in Ethiopia (Jolly et al. 2008, Jolly et al. 2013) showed that adult male hamadryas and olive baboons varied with regard to metabolite levels of noradrenalin and dopamine. Accordingly, behavioral variation among baboon species could be correlated with differences in monoaminergic activity, possibly regulated by *MAOALPR* genotype. The examination of other regions in the *MAOA* and other genes linked to the monoaminergic system in baboons, and the investigation of such polymorphisms within polymorphic populations would be promising to obtain further insights into the genetic foundation of both, inter-individual and interspecific variation in aggressiveness in primates.

In addition to study the causes for variation in aggressiveness, it would be interesting to investigate proximate mechanism promoting affiliative behavior and higher spatial tolerance in male Guinea baboons. In that context, the neuropeptides oxytocin and arginine vasopressin are promising to look at; both of them have been associated with maternal- and general bonding behavior, respectively, in mammals (Curley & Keverne 2005). For instance, in voles (*Microtus* spp.) the density of oxytocin and vasopressin V1a receptors in the brain apparently regulates interspecific variation in pair-bonding behavior (reviewed in Insel et al. 2010). Interestingly, length polymorphisms in promoter regions of the respective receptor genes likely affect the expression of these proteins. Oxytocin levels have also found to be correlated with bonding behavior in cotton-top tamarins (*Saguinus Oedipus*; Snowdon et al. 2010) and in chimpanzees (*Pan troglodytes*; Crockford et al. 2013). Accordingly, the investigations of oxytocin and arginine vasopressin profiles in baboons and interspecific comparisons of genes encoding for respective receptors could reveal further insights about the genetic and physiological basis of variation in affiliation and bonding in primates.

Taken together, the results of my thesis corroborate the assumption that testosterone promotes aggression in male chacma baboons, but there was no correlation in Guinea baboons. A comparison of five species of baboon indicates that *5-HTTLPR* alleles are not linked to behavioral variation. However, *MAOALPR* is highly variable in baboons and the genotype may contribute to interspecific and inter-individual variation in behavior in baboons. Future studies should further investigate this link, but may also examine proximate causes for variation in affiliation and social bonding in baboons, for example by studying genetic variability in oxytocin and arginine vasopressin related genes.

Adaptiveness

Within his social environment, a male chacma baboon may only obtain mating opportunities by aggressively challenging a high ranking male (e.g. Kitchen et al. 2005; see General Introduction, CHAPTER ONE). Even after successful reproduction, some males may need to aggressively defend their offspring against infanticidal immigrants (e.g. Palombit et al. 1997). An aggressive reproductive strategy is accompanied by high potential costs: (i) males risk regular injuries caused by intense fights (chapter 1; Kitchen et al. 2005), (ii) larger males are favored by sexual selection in case of intense contest competition resulting in increased body size dimorphism in primates (Plavcan & van Schaik 1997), which also increases energetic demands (Key & Ross 1999) and (iii) if the acquisition and maintenance of high rank is associated with overt aggression, dominant individuals may also carry high allostatic loads expressed by increased levels of glucocorticoids (Goymann & Wingfield 2004). In two studies on chacma baboons (Bergman et al. 2005, Cheney et al. in preparation), glucocorticoid levels of all males in a group were increased during periods of rank instability and this effect was more pronounced in high ranking individuals. During the present study, dominant individuals had generally higher glucocorticoid levels, which was probably related to the recent fission event of the group (see discussion CHAPTER TWO). Overall, it appears that during stressful events, in which glucocorticoids levels of all males are already strongly increased (Bergman et al. 2005, Cheney et al. in preparation), higher ranking males carry the highest allostatic load. Indeed, subordinate males may show slightly higher levels during stable periods (Bergman et al. 2005, but see Cheney et al. in preparation) when the allostatic load of all individuals is relatively low. However, generally, high ranking chacma baboons may be most strongly affected by the negative deleterious effects of increased glucocorticoid levels (reviewed in Sapolsky 2005). In sum, the prevalent male reproductive strategy in chacma baboons appears to be related to high costs, which may explain that male chacma baboons apparently have a shorter life span than, for example, male yellow baboons (Beehner et al. 2009). Nevertheless, for a male chacma baboon it seems to represent the best, or only, strategy to maximize his reproductive success.

Affiliation and high spatial tolerance among males, as observed in Guinea baboons, is usually rare among primates and has been interpreted as the expression of social bonds (van Hooff & van Schaik 1994). Bonds are, moreover, also characterized by cooperative behaviors and first observations on Guinea baboons showed that dyadic affiliation rates were positively correlated with the number of support events (Patzelt et al. in revision). Whether such relationships among males also meet other criteria usually applied to define a bond, including its temporal stability, balanced gives and takes, and strong in comparison to other relationships (Ostner & Schuelke 2014), remains to be investigated. Previous observations also suggested that Guinea baboon parties regularly include closely related dyads but kinship was not predictive for interaction patterns (Patzelt et al. in revision); however, male philopatry within the community may generally favor more tolerance and cooperative relationships. Further research is required to investigate the consequences of cooperative relationships with regard to access to receptive females, and, in the long term, for reproductive success.

Despite engaging in cooperative behaviors males could fiercely fight each other leading to the further question why male Guinea baboons show lower rates of agonistic behavior. The analysis of agonistic interactions among reproductively active male Guinea baboons revealed little about their dominance relationships, and this was supported by the observations that derived dominance ranks did not correlate with glucocorticoid levels (CHAPTER TWO). It is, however, likely that the access to females is regulated by other, more subtle, mechanisms, which could replace overt agonistic interactions. The same question has been discussed for male hamadryas baboons, in which leader males are dominant over followers (Colmenares 1991, Kummer 1995), while among leader males no clear dominance relationships could be detected (e.g. Romero & Castellanos 2010). For a male hamadryas baboon, a fight can result in the loss of one or more of his females (Swedell 2006), and the deaths of dependent infants (Swedell & Tesfaye 2003) which may explain the ‘respect’ of ownership described in this species (Kummer 1974). A single fight may therefore end his reproductive career and significantly diminish the number of already produced offspring. The non-agonistic negotiation of dominance relationships (or whatever factor is regulating access to females), might therefore be extremely important. Ritualized greeting behavior has been suggested to represent one such mechanism in hamadryas baboons (e.g. Colmenares 1991). Furthermore, manes could function as honest signals to indicate ‘condition and durability’ of a male (Jolly 2007) similar to the mane of male lions (*Panther leo*; West & Packer 2002). Finally, male hamadryas baboons often present their red buttocks during greetings and the color could represent an honest signal of competitive ability (Jolly 2007) as suggested for the redness of the chest patches in male geladas (*Theropithecus gelada*; Bergman et al. 2009) or the facial redness of male mandrills (*Mandrillus sphinx*; Setchell et al. 2008). Interestingly, testosterone levels of male mandrills were found to be correlated with their facial redness.

In Guinea baboons the relatively long lasting associations between males and females (often several months or years) are not characterized by a strong spatial cohesiveness, and there are no reports on infanticide, which indicates that overt agonistic interactions would not have the same consequences for a male as in hamadryas baboons. The low rate of agonistic interactions, however, indicates that in Guinea baboons there might also be alternative mechanism regulating the access to mating partners and other resources. It seems that there are slight individual differences in the color of buttocks and the appearance of manes - though much less pronounced than in hamadryas baboons - and this variation could reveal some information about the condition of a male. Furthermore, the regular greetings between males may also function to negotiate relationships.

Finally, relative canine size is reduced in primate species that form coalitions (Plavcan et al. 1995) suggesting that contest competition is generally reduced when cooperative strategies are available. Relative canine size is also reduced in male Guinea baboons compared male chacma baboons (Patzelt 2013), and likewise, selection pressures could have reduced the motivational disposition to act aggressively. Because of the high potential costs of aggressive strategies (see above), selective pressures may act strongly against traits favored by contest competition, like canines and aggressiveness, once cooperative strategies become an option.

Taken together, an aggressive reproductive strategy seems to be the best way for a male chacma baboon to maximize his reproductive success despite the high costs of this strategy. Male Guinea baboons may have more relaxed and cooperative relationships, though there will be still competition over females and other resources. Males may employ cooperative behaviors and subtle interactions to negotiate this, or they may have evolved honest signals to show their quality and competitive ability to others, but this needs to be investigated.

Evolutionary scenarios

Peter Henzi and Louise Barrett (2003, 2005) provided two comprehensive reviews on socio-ecological attempts to explain the variation in baboon social systems, and they stressed some inconsistencies between predictions made by these models and observed variation. Previous models were centered on the behavior of typical ‘savanna’ baboons and derived the conspicuous social organization of hamadryas baboons from this template. Henzi and Barrett pointed out that behavior of chacma baboons could actually not be derived from the typical savanna baboon template and suggested that chacma baboons as well show distinct social reaction norms. They proposed that variation in historical ecological conditions between different species of savanna baboons may have brought about these differences.

The starting point of the Henzi-Barrett scenario is the assumed split of different baboon lineages in southern Africa about 2 mya (Newman et al. 2004, Zinner et al. 2013b), which concurred with a global decrease in temperatures and rainfall, as well as a low habitat productivity (see Henzi & Barrett 2003, Henzi & Barrett 2005 and references therein). Under such conditions, contemporary chacma baboons form smaller and more-female biased groups. Henzi and Barrett suggested that ‘ancestral chacma baboons’ were adapted to the social life in such groups. Under the assumption that baboons were already non-seasonal breeders a single male may have monopolized most of the matings resulting in a high paternity certainty. Such conditions made infanticide a beneficial tactic for immigrated males, while the small number of males and high paternity certainty made concerted actions of multiple resident males against infanticidal immigrants unlikely. This created the need for counterstrategies, including ‘friendships’ between lactating females with the putative father (Palombit et al. 1997, Moscovice et al. 2010) or the engagement of females in proactive promiscuity (e.g. by soliciting several males for copulations) to decrease the paternity certainty (Henzi & Barrett 2003). Dominant males, however, acted against promiscuity by forming long lasting consortship and herding of females during group encounters as seen in contemporary chacma baboons (Henzi & Barrett 2003).

Current climatic conditions of many chacma baboon populations are still less productive than of olive or yellow baboon habitats (Henzi & Barrett 2005), but in some ‘good’ habitats, for example Moremi, groups contain a large number of males (Cheney & Seyfarth 2007). Male-male coalitions could therefore be advantageous, especially for subordinate males, but following the authors they may have never acquired the ability to do so: *“Put simply, male chacma baboons are not predisposed to interact with other males, or to respond to any interaction, in a manner that leads to cooperative behaviour.”* (Henzi et al. 1999, p. 241).

Following the scenario described above, the ancestors of olive and yellow baboons dispersed in more productive habitats, where they could form larger groups with more balanced sex ratios (Henzi & Barrett 2003). The large number of females resulted in overlapping periods of receptivity, which decreased the ability of a dominant male to monopolize receptive females. Furthermore, the larger number of males facilitated the evolution of cooperative strategies to take over consortships which in turn became shorter. As a result, paternity certainty decreased, and thus, males within the group had less inclination for infanticide while more males would aggressively protect infants against infanticidal immigrants. Friendships lost their initial importance but evolved into a male tactic to increase future mating opportunities as suggested for olive baboons (Strum 1982, Smuts 1985).

Henzi and Barrett (2003) directly derived the behavior of hamadryas baboons from the ancestral chacma baboon pattern described above. The harsh ecological conditions of north-eastern Africa and Arabia resulted in even smaller and more female-biased groups, with increased paternity certainty, and therefore higher risk of infanticide. This made it more beneficial for a male to permanently associate with his females and offspring rather than to pursue additional reproductive opportunities. As a consequence, assuring paternity became even more important which led to the evolution of the typical male herding behavior seen in hamadryas baboons (Kummer 1968). Finally, the ‘respect’ of ownership (Kummer 1974) and peaceful strategies to obtain females (Pines et al. 2011) evolved due to the high potential costs of fights (loss of females and offspring).

As data about social behavior from Guinea baboons were relatively scarce, Henzi and Barrett did not include the species into their hypothesis. Based on their scenario for chacma, olive, and yellow baboons, Clifford Jolly proposed his ‘frontier hypothesis’ which included Guinea baboons and disagreed with Henzi and Barretts hypothesis for the evolution of the hamadryas baboon society (Jolly 2007, Jolly 2009, Jolly, unpublished manuscript). Based on mitochondrial data, he assumed that baboons rapidly expanded from southern Africa northward into baboon-free territories which could have favored the evolution of male philopatry (Jolly 2009). During range expansion, neighboring groups were few and - especially in case that the frontier expanded in a ‘fanning out’ fashion - relatively distant, which made emigration more costly and favored those males who tend to remain in their natal-group. Jolly further argued that the propensity of a male to delay his emigration may have a genetic basis, which has been suggested for some primates (e.g. in rhesus macaques: Trefilov et al. 2000), and given a modest reduction of availability of neighboring groups, such a transformation could occur within a few (20-100) generations. The tendency for male philopatry would even be enforced (and after expansion maintained) by the concerted defense of males against ‘would-be immigrants’ (Jolly 2009), which also facilitated cooperation and enhanced tolerance among males. The formation of large groups was facilitated by the occupation of baboon-free areas which, in turn, attenuated the risk of inbreeding. During periods of poor ecological conditions, the maximum size for efficient foraging groups were diminished and, as a result, groups split up during the day to forage. In order to maintain the critical size of a breeding group, however, the subgroups maintained social contacts, for example at sleeping sites, which led to the well-known multi-level systems of hamadryas (Schreier & Swedell 2009) and Guinea baboons (Sharman 1981, Patzelt et al. in revision).

While Jolly assumed that Guinea baboons are probably more similar to these frontier populations, the hamadryas society came about after entering into the harsh ecological conditions of semi-deserts (Jolly, unpublished manuscript). This favored even smaller and more cohesive foraging units which evolved into polygynous reproductive units with intense herding behavior of males. Due to the high risk of fights for hamadryas leader males, they developed non-agonistic mechanisms to negotiate dominance relationships (i.e. greetings, manes, and red buttocks; see above), the ‘respect’ of ownership (Kummer 1974), and non-agonistic tactics, mainly ‘following’, to obtain access to mating partners (Pines et al. 2011). However, even in Guinea baboons which show less cohesive subgroups, the small testis size indicates a low degree of sperm competition (Patzelt 2013) and therefore a high degree of polygyny. This suggests that also in male Guinea baboons, a non-agonistic mechanism (e.g. greetings, manes) could have evolved to regulate the access to mating partners, and there is some sort of 'respect' of ownership. In both species, the large size of social groups made honest signals and non-agonistic interactions to negotiate social relationships even more important as many individuals would not be entirely familiar with each other (Jolly 2007).

Taken together, the behavior of contemporary chacma baboons was interpreted as adapted to small groups with male dispersal, in which one or few males monopolize most of the matings resulting in a high paternity certainty, high risk of infanticide, and associated counter-strategies (Henzi & Barrett 2003, Henzi & Barrett 2005). Even if demographic situations would allow cooperative behavior among present-day male chacma baboons, they do not form coalitions as their behavior is adapted to a single-male competition strategy. According to Jolly, the evolution of rather relaxed dominance relationships among male Guinea baboons and the (potential) formation of male bonds was mainly driven by male philopatry which occurred at the 'frontier' during range expansion of baboons (Jolly 2007, Jolly 2009, Jolly, unpublished manuscript). The frequency and intensity of overt aggressive interactions could have been further attenuated by the evolution of non-agonistic mechanisms to negotiate dominance relationships, and non-agonistic tactics by young males to obtain access to mating partners.

These scenarios are highly hypothetical and especially the lack of male coalitions in large groups of chacma baboons remains puzzling. Henzi and Barrett base their assumption on presumed historical ecological conditions which may have caused phylogenetic constraints on cooperative behaviors in male chacma baboons. It is without doubt that social style may show a phylogenetic signal (e.g. reviewed in Thierry 2013). However, it also would be promising to investigate variation in other factors that may explain the difference in male cooperation among contemporary chacma, olive, and yellow baboons. For example, the duration of the breeding season, average inter-birth interval, reliability of female fertility signals, and group size are thought to affect the potential for male contest competition, which is assumed to determine whether male cooperative behaviors are beneficial (reviewed in Ostner & Schülke 2014). Different species of savanna baboons may show subtle variation in one or more of these factors, which may also cause the absence of coalitions in male chacma baboons.

When Jolly proposed his 'frontier' hypothesis (Jolly 2007), data on both individually identified males and dispersal patterns of Guinea baboons were not yet available. Since then, several of his assumptions can be confirmed: data from several 'communities' indicated that male Guinea baboons are indeed philopatric (Kopp et al. under review), and, more specifically, closely related males sometimes remain within the same 'party' (Patzelt et al. in revision). Quantitative data collected during my thesis confirm that male social relationships are indeed more relaxed in Guinea than in chacma baboons. In sum, these observations further support the view that male baboons show a gradient in social behavior associated with variation in male philopatry, and this transition may potentially have evolved due to demographic effects during the historical dispersal of the genus.

Conclusion & Outlook

Based on behavioral observations, we could confirm the assumption that male chacma baboons in the Okavango Delta and male Guinea baboons in the Niokolo Koba differ considerably in aggressiveness, spatial tolerance, and characteristics of their dominance relationships. Overall, the intensity of male contest competition appeared to be higher in chacma than in Guinea baboons. This variation presumably holds for other populations of chacma and Guinea baboons as well, though observations on other wild populations of Guinea baboons are still lacking. In Guinea baboons, cooperative tactics and other factors than overt aggression may regulate access to females. For instance the function of greetings is not well understood but may be a promising factor to consider in further studies.

Testosterone levels did not correlate with age category or dominance status. Long-term data on Guinea baboons will be needed to confirm the assumption that males have a longer tenure, and to test whether differences in male reproductive trajectories between Guinea and other baboon species are associated with patterns of testosterone levels. With regard to the relation between testosterone and dominance position, it would be interesting to know whether testosterone levels are predictive for changes in the number of females a male can monopolize, similar to the effect of testosterone on future rank in chacma baboons.

Concerning the link between testosterone and aggressiveness, there was a trend that testosterone levels of male chacma baboons correlated with expressed agonistic behaviors, but no correlation was present in Guinea baboon. This confirms previous observations that testosterone promotes agonistic behaviors in chacma baboons. In Guinea baboons, agonistic behaviors apparently represent no major factor in mate competition which may explain the lack of a correlation with testosterone levels, though future studies need to confirm these results.

The lack of genetic variability in *5-HTTLPR* between different species of baboons indicate that this polymorphism is not linked to interspecific variation in behavior. However, an investigation of this locus among 19 papionine species revealed that variation in this locus may have occurred in macaques after their dispersal into Asia, though the functional consequences of these new alleles remain to be investigated.

The variability of *MAOALPR* among baboons implies that this polymorphism may underlie behavioral variation among baboons through regulation of monoaminergic activity. A further investigation of the relationships between genetic variability, monoaminergic neurotransmitter functioning and behavior in baboons could therefore be promising to obtain more insight into the genetic foundation of variation in aggressiveness in primates.

Finally, the correlation between dominance rank and glucocorticoid levels could be confirmed in chacma baboons and high ranking males carried a higher allostatic load. No correlation was found in Guinea baboons which could be caused by the lack of the importance of dominance positions in that species, or by the fact that such positions are not derivable from obvious agonistic interaction, such as supplants, as in other baboon species. By identifying the mechanisms that regulate the access to females in Guinea baboons, it could be tested whether these factors affect the allostatic load of males.

In conclusion, with my thesis I provide first data about the differences in several characteristics of dominance relationships between male chacma and Guinea baboons. There were some indications that these may be linked to testosterone levels, and that they moreover have repercussions for the distributions of allostatic load of social status as assessed by glucocorticoids. Furthermore, variation in *MAOALPR* within and between different species of baboons suggests that the activity of this gene may be linked to the observed behavioral variation in baboons. Future examinations of the effect of different alleles on neurotransmitter levels and behavior in polymorphic populations of baboons may reveal further insights into the genetic foundation of variation in aggressiveness in primates. I suggest that future studies should investigate the mechanisms regulating the access to receptive females in Guinea baboons in relation to physiological parameters as this may further improve our understanding of causes and mechanism of variation in male aggressiveness and tolerance among primate males.

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