The Social System of Guinea Baboons (*Papio papio*) With a Focus on Male-Male Relationships

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TABLE OF CONTENTS

SUMMARY

Understanding the driving forces in human social evolution is still a major aim in anthropological and primatological research. Baboons (*Papio* spp.) have traditionally served as a model in this context. Originating in southern Africa, during the Pleistocene members of the genus dispersed into large parts of sub-Saharan Africa and the southwestern part of the Arabian Peninsula. Guinea baboons (*P. papio*) constitute the northwestern and hamadryas baboons (*P. hamadryas*) the northeastern extreme of this dispersion. While most baboon taxa have been well studied, comparable data on Guinea baboons were missing as quantitative data from wild animals were absent. So far two types of social systems have typically been distinguished in baboons; female-bonded multi-male multi-female groups in the so- called ´savanna´ baboons (*P. anubis*, *P. cynocephalus* and *P. ursinus*), and multi-level societies based on one-male units (OMUs) in hamadryas baboons. Prior to this study, Guinea baboons were thought to show some similarities to the hamadryas baboon system, as previous observations indicated a multi-level organization. However, males were described as being exceptionally tolerant of one another, suggesting that their social system is unique among baboons. Concerning the characteristics of male behavior in the genus *Papio*, some authors introduced the idea of an evolutionary trend*,* with an increasing disposition for male philopatry and male-male tolerance and coalition formation along a south-to-north gradient according to the genus' dispersal pattern over the African continent. Due to their position at the frontier of the northwestern distribution, comparable data on the characteristics of male-male relationships in Guinea baboons are essential to test that assumption.

In my thesis I studied the social system of Guinea baboons with a focus on males, in order to investigate whether males influence aspects of the species` social system in a comparable way to that seen in hamadryas baboons. This focus moreover allowed testing of whether male Guinea baboons would fit into the above mentioned south-to-north gradient, according to which baboon males in northern species are expected to be more tolerant and cooperative among each other. Since kinship is predicted to have an important impact on social interaction patterns (*kin selection hypothesis*) and has been suggested to structure male- male relationships in hamadryas baboons, I furthermore investigated whether genetic relatedness correlates with spatial and social interaction patterns among Guinea baboon males. This is the first study on social behavior of Guinea baboons which is largely based on data of individually recognized subjects in their natural habitat.

Initially, we observed unhabituated members of the population (*community*) ranging next to our field site and recorded subgroup sizes and compositions at a water source. Spatial grouping patterns of unidentified individuals suggested a complex social organization with very variable group composition, on both, a daily and a seasonal basis. After completion of habituation of two subgroups, we investigated spatial association patterns among individually recognized adult males. To do this we used cluster analyses based on association frequencies calculated from Global Positioning System (GPS) data, as well as proximity measures from focal observations. Finally, male-male interaction patterns were studied in detail and related to spatial grouping patterns to investigate how male relationships are linked to their social organization. To examine whether kinship plays a role in shaping the Guinea baboon social system, we genotyped several adult males within the study community and correlated genetic relatedness to spatial association and social interaction patterns, respectively.

The results obtained from this study indicate a three-level social organization: *parties* consist of 3 or 4 males (plus several females and immatures) and seem to constitute the core unit of the society, as most social interactions, close bonding and coalition formation among adult males takes places at this level. Two or three *parties* may form a *gang* within which males were more related to each other than males belonging to different *gangs*. Social interactions were generally restricted to the *gang*-level. The *community* constitutes the next level and refers to all individuals sharing the same home range. We could not confirm that Guinea baboons show distinct OMUs as the smallest organizational units comparable to hamadryas baboons. However, we do not yet know how paternities are distributed among males.

Based on an analysis of social interaction patterns in combination with genetic networks, we found that strong bonds and high tolerance exists among male Guinea baboons within and between *parties*, regardless of kinship. Males thus seem to contribute actively to the cohesion of *gangs* and play an important role in the maintenance of the multi-level society they live in. Furthermore, rates of affiliation among adult males were far higher than reported for other baboon taxa. In concordance with this observation, a comparison of body measurements to those of other baboon taxa revealed that traits associated with intra-sexual competition were clearly reduced in male Guinea baboons. Thus, the social relationships of male Guinea baboons appear to differ strikingly from those of other members of the genus.

In conclusion, this study highlights the diversity of baboon social systems, in particular with regard to the quality of male-male relationships, and strongly supports the assumption that the genus encompasses at least three, rather than two, different types of social system. While the multi-level organization is superficially similar to the hamadryas system, it is unique with regard to the frequency of affiliative interactions among males. The results corroborate the supposed south-to-north gradient of a decrease in male despotism and an increase in male-male coalition formation, and thus indicate the importance of including the phylogeny and historical environments of a species, in addition to current ecological factors within the study of social evolution.

ZUSAMMENFASSUNG

Paviane (*Papio* spp.) gelten als wichtiges Modell für die Evolution menschlicher Sozialsysteme. Im Pleistozän hat sich die Gattung *Papio* ausgehend vom südlichen Afrika über große Teile Afrikas südlich der Sahara sowie Teile der Arabischen Halbinsel ausgebreitet, wobei Guineapaviane (*P. papio*) die nordwestlichsten und Mantelpaviane (*P. hamadryas*) die nordöstlichsten Gebiete besiedeln. Im Vergleich zu anderen Pavianarten, deren Ökologie und Sozialsystem seit vielen Jahrzehnten umfangreich untersucht werden, waren zu Guineapavianen bisher nur wenige und zudem widersprüchliche Kenntnisse vorhanden. Dies ist vor allem darauf zurückzuführen, dass von ihnen quantitative Freilanddaten fehlten. Bisher wurden für Paviane zwei Typen von Sozialsystemen beschrieben: Die sogenannten *Savannenpaviane* (*P. anubis, P. cynocephalus* und *P. ursinus*) im südlichen und östlichen Afrika leben in Gruppen mit mehreren Männchen und mehreren Weibchen, wobei Netzwerke nahverwandter Weibchen den sozialen Kern bilden. Mantelpaviane in Nordost-Afrika und Arabien leben dagegen in einer mehrschichtigen Gesellschaft, in denen Ein-Mann-Gruppen die kleinste soziale Einheit darstellen. Ergebnisse früherer Studien an Guineapavianen deuteten darauf hin, dass ihre Gesellschaft auch mehrschichtig ist, ähnlich der von Mantelpavianen. Allerdings wurden Guineapavianmännchen als untereinander außergewöhnlich tolerant beschrieben, was zu der Vermutung führte, dass ihr Sozialsystem innerhalb der Gattung *Papio* einzigartig ist.

Zudem scheinen Männchen verschiedener Pavianarten bezüglich der Konsistenz ihrer Hierarchien, der Häufigkeit von Koalitionsbildung und Infantizidrisiko zu variieren. Diese Beobachtung führte zu der Vermutung, dass im Zusammenhang mit der Ausbreitung der Gattung über den afrikanischen Kontinent entlang eines Süd-Nord-Gradienten eine Evolution hin zu mehr Toleranz und Koalitionensbildung zwischen Männchen stattgefunden hat. Da Guineapaviane an der nordwestlichsten Grenze des Verbreitungsgebietes der Gattung leben, ist hier eine Charakterisierung der Beziehungen zwischen Männchen wichtig, um diese Annahme zu überprüfen.

In meiner Dissertation habe ich verschiedene Aspekte des Sozialsystems der Guineapaviane untersucht. Dabei habe ich mich im Besonderen auf Männchen fokussiert, um zu prüfen, ob diese eine ähnlich einflussreiche Rolle in ihrer Gesellschaft einnehmen, wie es bei Mantelpavianmännchen beobachtet wird. Der Fokus auf Männchen erlaubte außerdem den angenommenen Süd-Nord-Gradienten bezüglich der Qualität der Beziehungen zwischen Männchen zu testen. Demnach sollten Guineapavianmännchen als Angehörige einer nördlichen Art im Vergleich zu südlicheren Arten toleranter und kooperativer untereinander sein. Da allgemein angenommen wird, dass Verwandtschaft einen bedeutenden Einfluss auf soziale Interaktionsmuster haben kann (Verwandtenselektion) und auch in sozialen Interaktionen zwischen Mantelpavianmännchen eine wichtige Rolle spielt, habe ich darüber hinaus geprüft, ob genetische Verwandtschaft die räumlichen und sozialen Interaktionsmuster von Guineapavianmännchen erklären kann. Meine Studie ist die erste über Guineapaviane, die überwiegend auf quantitativen Daten zum Sozialverhalten individuell bekannter Tiere in ihrem natürlichen Lebensraum basiert.

Zu Beginn des Projektes haben wir nicht habituierte Guineapaviane untersucht, die zu einer Population (*Community*) von Tieren gehören, deren Streifgebiet sich in der Nähe unserer Feldstation im Niokolo Koba Nationalpark im Senegal befindet. Dazu notierten wir die Größe und Zusammensetzung von Untergruppen an einer Wasserstelle. Es zeigte sich, dass diese Untergruppen je nach Tages- und Jahreszeit sehr variabel in ihrer Größe sowie der Zusammensetzung verschiedener Geschlechts- und Altersklassen waren. Nachdem wir zwei Untergruppen habituiert hatten und die Tiere individuell unterscheiden konnten, wurden anhand räumlicher Daten von mit GPS-Sendern ausgestatteten Tieren sowie mit Hilfe von Verhaltensbeobachtungen soziale Interaktionen und räumliche Assoziationen zwischen adulten Guineapavianmännchen untersucht. Um den Einfluss von Verwandtschaft auf das Sozialsystem zu prüfen, haben wir zudem mehrere adulte Männchen aus der untersuchten *Community* genotypisiert und genetische Verwandtschaft mit räumlichen Gruppierungs- bzw. sozialen Interaktionsmustern in Bezug gesetzt.

Die Ergebnisse meiner Arbeit deuten darauf hin, dass die soziale Organisation der Guineapaviane mindestens drei Ebenen umfasst: Sogenannte *Parties* bestehen aus drei oder vier adulten Männchen (plus mehrere Weibchen und deren Jungtiere). Innerhalb dieser Ebene fand der Großteil der Interaktionen statt und es wurden enge soziale Bindungen sowie Koalitionen zwischen Männchen beobachtet. *Parties* scheinen daher die zentrale Einheit der Guineapaviangesellschaft zu bilden. Zwei oder drei *Parties* formen eine *Gang*, innerhalb derer die Männchen enger miteinander verwandt waren als Männchen verschiedener *Gangs*. Allgemein waren soziale Interaktionen auf die Ebene der *Gang* beschränkt. Die *Community* stellt die dritte Ebene dar und umfasst alle Individuen, die im gleichen Streifgebiet leben. Im Unterschied zum Mantelpaviansystem scheinen daher Ein-Mann-Gruppen bei Guineapavianen keine Organisationseinheit darzustellen, wobei wir über die Verteilung von Vaterschaften noch keine Aussagen machen können.

Die Analyse sozialer Interaktionsmuster in Bezug auf Verwandtschaft ergab, dass Guineapavianmännchen unabhängig von Verwandtschaft starke kooperative Bindungen miteinander eingehen und sehr tolerant sind, sowohl innerhalb als auch zwischen *Parties*.

Männchen scheinen also aktiv zum Zusammenhalt der *Gangs* beizutragen und spielen daher eine wichtige Rolle in der Erhaltung der mehrschichtigen Gesellschaft in der sie leben. Außerdem interagieren Männchen weitaus häufiger freundlich miteinander als bei anderen Pavianarten. Im Einklang damit zeigt ein Vergleich von Körpermaßen innerhalb der Gattung, dass bei Guineapavianmännchen Merkmale reduziert sind, welche mit intrasexueller Konkurrenz in Verbindung gebracht werden. Die sozialen Beziehungen zwischen Guineapavianmännchen scheinen demnach entscheidend von denen der Männchen anderer Pavianarten abzuweichen.

Zusammengefasst belegt meine Studie, dass die Vielfalt von Sozialsystemen bei Pavianen, insbesondere die Variation in der Qualität der Beziehungen unter Männchen, größer ist als bisher angenommen. Die Gattung umfasst demzufolge vermutlich mehr als zwei, und mindestens drei, verschiedene Typen sozialer Systeme. Während die mehrschichtige Organisation der Guineapaviane oberflächlich dem Mantelpaviansystem ähnelt, unterscheiden sich die sozialen Beziehungen zwischen Guineapavianmännchen bezüglich der Intensität und Häufigkeit freundlicher Interaktionen auffallend von denen anderer Mitglieder der Gattung *Papio*. Diese Beobachtungen passen zu einem angenommenen Süd-Nord-Gradienten hinsichtlich einer erhöhten Häufigkeit von Koalitionsbildungen und einer gesteigerten Toleranz zwischen Männchen und betonen somit einmal mehr, dass es wichtig ist, die Stammesgeschichte und historischen Umweltbedingungen der untersuchten Arten neben derzeitigen Umweltbedingungen in die Untersuchung sozialer Evolution einzubeziehen.

RÉSUMÉ

Parvenir à comprendre les forces motrices de l'évolution sociale chez l'humain reste un enjeu majeur de la recherche anthropologique et primatologique. Les babouins (*Papio* spp.) ont traditionnellement joués un rôle de modèle dans ce contexte. Apparus au Sud de l'Afrique, durant le Pléistocène, les membres de ce genre se sont dispersés sur une grande partie de l'Afrique sub-saharienne ainsi que de la péninsule Arabe. Les babouins de Guinée (*P. papio*) au Nord-Ouest et les babouins hamadryas (*P. hamadryas*) au Nord-Est représentent les limites géographiques de cette dispersion. Alors que les babouins des savanes (*P. anubis*, *P. cynocephalus* et *P. ursinus*) ainsi que les hamadryas ont été étudiés en détails, les mêmes données étaient absentes pour le babouin de Guinée. Jusqu'à présent, deux formes de systèmes sociaux étaient traditionnellement différenciés chez les babouins: les groupes multimâles multifemelles, liés par des réseaux de femelles apparentées, pour les babouins des savanes et les sociétés à plusieurs niveaux dont l'unité de base est le harem (un mâle entouré de quelques femelles et des juvéniles) chez les babouins hamadryas. Avant cette étude, les babouins de Guinée étaient considérés comme socialement proches des babouins hamadryas, car des observations précédentes semblaient indiquer la présence d'une organisation à plusieurs niveaux.

Toutefois, les mâles ont été décrits comme étant extrêmement tolérant les uns envers les autres, suggérant un système social unique parmi les babouins. Concernant les caractéristiques du comportement des mâles du genre *Papio*, certains auteurs ont émis l'idée d'une tendance évolutive vers une propension croissante de philopatrie masculine, de tolérance entre mâle et de formation de coalitions, le long d'un gradient Sud-Nord qui suit le schéma de dispersion de ce genre au travers de l'Afrique continentale. En raison de leur positionnement à la limite Nord-Ouest de cette distribution, des données caractérisant les relations mâle-mâle des babouins de Guinée sont essentielles pour tester cette hypothèse.

Pour ma thèse, j'ai étudié le système social des babouins de Guinée, en me concentrant plus spécifiquement sur les mâles, afin de vérifier s'ils influencent certains aspects du système social de cette espèce de façon comparable à ce qui se passe chez les babouins hamadryas. De plus, cette focalisation a permis de tester si les babouins de Guinée mâles s'inscrivaient au sein du gradient Sud-Nord précédemment mentionné, qui prédit que les mâles des espèces septentrionales seraient plus tolérants et coopératifs les uns envers les autres. Puisque les liens de parentés sont considérés comme ayant un impact important sur les interactions sociales (*kin selection hypothesis*), j'ai aussi testée si la parenté génétique corrélait avec les interactions sociales et les modèles spatiaux entre babouins de Guinée mâles. C'est la première étude sur les comportements sociaux des babouins de Guinée essentiellement basée sur des données récoltées à partir de sujets individuellement reconnus, dans leur habitat naturel.

Initialement, nous avons observé les membres d'une population (*community*) non-habitués à l'homme, évoluant près de notre terrain d'étude, et avons enregistré la taille et la composition des sous-groupes à un point d'eau. Le schéma de distribution spatiale d'individus non-identifiés suggérait une organisation sociale complexe, avec des groupes de composition très variables aussi bien sur une échelle quotidienne que saisonnière. Après avoir réussi à habituer deux sous-groupes, nous nous sommes intéressés aux associations spatiales entre les mâles adultes individualisés. Pour ce faire, nous avons réalisé des analyses de partitionnement de données (*cluster analysis*) basées sur des fréquences d'association calculées à partir de données GPS (*Global Positioning System*) ainsi que des mesures de proximité obtenues par observations focales. Enfin, les interactions mâle-mâle ont été étudiées en détail et rapportés aux groupement spatiaux pour déterminer de quelles façons les relations inter-mâles étaient liées à l'organisation sociale.

Les résultats de cette étude démontrent une organisation sociale sur trois niveaux : les *parties* consistent en 3 ou 4 mâles (accompagnés de plusieurs femelles et juvéniles) et semblent former l'unité de base de la société puisque la plupart des interactions sociales, la formation de liens affectifs proches et de coalitions entre mâles adultes, se déroulent à ce niveau. Deux ou trois *parties* peuvent former un *gang*, au sein duquel les mâles sont plus apparentés les uns aux autres qu'aux mâles de différents *gangs*. Le nombre d'interactions sociales au niveau des *gangs* est assez restreint. La *community* constitue le niveau supérieur et renvoie à tous les individus partageant un même domaine vital. Nous n'avons pas pu confirmer l'existence de harems distincts, supposées former la plus petite unité d'organisation sociale, chez le babouin de Guinée contrairement à ce qui a été observé chez les babouins hamadryas. Cependant nous n'avons actuellement pas d'information concernant le succès reproducteur de chaque mâle.

De plus, en se basant sur l'analyse des interactions sociales combinées aux réseaux génétiques, nous avons pu déterminer que des liens forts et une haute tolérance existent entre les babouins de Guinée mâles au sein et entre les *parties*, indépendamment de leur affiliation. Les mâles semblent donc contribuer activement à la cohésion des *gangs* et jouent un rôle important dans le maintien des divers niveaux de leur société. Le taux d'affiliation entre mâles est beaucoup plus élevé que ce qui est observé pour les autres espèces de babouins. En accord avec ces observations, une comparaison des mesures corporelles entre les différentes espèces du genre *Papio* a montré que les traits physiques associés à la compétition sexuelle intra-sexe sont clairement réduits chez les babouins de Guinée mâles. Il semble donc que les relations sociales de ces babouins diffèrent étonnement de celles des autres membres de ce genre.

En conclusion, cette étude souligne la diversité des systèmes sociaux chez les babouins et, en particulier, la variation importante de qualité des relations mâle-mâle et apporte un soutien important à l’hypothèse que le genre possède au moins trois, plutôt que deux, types de systèmes sociaux différents. Bien que l’organisation à plusieurs niveaux est superficiellement similaire au système hamadryas, elle est unique au regard des relations entre mâles. Ces résultats renforcent l’hypothèse d’un gradient Sud-Nord de diminution du despotisme des mâles et d’augmentation de la formation de coalition entre mâles. Ils indiquent ainsi l’importance d’inclure la phylogenèse et l’environnement historique d’une espèce, en plus des facteurs écologiques actuels, pour l’étude de l’évolution sociale.

CHAPTER 1 – General Introduction

Primates display a large diversity of social systems (Kappeler & van Schaik 2002) with human societies representing the most complex of all primate social systems (Chapais 2011; Hill *et al*. 2009). Understanding the driving forces that shaped the differentiation of primate social systems is still a major aim in primatological and anthropological research. Since most evolutionary processes cannot be observed directly and archeological evidence is scarce (Jolly 2001), comparative studies on human hunter-gatherer societies and on non-human primates seem to be the most promising for investigating human social evolution (Boyd & Silk 2006; Chapais 2011; Potts 1987; Rodseth *et al*. 1991; Strum & Mitchell 1987). Baboons (*Papio* spp.) have traditionally served as a model in this context (e.g. de Vore & Washburn 1963; Jolly 2001). However, while most baboon taxa have been well studied, comparable data on Guinea baboons (*P. papio*) have been missing. In baboons, two major social systems have typically been distinguished: firstly, the female-bonded multi-male multi-female groups in ´savanna baboons´ (*P. anubis*, *P. cynocephalus* and *P. ursinus*) and, secondly, the multi-level social organization based on one-male units (OMUs) in hamadryas baboons (*P. hamadryas*; also referred to as ´desert´ baboons [Jolly 2007]). In my thesis, I investigated parts of the social system of Guinea baboons. I focused on male-male relationships for two reasons; regarding their multi-level structure and the characteristics of male–male relationships, Guinea baboons supposedly show some similarities to the hamadryas baboon society (Galat-Luong *et al*. 2006; Jolly 2007), which is described as “extreme male-dominated” (Swedell 2002; see also Kummer 1995). Moreover, there appears to be an evolutionary trend in the genus *Papio,* with an increasing disposition for male philopatry and male-male tolerance and coalition formation along a south-to-north gradient according to the genus’ dispersal pattern over the African continent (Jolly 2007, 2009, see also Henzi & Barett 2003, 2005). As Guinea baboons represent one of the northern extremes in the genus’ distribution, knowledge about male-male relationships is essential in order to test this idea. This is the first study of the social system of habituated and individually-recognized free-ranging Guinea baboons.

In the following, I will outline the key characteristics of human societies and highlight why baboons are considered to be excellent models in the study of human social evolution (section 1.1.). Moreover, I will review the theoretical framework commonly used in the study of primate social evolution (section 1.2.). Since males are the focus of my thesis I will also address factors that may shape the evolution of male-male relationships in section 1.3. I finally come back to the model species in section 1.4. and introduce baboons in more detail. The aims and approaches of my thesis are outlined in section 1.5.

1.1 Baboons as a Model in the Study of Human Social Evolution

Human societies

Human societies typically comprise several conjugal family groups forming stable communities (Chapais 2011; Grueter *et al*. 2012; Murdock 1949) within which individual members may form new temporary groups on a daily or hourly basis (Rodseth 1991). Sexual relationships are predominantly monogamous (Marlowe 2003; Rodseth *et al*. 1991) and individuals of both sexes can disperse from their family groups (Hill *et al*. 2011; Kramer & Greaves 2010). Most strikingly, humans maintain lifetime bonds with their natal kin, irrespective of spatial proximity (Hill *et al*. 2009). These bonds result in long-term alliances between family groups within the community based on kin and non-kin ties (Chapais 2008, 2010, 2011; Rodseth *et al*. 1991; Rodseth & Novak 2000). Multiple family groups, including several hundred individuals, gather occasionally for ceremonies, politics or trade (Durckheim 1915; Gat 2010; Gurven 2004; Hamilton *et al*.2007; Layton *et al*. 2012; Murdock 1949; Rodseth & Wrangham 2004; Steward 1969; Turnbull 1965). The advent of the exceptional cooperative relationships within human societies has been linked to this multi-level organization (Grueter *et al*. 2012a; Hill 2002; Rodseth *et al*. 1991; Silk & Boyd 2010). A very important step in this context was the emergence of affiliative bonds between men, since males are usually responsible for intergroup aggression, as for example in the strictly territorial chimpanzees (Chapais 2010).

Baboon models

Baboons (*Papio* spp.) are considered to be a valuable analogous model in the study of human social evolution since they probably evolved in the same savanna habitats and at the same time in southern and eastern Africa as early humans (Barton *et al*. 1996; de Vore & Washburn 1963; Jolly 2001; Strum & Mitchell 1987; Strum 2012; Swedell & Plummer 2012). Based on fossil records and mitochondrial sequence data, the genus *Papio* originated in southern Africa approximately 2.5 million years ago, from where it dispersed north- and westwards into savanna areas over large parts of sub-Saharan Africa during the Pleistocene (Newman *et al*. 2004; Zinner *et al*. 2009). Early humans are supposed to have appeared in African savanna habitats around the same time and to show a similar initial diversification (Henzi & Barrett 2005). Thus, baboons are the only living primates that were likely confronted with similar ecological conditions that acted as selective pressures as for early humans (Janson 2000; Jolly 2001). These conditions most likely included decreased rainfall, resulting in temporal and spatial variation and distribution of food sources, as well as confrontation with predators in open habitats (Henzi & Barett 2005). Baboons met these challenges by developing the ability to exploit a wide range of food sources (Washburn & de Vore 1963; Whiten *et al*. 1987; Zinner *et al*. 2013a) and the formation of complex multi-male groups (Crook & Gartlan 1966; Washburn & de Vore 1963), similar to the patterns expected for early humans (Henzi & Barett 2005; Susman 1987). Today the genus *Papio* is widely spread over sub-Saharan Africa and the southwestern part of the Arabian Peninsula, inhabiting a variety of habitats from semi-desert, savanna, and rainforest to high-altitude mountains (Barrett 2009; Barton 2000; Barton *et al*. 1996; Dunbar 1988; Henzi & Barrett 2005; Kingdon 1997; Kummer 1990, 1995, Zinner *et al*. 2013a), which provides an ideal situation for the study of social diversity in closely related primate species.

1.2 Framework for the Study of Primate Social Evolution

Primate social systems

A society is defined as a set of individuals who share a home range and interact more frequently among each other than with other conspecifics (Schülke & Kappeler 2003; Struhsaker 1969; Wilson 2000). Most primates are highly gregarious and live in permanent bisexual groups with at least three adult individuals. This pattern is unusual in mammals, where most males leave the females after fertilization (Clutton-Brock 1989; van Schaik & Kappeler 1997). Primate societies, as most other animal societies, can be structured into three components: the *social organization*, the *mating system* and the *social structure* (*sensu* Kappeler & van Schaik 2002). In order to gain a better understanding of the factors that may have led to the diversification of primate societies, these components should be analyzed independently, since their variation might be caused by different factors (Clutton-Brock & Janson 2012, Kappeler & van Schaik 2002; Schülke & Ostner 2012; Struhsaker 1969).

The *social organization* describes the size, spatiotemporal distribution, age and sex ratios, as well as the genetic structure of a society. Five types of social organization are usually distinguished (Kappeler & van Schaik 2002). In *solitary* species activity patterns of individuals are not synchronized, but home ranges may be overlapping (several nocturnal strepsirrhines). In *pair-living* species, one adult male and one adult female are permanently associated (e.g. most hylobatids). Yet, most primates live in groups that contain multiple males and females (i.e. *multi-male multi-female;* most cercopithecines). Other forms of group living are *one-male multi-female* groups (e.g. many colobines) and *one-female multi-male* groups (several callitrichids). Group size and composition can be either stable or may exhibit temporal variation (Kappeler & van Schaik 2002). In fission-fusion societies individuals may temporarily form subgroups of varying size and composition (Aureli *et al*. 2008), whereas in multi-level societies small and stable subgroups, typically OMUs, are nested within higher levels (Grueter & Zinner 2004;

Grueter *et al*. 2012b; Kummer 1968; Stammbach 1987). While recognizing a stable group is usually easy, it may be complicated by units varying in size and composition (Kappeler & van Schaik 2002).

Males usually compete over access to fertile females and therefore try to monopolize as many as possible (Altmann 2000). This pattern constitutes the basis for the formation of *mating systems*, which comprise a behavioral (i.e. matings) and a genetic component (i.e. reproductive consequences). Primates exhibit almost all mating systems found in mammals (Clutton-Brock 1989), for example *monogamous* (one male mates with one female), *polyandric* (one female mates with multiple males), *polygynous* (one male mates with multiple females), or *promiscuous* (multiple males mate with multiple females). The mating system has important consequences for the genetic structure of a society or population, as, for instance, genetic relationships within a group vary according to the distribution of successful matings (Ross 2001). Moreover, mating systems and accompanying intra- and intersexual selection may have a profound impact on the morphology of individuals (Kappeler 2006). The type of intrasexual competition (i.e. whether males can monopolize females in direct contest or not) may possibly favor character traits associated with reproductive success, such as male body and/or relative testis size (van Hooff & van Schaik 1994). In polygynous species or promiscuous mating systems, for example, males may compete aggressively over access to receptive females and, as a consequence, they may be larger and have longer canines than females (Plavcan & van Schaik 1994; Trivers 1972). For instance, a strong relationship between relative testis size and the degree of sperm competition imposed by their mating systems can be observed within the great apes (Short 1981).

The *social structure* describes the pattern and nature of the interactions among members of a society, which often have particular social relationships (Hinde 1976; Whitehead 2008), such as family bonds, friendships, dominance relationships or coalitions. Such relationships can be described by the frequency and quality of behaviors exchanged within dyads (Hinde 1976), including affiliative (friendly) and agonistic (aggressive and submissive) interactions (de Waal 1986, 1989). The three components of a social system may be interrelated (Kappeler & van Schaik 2002). This is most obvious when considering the social organization and the mating system. For example, if pair-living is the modal social organization then mating is most likely monogamous. Moreover, sex-biased dispersal (part of the social organization) often determines whether kin bonds (part of the social structure) will be formed among individuals. Accordingly, in many cercopithecine species, philopatric females form valuable bonds within their matrilines (Silk *et al*. 2006; Silk *et al*. 2010; Wrangham 1980).

Socio-ecological models and phylogenetic constraints

Despite a large number of studies investigating social evolution, the selective forces shaping the diversity of social systems are still disputed (Clutton-Brock & Janson 2012; Kappeler & van Schaik 2002, Koenig & Borries 2009). Socio-ecological models constitute the traditional theoretical framework to explain primate social diversity (reviewed e.g. in Janson 2000, Schülke & Ostner 2012). These models suggest that the interplay of food distribution, predation and infanticide risk shapes the grouping patterns and competitive regimes among females (e.g. Crook & Gartlan 1966; Emlen & Oring 1977; Isbell 1991; Sterck *et al*. 1997; van Schaik 1989; Wrangham 1980). Males, on the other hand, are supposed to distribute themselves according to female grouping patterns (Altmann 1990; Emlen & Oring 1977).

While several predictions of the model could be confirmed, a growing body of studies has revealed incompatible results (reviewed in Clutton-Brock & Janson 2012; Janson 2000; Schülke & Ostner 2012). One example is the observation that although primates generally show a large diversity in social systems, those of most cercopithecine species are very similar even though the different species occupy a variety of different habitats (di Fiore & Rendall 1994, Ménard 2004, Struhsaker 1969). Thus, primate social systems are perhaps less flexible than presumed by socio-ecological models, leading to the assumption that they may be partly genetically constrained (di Fiore & Rendall 1994; Kummer *et al*. 1970). Thus, traits that can be observed today may be a product of both evolutionary history and natural selection in current environments (e.g. Blomberg & Garland 2002; Chapman & Rothman 2009; Edwards & Naeem 1993; Singh & Sinha 2004).

Concepts to explain the evolution of cooperative relationships

As outlined above, socio-ecological models try to explain how association patterns among individuals generally arise. Looking further into the social structure of a group, there are more specific relationships among individuals that go beyond the scope of mating or common resource defense. Cooperative interactions, such as coalitions, grooming or the sharing of food resources affect the fitness of both partners. However, it appears that often only one partner immediately benefits while the other pays a cost (i.e. altruistic behavior; Boyd & Silk 2006; Clutton-Brock 2002), raising the question how cooperative behavior and social bonds, respectively, develop among group members. One important concept in this context is *kin selection theory* (Hamilton 1964), according to which genetic relatedness favors the development of cooperative bonds. It is based on Hamilton's rule, stating that altruistic behavior should be more likely among kin as this would result in increased *inclusive fitness* (Hamilton 1964). Examples of altruistic behaviors related to kinship have been observed in various species such as microorganisms, social insects, birds (see West *et al*. 2006 for a review), carnivores (Packer *et al*. 1991; Smith *et al*. 2010; Holekamp *et al*. 2011) and primates (reviewed in Chapais & Berman 2004; Silk 2002).

Kinship is, however, “not the only force at work” (Silk 2002, p.862). According to the concept of *reciprocal altruism* (Trivers 1971) altruistic interactions can also evolve among non-kin if fitness costs and benefits for both partners are balanced over time. One example for reciprocal altruism in primates may be the sharing of meat, common border controls, and the exchange of grooming and support among non-kin in chimpanzees (Mitani & Watts 2001, Watts 2002). However, the actual costs and benefits associated with specific behaviors are hard to quantify, since different ‘currencies’ may be used. For example, grooming can be reciprocated with support (Boyd & Silk 2006). This may explain why reciprocity has rarely been demonstrated in natural settings. It has also been suggested that pure reciprocal altruism only works among humans because the required preconditions, such as the possibility to interact regularly, the ability of individuals to track those interactions and to adapt their behavior accordingly, can be extremely complex (Clutton-Brock 2002, 2009; Dugatkin 1997; reviewed in West *et al*. 2007).

Another approach to understand altruism among non-kin is the *biological market-theory* (Noë & Hammerstein 1994), according to which animals act as participants on a ‘biological market’ where ‘commodities’ are traded among more than two individuals. Several potential ‘producers’ provide their offer, and ‘consumers’ are able to choose who to interact with, resulting in competition for the best partner. Biological markets have been used as an explanation for ‘altruistic behavior’ all over the animal kingdom, including primates (see Noë *et al*. 2001). *Mutualism* (i.e. both partners getting an immediate direct benefit through an interaction) is supposed to be another important mechanism in other animals (Dugatkin 1997), yet it has not been well studied in primates. Some forms of cooperation among chimpanzees have been assumed to be mutualistic rather than altruistic (Watts 2002; reviewed in Gilby 2012), however, this idea remains speculative (Gilby 2012).

1.3 Primate Males

One important aspect in the evaluation of social relationships is to consider the circumstances under which cooperative bonds may evolve, particularly with regard to the distinct interests of the two sexes. Reproductive success in male and female primates is determined by different factors. In females, it largely depends on the ability to produce eggs and to raise offspring (Trivers 1972), which requires a good physical condition. Accordingly, females mainly compete for food resources rather than for mating partners. Food can usually be divided between several individuals (Emlen & Oring 1977; Wrangham 1980). In contrast, male reproductive success mainly depends on the access to fertile females, which represents an indivisible resource (Hall & de Vore 1965; Packer 1979; van Hooff & van Schaik 1994), forcing males to primarily compete for mating partners rather than food resources. These differences are useful to consider when evaluating male-male relationships.

Sex differences in factors that favor social bonding

As a consequence arising from the different interests of males and females (described above), the two sexes apply different reproductive strategies. Males should engage in intrasexual competition for females, while females should be selective in their mate choice and employ counterstrategies against the risk of infanticide (Trivers 1972). Accordingly, the nature of male contest, and therefore the chance for male bonds to develop, is largely determined by the distribution of fertile females (Hill & van Hoof 1994; van Hoof & van Schaik 1994; Trivers 1972).

As mentioned earlier, sex-biased dispersal patterns may also strongly influence the nature of social relationships. Since most primate groups are characterized by female philopatry and male dispersal (Greenwood 1980; Pusey & Packer 1987), adult males generally live among unrelated and often unfamiliar individuals (Silk 1994). As a consequence, male bonds are usually weaker than those among females, who may live among close kin and peers. Furthermore, the formation of alliances among females may be more beneficial as they commonly defend divisible food resources. In contrast, in male coalitions only one partner finally benefits by fertilizing the female (Packer 1977). The effect of intrasexual competition on reproductive success is thus larger in males than in females (Boyd & Silk 2006; Strier 2007). This mostly prevents males from forming close social relationships among each other (Cords 1987; Silk 1994; van Hooff 2000).

Multi-male groups

Contrary to the predictions derived from sexual selection theory (Darwin 1871), according to which males should ideally exclude other males from reproduction, most primate groups contain multiple reproducing males (Altmann 2000; van Hooff 2000; van Hooff & van Schaik 1994; see 1.2). This is firstly related to the fact that a single male can only monopolize a limited number of females (Andelmann 1986; Mitani *et al*. 1996). Additionally, females for their part may have an interest to attract more than one male to their group, for example to increase their options for mate choice (Altmann 2000), leading to the possibility of enhancing the genetic quality of their offspring to gain fecundity advantages (sperm competition) (Andersson 1994; Mesnik 1996) and to be protected against predators and infanticidal males (Altmann 1990; Smuts & Smuts 1993). Moreover, multiple males in a group are beneficial for the defense of food resources against other groups (Altmann 2000; Stanford 1997; Sterck *et al*. 1997; van Schaik & van Nordwijk 1989; van Schaik & Hörstermann 1994; van Schaik 2000).

The formation of multi-male groups is a precondition for males to regularly interact among each other, facilitating the development of social bonds. The frequency and quality of exchanged affiliative behaviors vary across species, with bonds being either temporary or long-lasting (van Hooff & van Schaik 1994). Particularly in species where males are philopatric, and thus generally have more kin in their group (Sterck *et al*. 1997), grooming bonds and coalitionary behavior among males are well-developed and may result in increased reproductive success of relatives (Pope 2000; Strier 1994). But unrelated males may also cooperate. For example, in some baboons, males may form coalitions in the reproductive context (e.g. Noë 1986, Noë & Sluijter 1990; see below). Since male coalitions may also be directed against infanticidal males and predators, both males and females living in multi-male groups eventually benefit from increased reproductive success (Altmann 2000; Kappeler & Ostner 2004; van Schaik & Hörstermann 1994).

Hierarchies

While the cooperative antipredator behavior and resource defense against other groups is assumed to lead to the formation of multi-male groups, individuals within groups still have to compete for resources. However, it would be too costly for males to fight each time they face a competitive situation, thus male-male competition in multi-male groups is usually regulated by dominance relationships (hierarchies) that mostly reflect fighting abilities. High-ranking males generally have priority of access to females and other resources (e.g. Alberts *et al*. 2003; Altman 1962; Bulger 1993; Kutsukake & Nunn 2006). However, as indicated above, some subordinate males may form reproductive coalitions against dominant males. Consequently, they may obtain more mating opportunities than predicted by their rank. The effect of rank or coalitions on male reproductive success may further be blurred by ‘female choice’ (Strier 2001). In the case that aggressive contest among males does not improve access to individual females, egalitarian relationships among males are presumed to occur (van Hooff & van Schaik 1992). Thus, male dominance relationships should reflect the degree to which individual females can be monopolized by males within a group.

1.4 The Comparative Approach - A Short Introduction to Baboons

For reasons defined earlier, baboons have traditionally served as a model in the study of social evolution. To date, six distinct morphotypes are recognized in the genus *Papio* (Jolly *et al*. 2011; Zinner *et al*. 2009, 2013b; see Fig. 1.1): chacma (*P. ursinus*), olive (*P. anubis*), yellow (*P. cynocephalus*), Kinda (*P. kindae*), Guinea (*P. papio*) and hamadryas baboons (*P. hamadryas*). These are not true biological species because they form hybrid zones (Alberts & Altmann 2001; Burrell 2008; Jolly *et al*. 2011; Nagel 1973; Phillips-Conroy *et al*. 1992). However, following the phylogenetic species concept (Cracraft 1989), the term 'species' will be used hereafter to refer to the different morphotypes. The different species vary in their social organization and mating systems, including the identity of the dispersing sex, resulting in variation of genetic relatedness and familiarity between females as well as between males within groups. This may have affected the evolution of social bonds and the characteristics of dominance hierarchies among males.

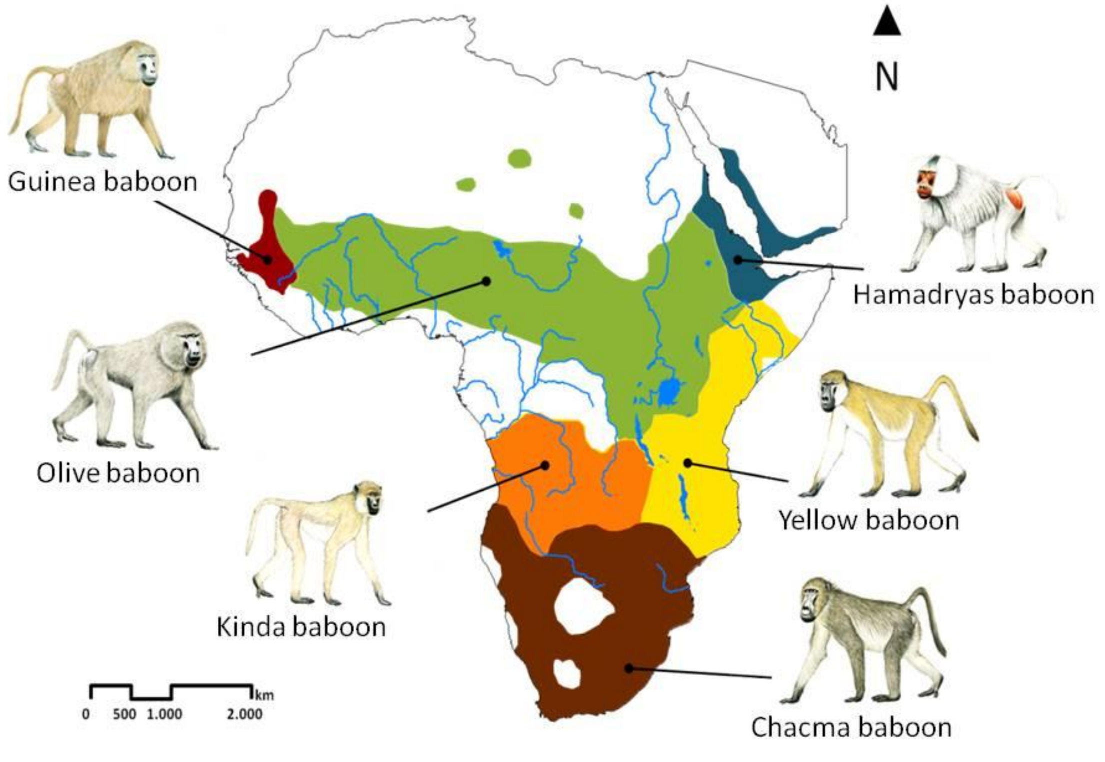

Figure 1.1 Geographical distribution of the six currently recognized baboon species (map based on Kingdon 1997; Jolly 2007; Zinner *et al*., 2009; illustrations © 2013 Stephen D. Nash / IUCN/SSC Primate Specialist Group. Used with permission).

Baboon social systems

Olive, chacma, and yellow baboons are commonly regarded as ´savanna baboons´ (ignoring the fact that within each species, some populations live in savanna habitats whereas others do not [Swedell 2011; Whiten *et al*. 1991]). Savanna baboons usually live in stable multi-male multi-female groups (Barton *et al*. 1996; Henzi & Barrett 2003; Melnick & Pearl 1987). Males disperse from their natal groups while philopatric females constitute the stable core of the group (Barton 2000; Dunbar 1988; Packer 1975, 1979; Silk 2007). The mating system is promiscuous and dominant males have a 'priority of access' to receptive females (Altmann 1962). During receptive periods, males intensively guard females in 'consortships' (Alberts *et al* 1996; Forster & Strum 1994; Smuts 1985). Lactating females may form close, non-sexual bonds ('friendships') with specific males who are often their infants' fathers, presumably as prevention against infanticide (Palombit *et al*. 2001) or as a strategy against harassment in general (Altmann 1980; Smuts 1985). The less-studied Kinda baboons have been suggested to show a similar social system, yet their reduced dimorphism in body size and a high frequency of affiliative male-female interactions suggest stronger intersexual bonds (Phillips-Conroy *et al*. 2009; Weyher & Chiou 2013). In contrast to savanna baboons, hamadryas baboons live in a multi-level society (Abegglen 1984; Kummer 1968, 1990; Schreier & Swedell 2009; Sigg *et al*. 1982). OMUs constitute the smallest social entity. Most reproduction and almost all interactions take place between the leader male and his females (Kummer 1968), including strict herding behavior shown by the leader male. All adult females are members of OMUs. Some OMUs may contain an additional "follower" male that may socialize but usually does not mate with the females (Kummer 1968). Several OMUs aggregate into larger *clans* (Abegglen 1984; Schreier & Swedell 2009). Several clans and additional "solitary" males form a band. Such bands share a common home range and travel pattern (Abegglen 1984; Kummer 1968) and may join other bands at sleeping sites forming *troops* containing up to 700 individuals (Kummer 1968; 1995). Both sexes are said to be philopatric within bands (Sigg *et al* 1982; Swedell *et al*. 2011). Males within clans are assumed to be related, and females within OMUs are probably non-kin (Abegglen 1984; Sigg *et al*. 1982; Stolba 1979). However, these assumptions are not yet supported by genetic data.

In contrast to the other baboon species, prior to this study little was known about Guinea baboons (e.g. Galat-Luong *et al*. 2006; Maestripieri *et al*. 2007). Available studies originate either from short field stints where individuals were not recognized (Anderson & McGrew 1984; Bert *et al*. 1967; Boese 1973; Dunbar & Nathan 1972; Sharman 1981) or from observations of captive groups (Boese 1973, 1975; Maestripieri *et al*. 2007). While data on captive animals are unreliable to estimate the natural group composition or size, studies of wild

Guinea baboons reported multi- male multi-female troops of up to 350 individuals (Galat-Luong *et al*. 2006; Sharman 1981). Some features were described consistently, such as the observation that individuals aggregate in large groups when travelling and at sleeping sites, while foraging and resting seem to take place in smaller groups (Anderson & McGrew 1984; Boese 1973; Dunbar & Nathan 1972; Galat-Luong *et al*. 2006; Sharman 1981; but see Bert *et al*. 1967 and Dupuy & Gaillard 1969). Moreover, most authors reported OMU-like subgroups as the smallest entities (Boese 1973; Galat- Loung *et al*. 2006; Sharman 1981); however, it remained unclear whether these OMUs represent reproductive units as in hamadryas baboons (Kummer 1968). Based upon observations on captive animals, Maestripieri and colleagues (2007) assumed the latter, but Sharman (1981) observed females mating with multiple males in the wild, which is typically found in savanna baboon societies but not in hamadryas baboons. Aggressive herding, as in hamadryas baboons, was observed in some studies (Boese 1973, 1975; Maestripieri *et al*. 2007), but not in others (Sharman 1981; Galat-Luong *et al*. 2006). Yet, all authors highlighted that females moved freely between subgroups (Anderson & Mc Grew 1984; Boese 1973, 1975; Dunbar & Natan 1972; Galat-Luong *et al*.2006; Maestripieri *et al*. 2007; Sharman 1981). Boese (1973) concluded that the Guinea baboon social organization represents an evolutionary precursor to the more rigid multi-layered social organization of hamadryas baboons (but note that he only collected 3 months of data in the wild). The assumption that Guinea baboons may constitute precursors to hamadryas baboons does not, however, fit with current phylogenetic evidence (Zinner *et al*. 2009). In contrast to Boese`s assumption, Sharman (1981), who observed wild Guinea baboons over a period of 19 months, suggested that the male-centered units in Guinea baboons more likely represent maternal kin groups (Sharman 1981), thus rather resembling the social organization of geladas, where related females form the core of OMUs within the larger troop (Dunbar & Dunbar 1975; le Roux *et al*. 2012). In sum, there was large disagreement about the Guinea baboon social system.

Social relationships among male baboons

In conjunction with variation in the social organization and mating system male-male relationships in baboons differ across species. As mentioned earlier, this variation appears to follow along a south-to-north gradient according to the expansion pattern of the genus during the Pleistocene (Jolly 2009). Among savanna baboons, hierarchy steepness appears to decrease from south to north accompanied by a lower mating skew in northern species (Alberts *et al*. 2003; Bulger 1993; Weingrill *et al*. 2003). Since mating opportunities in baboons are presumably related to reproductive success (Alberts *et al*. 2006; Moscovice *et al*. 2010), the lower mating skew is supposed to be associated with a higher frequency of coalition formation, which enables subordinate yellow and olive baboon males to take over receptive females from dominant males (e.g. Bercovitch 1988; Bulger 1993; Hall & de Vore 1965; Hausfater 1975; Noë & Sluijter 1990, 1995; Packer 1979; Smuts 1985). Chacma baboon males however, representing the most southern species with the most pronounced mating skew, were never observed forming coalitions (Bulger 1993; Henzi & Barrett 2003). Infanticide by males occurs less frequently in olive and yellow baboons (Broom *et al*. 2004), while it occurs regularly in some populations of chacma baboons (Palombit *et al*. 1997). Moreover, savanna baboon males are generally intolerant of one another and rarely spend time in close proximity (*P. ursinus*: Saayman 1971; *P. cynocephalus*: Hausfater 1975; Noë & Sluijter 1995, *P.anubis*: Alberts 2012; Harding 1980; Smuts 1985; but see Sapolsky who occasionally observed grooming between adult males [Sapolsky pers. comm.]). In hamadryas baboons male-male relationships have evolved differently, showing both tolerance and cooperation. This is suggested to be related to male philopatry, resulting in higher genetic relatedness among males (Abegglen 1984; Hammond *et al*. 2006; Kummer 1968). In contrast to other baboons, they do not exhibit “typical” dominance hierarchies across several males. Yet, "leader males" of OMUs are dominant to follower and solitary males and (almost) completely monopolize reproduction of females within the OMU (Abegglen 1984; Kummer 1968, 1973). Males may engage in ritualized behaviors (´notifications´), most likely to test a rival's tendencies in a competitive situation (Colmenares 1990). Adult males may groom each other and maintain affiliative relationships, but become less tolerant (Abegglen 1984; Colmenares 1990, 1991) and are very rarely observed to groom from the moment when they acquire females (Schreier & Swedell 2009). In hamadryas baboons, infanticide has been observed in relation to take-overs of OMUs (Swedell & Saunders 2006).

Observations of male Guinea baboons by Sharman (1981) and Galat-Luong *et al*. (2006) suggest that they maintain more relaxed relationships among each other compared to other savanna baboon taxa. However, data on wild, individually identified Guinea baboons had not been collected. Therefore, the social structure of male Guinea baboons was still unknown.

1.5 Aims and Approaches

The overall aim of my thesis was to contribute to the resolution of the dispute about the social system of Guinea baboons. Based on the assumption that hamadryas and Guinea baboon social systems share some similarities, I focused on males since these play an important role in structuring the society of hamadryas baboons (Colmenares 1992; Kummer 1968, 1995). This focus moreover allowed testing of whether Guinea baboons would fit into the above-mentioned south-to-north gradient, according to which baboon males are expected to be more tolerant and cooperative among each other in the northern species (Jolly 2007, 2009; see also Henzi & Barrett 2003, 2005). Since kinship is expected to have an important impact on social interaction patterns (*kin selection hypothesis*; Hamilton 1964) and has been suggested to structure male- male relationships in hamadryas baboons (Abbegglen 1984), I furthermore investigated whether genetic relatedness correlates with spatial and social interaction patterns.

My project consisted of three parts. The first part (chapter 2 [Patzelt *et al*. 2011]) focused on the social organization (i.e. group size and composition) of Guinea baboons. As an initial approach at the beginning of the research project, we observed unhabituated members of the baboon community ranging next to our field site when crossing an open area (fixed point observation). The aim of this study was to determine the size and composition of (sub-) groups at the water source. Individuals were counted and changes in composition of both arriving and departing parties were recorded and compared. In part 2 (chapter 3 [Patzelt *et al*. under review]), we described association patterns among individually-recognized adult males within the Guinea baboon community and correlated them to kinship coefficients, using ranging data collected from animals equipped with Global Positioning System (GPS-)collars, proximity measures recorded during focal observations, and genetic analyses based on individual microsatellite genotyping. We quantified and visualized spatial interaction patterns using cluster analyses based on association frequencies calculated from GPS data as well as proximity measures from focal observations. Grouping patterns were correlated to genetic relatedness to identify whether related males form the core of the Guinea baboon society. However, spatial associations alone may not necessarily reflect social preferences, but can simply mirror similar physiological needs, which have to be satisfied at the same time in the same place (Bercovitch & Berry 2013; Mitani *et al*. 1991; Snyder-Mackler *et al*. 2012; see also Wrangham & Rubinstein 1986), such as gathering at a water place for drinking. Behavioral interactions, close proximity, and nearest-neighbor measures are supposed to be a more reliable indicator for social bonding (Lehmann & Boesch 2009; Wilson 2000). Therefore, we additionally applied 1-m scans to assess the quality of male-male relationships. In part 3 (chapter 4 [Patzelt *et al*., prepared for submission]) we studied male-male interactions in more detail. We related social interactions to spatial grouping patterns to investigate how male relationships (as part of the social structure) are linked to their social organization (*sensu* Kappeler & van Schaik 2002). To evaluate whether genetic relatedness explains male interaction patterns in Guinea baboons, we correlated interaction frequencies with genetic relatedness coefficients on a dyadic level. Moreover, we compared body measurements that are supposed to be correlated with intrasexual competition to that of other baboon taxa in order to evaluate the degree of sexual competition among Guinea baboon males.

This project was part of a long-term study on the diversity of social behavior and vocal communication of baboons initiated by our laboratory in the Niokolo-Koba National Park in Senegal. In 2007 we established the field site “Centre de Recherche de Primatologie (CRP) Simenti” located near the Gambia River (13°01’34’’ N, 13°17’41’’ W) and habituated subjects belonging to a community of approximately 350 baboons ranging nearby. From previous studies we knew that Guinea baboon groups are not stable but show some structuring (see above). However, nothing was known about the composition or the relationships among as well as within such subgroups. Ultimately, in combination with studies on phylogeography and ecology, the results of my thesis should lead to a better understanding of the diversity within baboon social systems. Ultimately, this may help to identify the driving forces shaping social systems in savanna habitats, leading to a better understanding of our own social evolution (Janson 2000).

CHAPTER 2

Group Composition of Guinea Baboons (*Papio Papio*) at a Water Place Suggests a Fluid Social Organization

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ABSTRACT

Baboon social systems are among the most studied in primates. Solid knowledge of the hamadryas and savannah baboon systems has accumulated, leading to a dichotomic view of baboon social systems. Hamadryas baboons live in multilayered troops based on 1-male units whereas savannah baboons live in multimale multifemale groups based on a network of related females. Less attention has been paid to their West African congenerics, the Guinea baboons, *Papio papio*. To fill this gap, in 2007 we initiated a long-term study of a baboon troop ranging in the Niokolo Koba National Park in southeastern Senegal. Earlier studies suggested a tendency for a multilayered social system in Guinea baboons, similar to the hamadryas baboon organization. Therefore, as a first approach to analyzing variability in party size and composition, we observed members of the troop crossing an open area from a fixed point for 3 mo during the dry and wet seasons. We counted individuals and recorded changes in composition of both arriving and departing parties. Party size and composition were highly variable on both a daily and a seasonal basis; 45.9% of the arriving parties changed in composition while crossing the open area, either splitting into smaller parties or fusing into larger ones, suggesting a fluid organization. Our data support the existence of neither a hamadryas baboon-like multilayered social organization nor a stable medium-sized multimale multifemale group as in savannah baboons. In light of our data we may need to revise the dichotomic view of baboon social systems and include space for greater variability of their social systems.

Keywords: Fixed-point observation, Guinea baboons, *Papio papio*, Social organization

INTRODUCTION

Baboons are among the most extensively studied primate taxa, and data on their ecology and social systems have been used in comparative socio-ecological analyses to assess the variability and plasticity of social systems in closely related primate species (Barrett 2009; Barton 2000; Barton *et al.* 1996; Dunbar 1988; Henzi & Barrett 2005; Kummer 1990, 1995). However, compared to other baboon species, little is known about Guinea baboons (*Papio papio*; Barton 2000; Galat-Luong *et al*. 2006; Henzi & Barrett 2003; Maestripieri *et al.* 2007). Despite several studies, a great deal of inconsistency remains within the scientific literature concerning the social organization and group structure of this species. It is essential to understand better the social organization of Guinea baboons to gain a more complete understanding of the evolutionary history of baboon social systems. Olive (*P. anubis*), yellow (*P. cynocephalus*), and chacma baboons (*P. ursinus*), referred to as savannah baboons, live in multimale, multifemale groups (MMUs) of medium size (mean 50 individuals, based on data in Swedell 2011). However, group sizes are variable, mainly due to habitat conditions such as food availability or predation risk (Melnick & Pearl 1987). Savannah baboon groups are usually stable but may split up for short periods (Henzi & Barrett 2003), e.g., when foraging in harsher habitats (Barton *et al*. 1996). Females are predominantly philopatric, and a network of related females comprises the core of the MMU (Barton 2000). Female– female bonds are strongest between close kin, and stable dominance hierarchies exist (Barton 2000; Gouzoules & Gouzoules 1987; Hausfater *et al*. 1982). Females have multiple mating partners (Melnick & Pearl 1987), and males and females form sexual consortships during females' receptive periods (Smuts 1985). These consortships are exclusive pair bonds lasting from several hours up to 6 d, during which most of the matings are performed. In addition, females' intersexual social interactions are focused on only one or a few males with which they may form "friendships" that last beyond phases of sexual receptivity (Barton 2000; Huchard *et al*. 2010; Nguyen *et al*. 2009; Palombit 2009). Adult sex ratios are 1:1.1 (*P. anubis*; Rowell 1966 [cited in Swedell 2011])–1:3.3 (*P. ursinus*; Hall & de Vore 1965).

In contrast, hamadryas baboons (*P. hamadryas*) live in a multilayered organization, i.e., smaller social units are nested within larger ones. The basic social entities are stable 1-male, multifemale units (OMUs), consisting of 1 male (Kummer 1968), 1–10 females, and their offspring (for an overview of multilayered societies including hamadryas baboons see Grueter & Zinner 2004; Stammbach 1987). Some OMUs may contain an additional follower male (Kummer 1968). These OMUs are distinguishable through spatial and social segregation (Grueter &Zinner 2004; Kummer 1968; Stammbach 1987). Two or three hamadryas OMUs associate, forming the next higher layer, a clan (Abegglen 1984; Schreier & Swedell 2009). Several clans and additional single males form a band, which is a stable and exclusive unit and constitutes the next layer. This layer is thought to be homologous to the multimale units of savannah baboons (Dunbar 1988). Up to 4 bands may form a sleeping unit, the troop (Stammbach 1987). Bands often fission into clans or single OMUs when foraging (Kummer 1968). Males within a clan are assumed to be related (Abegglen 1984; Stolba 1979), but so far there is no genetic evidence confirming this assumption. Mean OMU size is ca. 7 (range 5–9) individuals, clan size ca. 24 (range 20–29), and band size ca. 86 (range 40–165) (Hill *et al*. 2008), and troops may contain several hundred (up to 800) individuals (Kummer 1968; Zinner *et al*. 2001). Females leave their natal OMU when sexually mature, but mostly stay within their bands (Sigg *et al*. 1982). Adult sex ratios are similar to those in savannah baboons: 1:1.3 (Swedell 2006) – 1:2.9 (Zinner *et al*. 2001).

The data available for Guinea baboons suggest that their society differs from other baboon social organizations. Studies of free-ranging Guinea baboons report multimale troops of up to 300 or even more individuals in a multilayered organization (Sharman 1981). Individuals aggregate in these large groups when traveling and at sleeping sites. Foraging and resting seem to take place in smaller groups (Anderson & McGrew 1984; Boese 1973; Dunbar & Nathan 1972; Galat- Luong *et al*. 2006; Sharman 1981). Contradictory suggestions have been made concerning their social organization. Some authors suggest that they are organized in OMUs that aggregate into larger parties, resembling the social organization of hamadryas baboons. For instance, Boese (1973, 1975) observed that the composition of OMUs in a zoo population remained stable over a longer period of time, that female–male bonds are strong, and that males show herding behavior, like hamadryas males. However, he also reported that females interact freely with females of other OMUs and also with other males besides their OMU males; traits that are uncommon in hamadryas baboons (Kummer 1968). Boese also observed OMUs aggregating into larger parties in a field study (Boese 1973). In a more recent study of captive Guinea baboons, Maestripieri *et al*. (2007) observed both mating and social activity taking place within OMUs, and just 1 of 16 sexually active females copulating with >1 male. However, the OMU male threatened “his” females more often than other individuals did and the females did not threaten the male. Again, the researchers observed no typical hamadryas herding behavior, which was also confirmed in a study on free-ranging groups by Galat-Luong and colleagues (2006). Similarly, Dunbar and Nathan (1972) and Anderson and McGrew (1984) describe OMU-like subgroups in free-ranging Guinea baboons, but emphasize that females have more freedom in their social interactions than hamadryas baboon females. Sharman (1981) even observed females copulating with >1 male and, moreover, he reported consortships when females were in estrus, suggesting direct competition among males for receptive females, a trait typically found in savannah baboon multimale societies and not in hamadryas baboons. Boese (1973) suggested that the social organization of Guinea baboons represents an evolutionary precursor to the more rigid multilayered social organization of hamadryas baboons. Sharman (1981), in contrast, maintained that the male-centered units in Guinea baboons more likely represent maternal kin groups than male-policed harems as in hamadryas baboons, thus possibly resembling the social organization of the geladas (Dunbar 1978, 1983a, b, 1988).

We observed a large troop of Guinea baboons when they crossed an open area. This condition allows for better visibility than previous studies that estimated group size in a forested habitat (Bert *et al*. 1967; Dunbar & Nathan 1972; Galat-Luong *et al*. 2006) and allowed us to obtain more detailed data on group composition. Researchers have used similar fixed-point observation to detect temporal and spatial organization patterns in groups of other nonhabituated primates (*Pan troglodytes*: Itani 1966 [cited in Sugiyama 1968]; *Mandrillus sphinx*: Abernethy *et al*. 2002; *Rhinopithecus bieti*: Zehua *et al*. 2007) and other mammalian taxa, e.g., chital (*Axis axis*: Barrette 1991).

We focus on the question of whether Guinea baboon social organization resembles that of savannah or hamadryas baboons (Fig. 2.1) and test the following predictions:

1) If Guinea baboons constitute a coherent social group of medium size similar to that of savannah baboon bands, we expect a steady flow of complete, discrete groups crossing the open area, with stable group sizes over time. This does not exclude the possibility that we may occasionally observe subunits of this medium-sized group. However, OMUs should rarely occur. Thus we predict a narrow unimodal distribution of group size with only small variation over the observation period.

2) If Guinea baboons are organized in a multilayered way, similar to hamadryas baboons, we expect them to either enter or cross the open area as a coherent band of large size, as clans of medium size or as single OMUs. This predicts (a) a bi- or trimodal frequency distribution of party size with maxima for OMU size, possibly clan size and band size (Fig. 2.1). (b) If subgroups are predominantly organized as OMUs, we expect to find specific spatially or temporally segregated clusters of 1 adult male, possibly subadult followers, and several adult females and their offspring in the same composition throughout all observations. Moreover, (c) if larger subgroups reflect a temporary association of several OMUs a comparison of sex ratios in OMUs and these larger MMUs should reveal no difference (Abernethy *et al*. 2002).

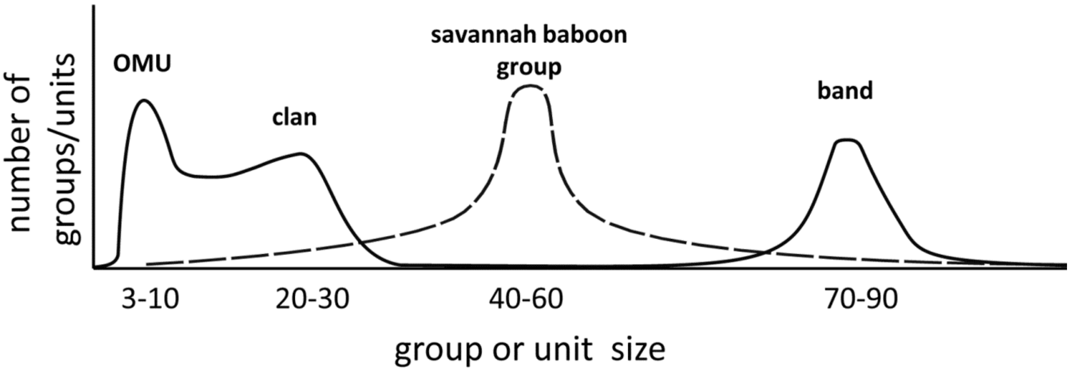

Figure 2.1 Examples of potential distributions of unit or group sizes for (1) a bi- or tri-modal distribution similar to a hamadryas-like organization (black line) where OMUs join up into larger clans and bands, and (2) for a uni-modal distribution as expected for a savannah baboon organization (broken line).

METHODS

Study Site

Our focal troop ranges close to the field station of the German Primate Center (DPZ), the Centre de Recherche de Primatologie (CRP) at Simenti (13°01′34′′N, 13°17′41′′W) in the Niokolo Koba National Park in southeastern Senegal. The climate is highly seasonal with a dry season from November until June. The mean annual rainfall of 1000–1100 mm (Dupuy 1971) is mostly concentrated in the rainy season from July to October. Vegetation varies from grassland savannah, dry and evergreen, to deciduous and palm tree forest as well as gallery forest along the banks of the Gambia River. Galagos (*Galago senegalensis*), green monkeys (*Chlorocebus sabaeus*), Western red colobus (*Piliocolobus badius*), and patas monkeys (*Erythrocebus patas*) occur sympatrically with Guinea baboons. Potential predators are lions (*Panthera leo*), leopards (*Panthera pardus*), and spotted hyenas (*Crocuta crocuta*) (Galat-Luong *et al*. 2006).

We conducted the study at the Mare de Simenti. The Mare is a seasonally flooded plain of ca. 6.6 ha next to the field station, with mainly herbaceous vegetation, surrounded by bushes and palms as well as deciduous forest. It is used by grazers such as warthogs (*Phacochoerus africanus africanus*) and kobs (*Kobus kob kob*). A muddy pool usually remains in the center during the dry season and is used for wallowing by warthogs and for drinking by other animals, including the baboons.

Data collection

Observations took place while habituation was still under way. We collected data over 3.5 mo in the dry and rainy seasons. We observed and recorded the arrival and departure of baboons using binoculars (10×40) from an outlook used as a hideout by tourists. Our observation post was situated at the edge of the Mare, between the sleeping site and the forest. The baboons usually crossed the Mare in the morning before foraging in the forest and crossed back again on returning to the sleeping trees (Fig. 2.2). They occupied an area of short grass at a distance of 30 to ca. 320 m from our observation point. Visibility was unobstructed. Two observers collected data on size and composition of arriving and departing parties independently for 2 wk to check for concordance, which was 93.5%. For the rest of the observation period the 2 observers collected data alternately.

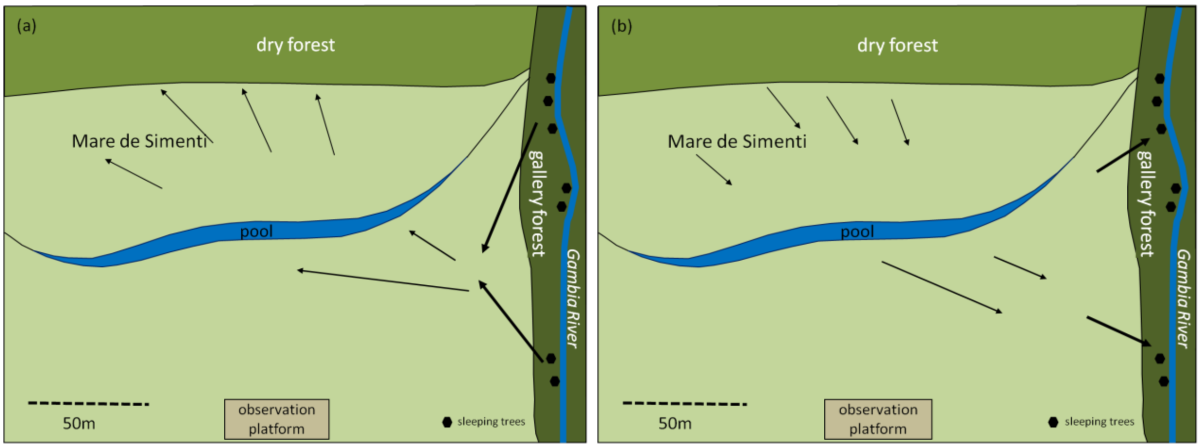

Figure 2.2 Movement directions of the baboon troop when (a) leaving the sleeping site in the morning, and (b) coming back from foraging in the afternoon. Location of observation platform is also indicated.

Next to the Mare the baboons use large trees along the Gambia River as sleeping sites (Fig. 2.2). We refer to these baboons as a troop, and to any cluster of ≥4 individuals as a party. We preferred the term party instead of group or subgroup because the term is generally used to describe social entities of fission–fusion societies (Aureli *et al*. 2008). Once we recorded a party comprising 330 individuals in the rainy season leaving the Mare. Our estimation of the total troop size is thus based on this maximum count.

The troop's sleeping site extends over ca. 500 m of the Gambia River, and the baboons pass the night resting in tall trees, e.g., *Borassus aethiopium*, *Ceiba pentandra*, that are difficult to access for predators. In the mornings scattered parties arrived at the Mare. The baboons either crossed the Mare immediately or spent some time in the open field and used the Mare for foraging, drinking, and socializing (median 10 min; range 0–122 min; N=163 of 198 parties entered and left the Mare in the same composition. For the remaining 35 parties the data set was not complete.). They stayed either as 1 party or mingled or later moved on into the forest with other parties. Further, some parties left the sleeping site at the Gambia into other directions without crossing the Mare. In the afternoon, scattered parties returned from foraging in the forest. As in the morning, the baboons spent time on the Mare for foraging, drinking, and socializing before they took off to their sleeping trees. Because of this pattern we hardly ever saw all the ca. 330 individuals within 1 session.

We collected data on 78 d from April 30, 2007 to August 12, 2007 when the Mare flooded and baboons were no longer able to cross it. We classed data collected until the first heavy rain (June 16, 2007) as dry season data and data collected thereafter as rainy season data (Fig. 2.3). We gathered data during 20 morning and 32 afternoon observation sessions in the dry season and 28 morning and 29 afternoon sessions in the wet season (total=109 sessions).

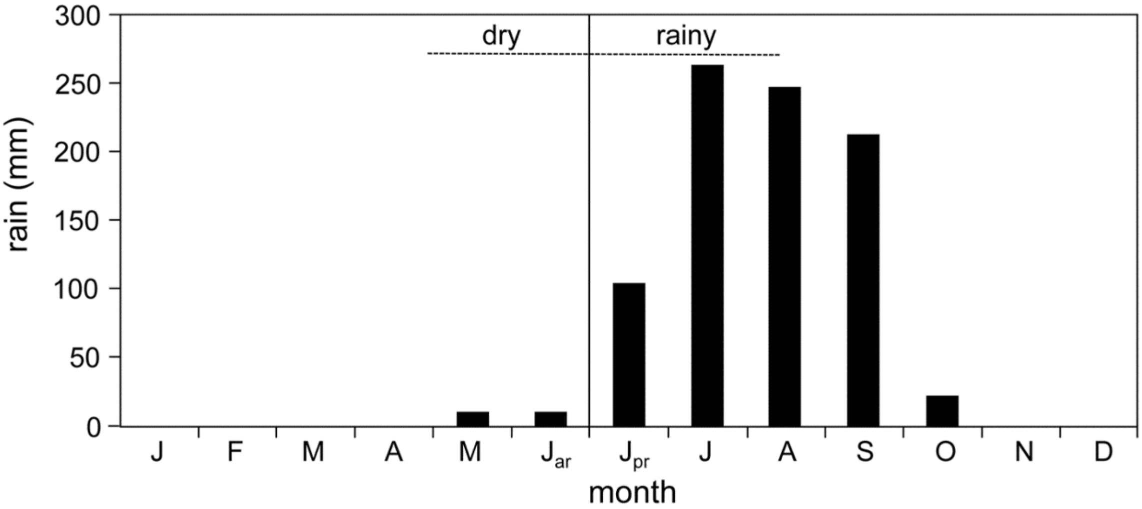

Figure 2.3 Precipitation in 2007. J_{ar} = June before first heavy rain, J_{pr} = June after first heavy rain. The dashed line marks the observation period in the dry and rainy seasons.

Morning observation sessions started at dawn (between 06:15 h and 07:00 h, depending on sunrise) and lasted until 10:00 h. We resumed our observations when the baboons started to return to their sleeping site and crossed the Mare in the afternoon (15:00 h–17:00 h). Observations lasted until darkness (18:30 h–19:15 h, depending on the season). Whenever the baboons entered or left our field of view, we recorded their arrival and departure times respectively, direction of movement, party composition (number of males, females, juveniles, and infants), and fission and fusion events. We recorded a fission event when one part of a party left the area while the other part stayed behind, and a fusion event when 2 parties entered the area at different times or from different directions but left the area together at the same time and in the same direction. It was difficult to obtain an exact head count at times, especially when parties were large, dense, or in motion (Sharman, 1981). In such cases, we estimated party size to the nearest 10, e.g., 100–110 individuals; 68 of 366 events with parties >50 individuals, and used the intermediate value in analysis (thus, in the former example we would have taken 105 as party size value). Moreover, we may have missed individuals or counted them twice. Thus the error in estimating exact party size and composition likely increased with party size.

Guinea baboons show a pronounced sexual dimorphism, which makes identification of the adult sexes easy. Males are much larger than females (males on average 21 kg, females 14 kg; Boese 1973) and have a shoulder mantle, which is not as pronounced as in hamadryas baboons, but more developed than in olive baboons. However, distinguishing females from juvenile males was sometimes difficult when the baboons were in greater distance and might have resulted in an over- or underestimation of females and subadult males. However, because this error should apply for all types of clusters in the same magnitude, it should not bias sex-ratio estimations for OMUs and MMUs. We used temporal or spatial criteria, or both, to distinguish one party from another and defined parties as:

1) Clusters of ≥4 individuals if these clusters came from (or left in) the same direction but were separated by an interval of ≥5 min. 130 of the 132 recorded time gaps between 2 consecutively arriving clusters were ≥5 min.
2) Clusters of ≥4 individuals if these clusters came from or left in different directions (defined as >45°), even if they arrived or left at the same time. While resting at the Mare, parties were not only spatially separated, with a spatial distance of <5 m among but ≥50 m between individuals or clusters, but also behaviourally separated from each other, i.e., no interaction between the parties took place (Sharman 1981). This is also valid for newly formed aggregations in cases of fission and fusion taking place on the Mare.

Data Analysis

We determined the sizes of 496 parties, including 366 parties that entered the observation area (arriving parties). The remaining 130 parties were departing parties that resulted from fission–fusion events on the Mare. To avoid inflating sample size by counting the same party when it arriving, rested in, and left the observation area, we used only data for arriving parties in the analysis. We were able to determine the group composition of 241 of 366 arriving parties, i.e., all individuals within a party could be assigned to an age/sex class.

We explored the impact of time of day on the number of parties arriving and party size with a Mann-Whitney U test (Statistica 9.0, StatSoft Inc., www.statsoft.com). We used 1 data point for each party during each observation period, resulting in a sample size of 109. We used a t-test to compare sex ratios in OMUs and MMUs (Statistica 9.0, StatSoft Inc., www.statsoft.com). We compared the frequency distributions of party sizes in the rainy and dry seasons with an exact χ^2 test (SsS 1.0b Rubisoft Software GmbH).

To test whether the observed distribution of party sizes of Guinea baboons is due to a random process of general attraction to a group or whether they form any higher social organization, we fitted the observed distribution with a 0- truncated Poisson distribution and a 0 truncated negative binomial distribution (StataCorp. 2010. Stata Statistical Software: Release 11.1.). We compared models using Akaike's Information Criteria (AICs). The model having the lowest AIC is regarded as a better fit (Akaike 1973), and a difference in AIC of >10 suggests virtually no support for the model with the larger AIC (Burnham & Anderson 2002). If the membership or size of a group does not influence the attraction of an individual to join a group, then the frequency distribution of the group should follow a 0-truncated Poisson distribution (Cohen 1971; Wilson 2000). If individuals join a group because of specific membership or the size of the group, then the frequency distribution should follow a 0-truncated binomial distribution. If this is the case, we can conclude that Guinea baboons form higher social aggregations. Descriptive data are presented as means and standard deviations (SD), median, and IQR or proportions.

RESULTS

Troop cohesion was rather loose, and the composition of arriving parties was highly variable, both on a daily and on a seasonal basis. In the dry season we observed only 1 arriving party >100 (in that particular case, 125) individuals (0.5% of 191 parties), whereas in the rainy season 13.1% of the parties (23 of 175) comprised >100 individuals.

Using our 2 criteria for different occasions, we identified 212 arriving parties according to our spatial criterion, arriving from different directions, and 132 by our temporal criterion (≥5 min lag). Time intervals between arriving parties ranged from 5 to 113 min (median 20 min; IQR 10–30; N=131). In 22 of 109 observation sessions, only 1 party passed the observation area, which adds to a total of 366 arriving parties. The average size of arriving parties was 20.0 (median; IQR 11–40; range 4–300). 58.5% (214/366) of all arriving groups comprised 6–25 individuals, while 12.3% (45/366) comprised 40–60 individuals (the equivalent of savannah baboon groups) and 4.9% (18/366), 70–90 individuals (the equivalent of hamadryas bands).

A 0-truncated negative binomial distribution (AIC=3325.3) fitted the distribution of sizes for arriving parties better than a 0-truncated Poisson distribution (AIC= 14089.6; Fig. 2.4), suggesting that party size was not random.

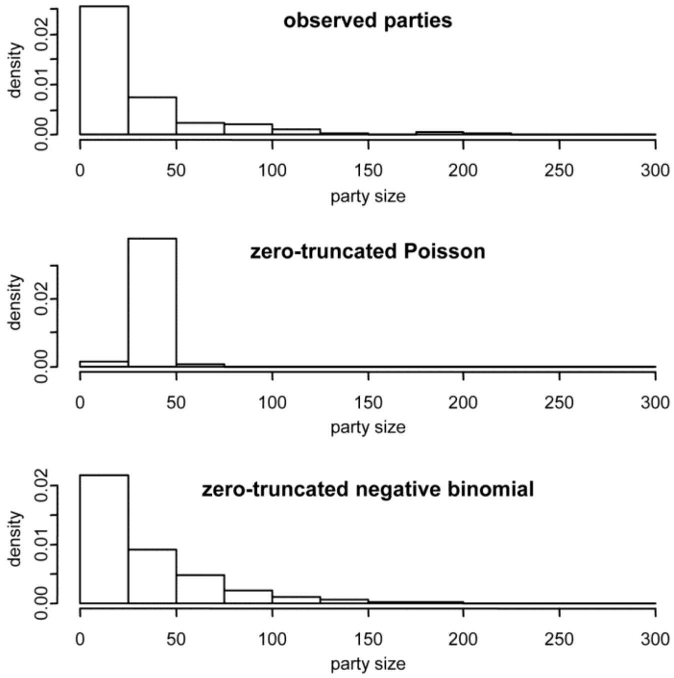

Figure 2.4 Comparison of observed data with zero-truncated Poisson and zero-truncated negative binomial distributions.

The negative binomial dispersion parameter (α) of the 0-truncated model was 0.88 (95% CI: 0.75–1.04) and significantly larger than 0 (z=12.1, p<0.001). This further suggests that there is overdispersion in the data set and a 0-truncated Poisson model is not appropriate (when the overdispersion parameter is 0 the negative binomial distribution is equivalent to a Poisson distribution.) The observed distribution matched neither the bi- or trimodal distribution expected for hamadryas baboons nor the unimodal distribution expected for savannah baboons (Fig. 2.5).

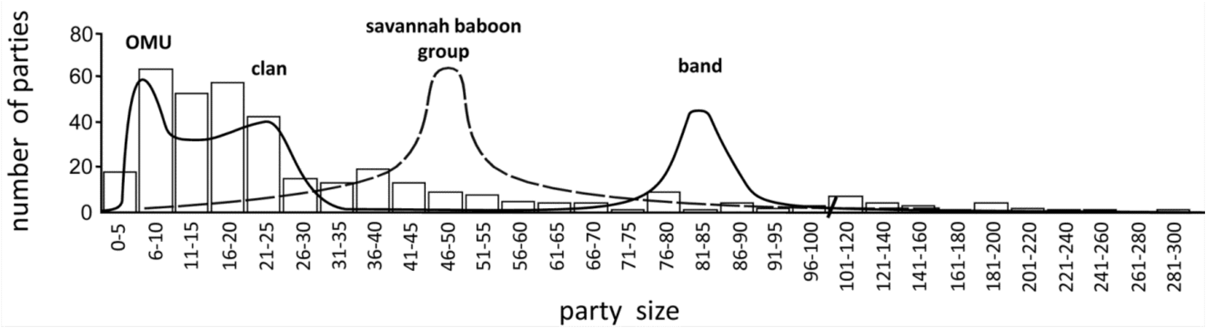

Figure 2.5 Frequency distribution of party size categories (histogram; N = 366 arriving parties) in relation to an expected bi- or tri-modal distribution for a hamadryas-like organization (black line) where OMUs join up into larger clans and bands and a uni-modal distribution expected for a savannah baboon organization (broken line). The distribution of hamadryas baboon unit sizes is based on data in Hill *et al.* 2008 (summary of 8 different study sites); the distribution for savannah baboons is based on data in Swedell 2011 (summary of 11 *P. anubis,* 2 *P. cynocephalus* and 10 *P. ursinus* study sites).

Party Composition and Sex Ratio

The average party size was 16 individuals (median; IQR 9–23; range 4–90; N=241),with a mean of 3.1 adult males (17.1%; SD 2.6; range 0–18; N=241). 63 of 241 parties with known composition (26.1%) included only 1 adult male, whereas 175 parties were MMUs (Table 1). Three of 241 parties (1.2%) included no adult males. A large proportion (65.0%, 52/80) of the small parties (≤10 individuals), however, were OMUs. The number of females per male was lower in MMUs than in OMUs (sex ratio: 1:2.5 vs. 1:3.3; $t=4.35$, $p<0.001$, $N_{MMU}=175$, $N_{OMU}=63$).

We recorded 2 small all-male units (AMUs, i.e., units of exclusively adult males) containing 3 and 2 adult males, respectively. We also noted 16 solitary males, 15 of which we observed in the dry season. Although we observed some party compositions up to 6 times during our study period, we only once saw a party of the same size and composition twice on 2 consecutive days. The mean time lag between observations of the same party compositions was 25 d (median 13 d; IQR 8–35.6; range 1–86; N=78).

Table 2.1 Composition and sex ratio of multi-male units (MMU: *n* = 175) and 1-male units (OMUs: *n* = 63).

	Party Size	Adult males	Adult females	Adult sex ratio
MMUs				
Mean	23.0	3.8	9.1	1:2.5
SD	15.6	2.6	6.3	1:1.1
Range	4-90	2-18	1-40	1:0.5-1:7.0
OMUs				
Mean	8.8	1.0	3.3	1:3.3
SD	4.1		1.5	1.5
Range	4-24		1-7	1:1.0-1:7.0

Changes in Party Size by Time of Day and Season

More and smaller parties arrived in the afternoon than in the morning (Fig. 2.6). In the morning, an average of 2 parties (median; IQR 1–3; range 1–8; N=49) arrived at the Mare whereas 4 parties arrived in the afternoon (median; IQR 2–6; range 1–11; N=60; Z=–3.969; p<0.001).

Median party size was 25 in the morning (IQR 11.5– 78.5; range 5–300; N=115) and 19 in the afternoon (IQR 11.5–32; range 4–210; N= 251; Z=3.670; p<0.001).

Parties were larger during the rainy season vs. the dry season (Fig. 2.7; χ^2=205.6, df=3, p<0.001). Party size was 16 in the dry season (median; IQR: 8.5–24; range 4– 125; N=191), and 30 in the rainy season (median; IQR 16–58; range 5–300; N=175; Z=–7.28; p<0.001).

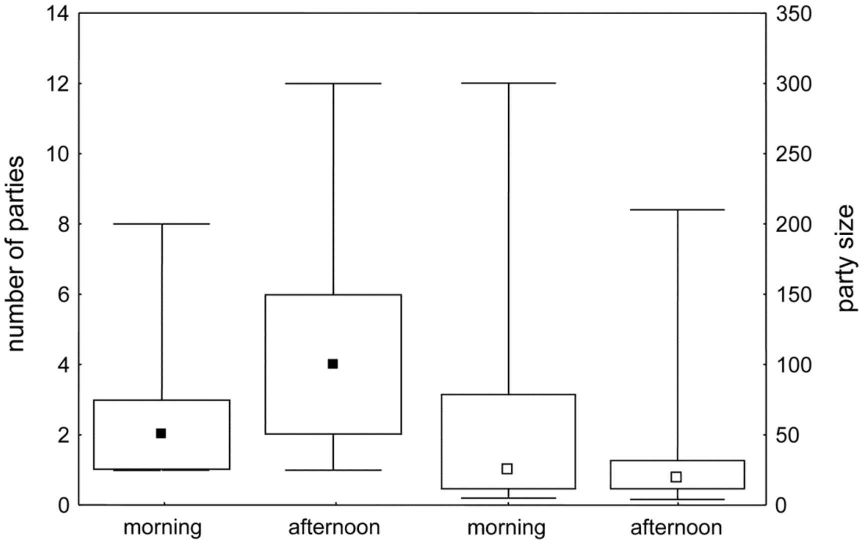

Figure 2.6 Number of parties arriving (black squares) and party size (white squares) according to time of day (morning and afternoon) (median, IQR, range).

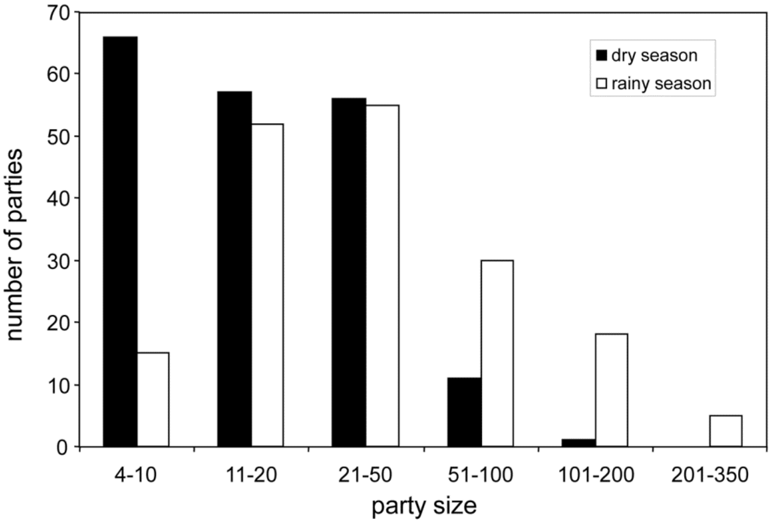

Figure 2.7 Frequency distribution of party sizes in the dry and rainy seasons (N = 366 parties).

Fission and Fusion

The fate of the parties arriving at the Mare is shown in Fig.2.8. 198 parties (54.1%) arrived and left the Mare without any change in size and composition. The average size of these parties was 19 (median; IQR 11–39, range 4–300; Fig. 2.8a). In the remaining 168 parties we observed fissions, fusions, and fusion–fission by intermingling of parties while the baboons crossed the Mare (Fig. 2.8b–d).

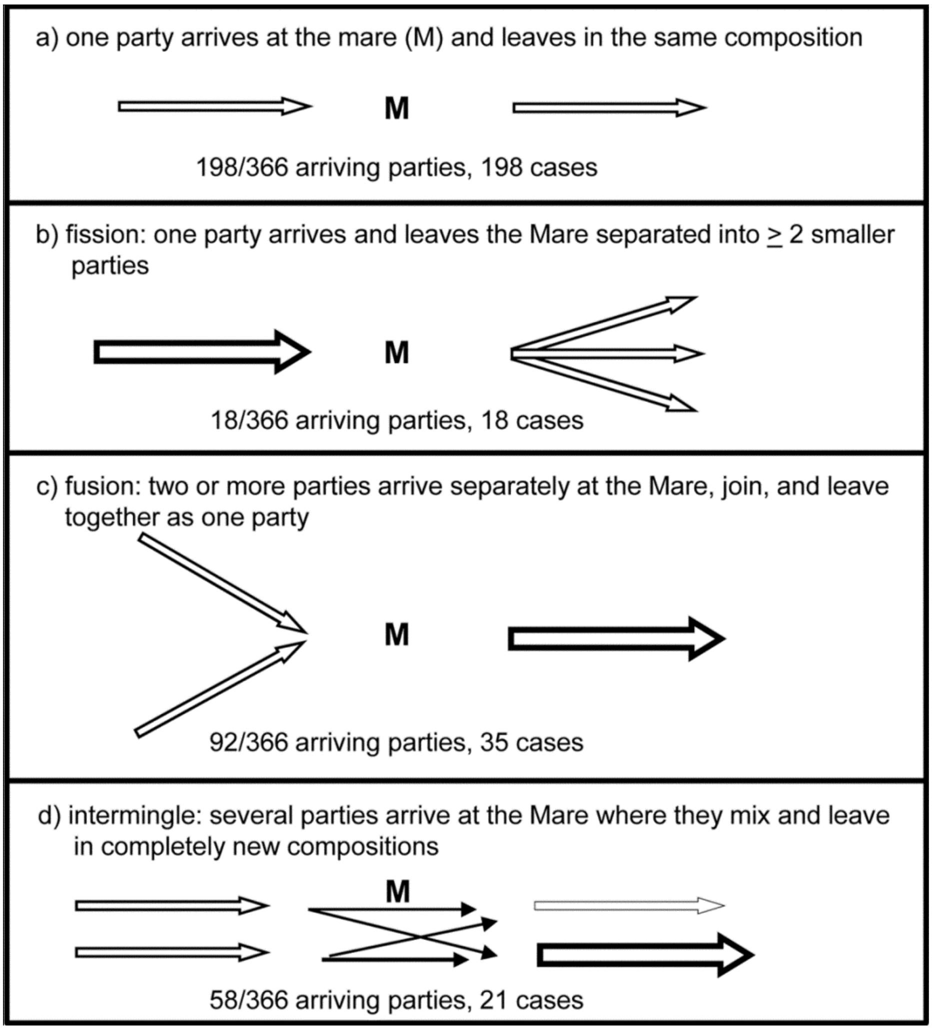

Figure 2.8 Fate of parties arriving at the "Mare" (M). Arrows indicate direction of movement and size of baboon parties. Total number of arriving parties = 366.

In 18 cases, 1 party arrived and left the Mare split into ≥2 smaller parties (Fig. 2.8b). The average size of these parties before splitting was 101 (median; IQR 46.5–151; range 9–220). On average, 2.7 (mean; SD 0.86; range 2–4; N=42) parties were formed out of 1 arriving party with an average size of 22 baboons (median; IQR 12.5–37.25; range 4–137).

In 35 cases, ≥2 parties arrived independently at the Mare, joined, and left together as 1 party (Fig. 2.8c). The mean number of parties to converge into a single party was 2.8 (mean; SD 1.37; range 2–7; N=95) with an average size of 20 individuals each (median; IQR 11–36; range 4–120), whereas the average size of the combined departing parties was 49 individuals (median; IQR 31–108; range 8– 330; N=38).

In 21 cases, several parties arrived at the Mare, where they mixed and then left as several newly composed parties (Fig. 2.8d). An average of 2.9 parties (mean; SD 1.59; range 1–6; N=58) with an average size of 22 individuals (median; IQR 13.5–38.5; range 4–80) arrived. Those parties split and individuals of several parties mingled and formed new parties. On average 2.8 parties (mean; SD 1.57; range 1–8; N=50) of 18 individuals (median; IQR 12–28.5; range 4–240) left.

DISCUSSION

Social Organization

The baboons came to the Mare from their various sleeping sites in scattered parties in the morning, and in the afternoon when distinct parties came back from foraging before moving back to their sleeping trees.We therefore only rarely saw the whole troop at the same time. We observed mainly parties of ≤25 individuals. Aggregations of ca. 40–60 and 70–90 individuals, as expected for savannah and hamadryas baboons respectively, were rare, suggesting that the troop most likely did not consist of several stable groups or bands, unlike savannah or hamadryas baboons (Fig. 2.5). Thus predictions 1 and 2a are not supported by our data. The observed distribution of party sizes was best described by a 0-truncated negative binomial distribution, suggesting that Guinea baboons join a group because they are attracted by its membership and that they do not associate in a random fashion, which would be the case if a 0-truncated Poisson distribution was a better fit (Cohen 1971; Wilson 2000).

Two thirds of the smaller parties (≤10 individuals) of known composition contained just 1 adult male and can be regarded as OMUs.We did not repeatedly observe specific spatially or temporally segregated clusters of 1 adult male, possibly subadult followers, and several adult females and their offspring in the same composition throughout all observations, contradicting prediction 2b. Moreover, the different sex ratios in OMUs and MMUs suggest that MMUs do not reflect a temporary association of several OMUs. Thus, prediction 2c is also not supported.OMUs seem not be the modal basal social unit in Guinea baboons, suggesting that the social organization of our focal troop seems to be different from hamadryas baboon organization.

However, these findings must be interpreted with caution as they do not exclude the possibility that observed MMUs do consist of several OMUs, but not always the same OMUs (unlike hamadryas baboons), resulting in a more flexible composition similar to that of geladas, as suggested by Sharman (1981). However, Sharman (1981) concluded that a harem structure (OMU organization) was improbable, as he frequently observed small social groups without any males, and argued that it would be impossible for males to control their females from a distance because visibility was highly restricted in the habitat where he studied the baboons. Similarly, at our study site, visibility is also largely restricted in certain habitat types.

An alternative explanation for the different sex ratios may be the presence of additional follower males that occasionally integrate into MMUs, which consist of OMUs, or defeated leader males that do not monopolize females anymore but remain attached to the unit, as is the case in both hamadryas and gelada baboons (Mori 1979; Stammbach 1987). However, because there is a large proportion of OMUs among the smaller parties, but also a high percentage of MMUs in the entire data set, we suggest that both kinds of parties occur and that the MMUs do not consist of OMUs. The simultaneous occurrence of OMUs and MMUs that are not composed of single OMUs would match neither the savannah nor the hamadryas baboon social organization, suggesting that Guinea baboons have a distinct system that cannot be integrated into the established dichotomic framework of baboon social systems.

Daily and Seasonal Variation in the Number of Parties Arriving and Party Size

The number and size of parties arriving varied on both a daily and seasonal scale. Fewer but larger parties arrived at the Mare and split for foraging in the mornings, whereas more but smaller parties came back from foraging in the afternoon. This seasonal fluctuation in party size corroborates Sharman's (1981) observations of increasing group sizes in the rainy season (Anderson & McGrew 1984; Galat-Luong *et al.* 2006). Boese (1973), Sharman (1981), and Galat-Luong *et al.* (2006) hypothesize that seasonal changes in group size are an adaptation to food scarcity in the dry season and conclude that Guinea baboons optimize group sizes according to a given situation, avoiding unnecessary demands on individual time budgets. Moreover, because food availability increases in the rainy season and, consequently, food competition decreases, groups may no longer be forced to split up for foraging (Anderson & McGrew 1984; Galat-Luong & Galat, 2003; Galat-Luong *et al.* 2006). This seems plausible, but both phenological data and quantitative records of seasonal changes in food availability are lacking for Guinea baboons. Another possible cause for the formation of larger groups in the rainy season is restricted visibility owing to denser vegetation, which may lead to higher predation risk as predators become harder to detect (Henzi & Barrett 2003; Sharman 1981).

About half of the arriving parties split up or merged with others when crossing or resting at the Mare. Thus troop cohesion was rather loose, and parties were highly variable in size and composition, both on a daily and seasonal scale. These findings suggest a flexible social organization with a high tendency for fission–fusion. However, it remains unknown whether parties are stable over time and whether the fission–fusion resembles a molecular organization, with particular independent subgroups, e.g., family or breeding groups such as OMUs in hamadryas baboons, or whether individuals decide when and where to go and with whom, in an atomistic organization similar to that of chimpanzees (Rodseth *et al*. 1991).

Our results regarding the apparently undifferentiated and highly flexible social organization of Guinea baboons are in accordance with those of other authors (Boese 1973; Sharman 1981). We were unable to distinguish the baboons individually, but we observed them intermingling on a daily basis, and party sizes and compositions were different before and after the intermingling of arriving parties. OMUs analogous to hamadryas OMUs may have aggregated before arriving at the observation site. However, we observed both males and females switching between multimale parties, with females grooming and even mating with different males, which is not characteristic of the hamadryas system. Further, male–male distances in our Guinea baboons were often very small and males interacted extensively (unpublished data), which also does not suggest a hamadryas-like OMU organization. We suggest that the basal social entities of Guinea baboons are OMUs and

MMUs, which are not made up of OMUs, i.e., some males may monopolize females whereas other males share females. Whether this social organization translates directly into the mating system and whether it represents 2 alternative male reproductive strategies needs to be explored.

CONCLUSION

We found no stable temporal or spatial patterns in Guinea baboon group composition. Guinea baboons appear to have a highly complex social organization with very variable group composition, on both a daily and a seasonal basis. Their social organization appears to resemble neither the strict multilayered OMU-based organization of hamadryas baboons nor the typical multimale organization of savannah baboons. It is likely that the social organization of Guinea baboons, and with it most likely the complete social system (*sensu* Kappeler & van Schaik 2002), is neither a precursor of the hamadryas system nor intermediate between savannah and hamadryas systems. In light of our data, we may have to revise our view of baboon social systems as a dichotomy, as they seem to be much more variable than previously assumed.

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CHAPTER 3

Spatial, Social and Genetic Relationships of Guinea Baboons (*Papio papio*) Suggest a New Dimension in Primate Social Diversity

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under review

ABSTRACT

Identifying the driving forces in social evolution is fundamental for understanding the emergence of cooperation, and ultimately human evolution. Baboons (*Papio* spp.) constitute an important model in this context. Traditionally, two different social organisations are distinguished: while savanna baboons (*P. anubis*, *P. cynocephalus*, *P. ursinus*) live in stable multi-male multi-female groups, the hamadryas baboon (*P. hamadryas*) society contains multiple levels based on one-male units. Little was known about Guinea baboons (*P. papio*), however. Here we report the results of the first study of individually recognized wild Guinea baboons, ranging in Senegal. Combining spatial and genetic data, we show that they exhibit a multi-level system consisting of subgroups ("parties") comprising 3-4 males and several females. Some but not all males in a given party are highly related. Specific parties regularly form a "gang". Several gangs utilizing the same home range constitute the "community". While the social organisation of Guinea baboons superficially resembles that of hamadryas baboons, we found stronger male-male affiliation, apparently higher female freedom, and more fluid grouping patterns. Our results support the notion that baboon social systems are more diverse than traditionally acknowledged, and raise important questions about the emergence of multilevel societies and primate social evolution in general

Keywords: Social evolution, Multi-level society, Male-male affiliation, Guinea Baboon, *Papio papio*

INTRODUCTION

Human societies are considered to be highly complex social systems, and a key question in anthropological research is how biological and cultural factors contribute to their differentiation. Traditional societies typically comprise several conjugal, predominantly monogamous families embedded in stable communities (Murdock 1949). Recent studies on contemporary hunter-gatherers have revealed a quite flexible bisexual dispersal pattern (e.g. Hill *et al*. 2011). Multiple family groups aggregate at higher levels, such as regional tribes of several hundred individuals who gather for rituals, politics or trade (Murdock 1949; Turnbull 1965; Steward 1969). Chapais (2008; 2011) suggested that this system evolved from groups composed of several males and females, characterized by a polygynandrous mating system, female dispersal, male philopatry and strong bonds between related males.

Attempts to uncover the driving forces in human social evolution have fuelled numerous comparative analyses of primate species (e.g. Kinzey 1987; Jolly 2009). In this context, baboons (*Papio* spp.) have been considered as a valuable model for investigating the influence of selection pressures and evolutionary constraints on the formation of social systems (de Vore & Washburn 1963; Dunbar 1988; Henzi & Barrett 2005; Jolly 2009; Swedell & Plummer 2012). The genus *Papio* evolved in a similar time frame and the same savanna habitats in southern and eastern Africa as early humans. To date, two main social systems have been contrasted in this genus: stable female-bonded social groups in the so-called savanna baboons, (*P. ursinus*, *P. anubis*, and *P. cynocephalus*) contrasting to a multi-level system in hamadryas baboons (*P. hamadryas*), where one-male units (OMUs) constitute the smallest social entity (Kummer 1968). OMUs aggregate into clans within which males are supposed to be related (Abegglen 1984). Several clans and additional single males form a band, which is a stable and exclusive unit, and thought to be homologous to the multi-male multi-female groups of savanna baboons (Dunbar 1988). Bands may aggregate into troops of up to 700 individuals at sleeping sites (Kummer 1968; Zinner *et al*. 2001). The closely related geladas (*Theropithecus gelada*) exhibit a superficially similar multi-level system. Yet, in contrast to hamadryas baboons, the base of an OMU is formed by closely related females and the aggregations of geladas are extremely fluid (Dunbar 1988; le Roux *et al*. 2011; Snyder-Mackler *et al*. 2012).

Comparatively little attention has been paid to the westernmost member of the genus *Papio*, the Guinea baboon (*P. papio*). While some previous studies, mainly from captivity or short field stints, suggested that Guinea baboon groups are based on OMUs that aggregate into larger parties, similar to the social organisation of hamadryas baboons (e.g. Boese 1973; Galat-Loung *et al*. 2006), others suggested a multi-male multi-female organisation comparable to that of savanna baboons (Dunbar & Nathan 1972) or one that differs from both, the savanna and the hamadryas baboon type (Shaman 1981; Patzelt *et al*. 2011). However, all authors agree in that females have more freedom in their social interactions than hamadryas baboon females, which are forcibly herded by their leader males.

In 2007, we initiated a long-term study in the Niokolo-Koba National Park in Senegal to investigate the social system of this species. We established the field station "Centre de Recherche de Primatologie (CRP) de Simenti" and began observations of a population ("community") of more than 350 individuals in the area. Observations during the time when individuals were still unhabituated showed that the community regularly splits into smaller subgroups of varying size, suggesting a relatively fluid system (Patzelt *et al*. 2011; see also Sharman 1981). Indeed, our first impressions mirrored those of Bert *et al*. (1967), who reported an "unstructured, anarchic appearance of the troops" (cf. Sharman 1981, p. 9.1). Here we provide the first systematic study on individually identified wild Guinea baboons. The specific aim of this paper is to resolve the debate regarding the species' social organisation. In the long term, this should contribute to our understanding of the factors that shape the social organisation of this genus specifically, and primate societies evolving in savanna habitats more generally. We used ranging data collected from animals equipped with Global Positioning System (GPS)-collars, proximity measures recorded during focal observations, and genetic analyses based on microsatellites to describe the association patterns of the animals in space and time, and in relation to genetic relationships, focusing on adult males. If Guinea baboons indeed live in a fluid and relatively unstructured fission-fusion society, as suggested by the highly variable subgroup size and composition observed by Patzelt and colleagues (Patzelt *et al*. 2011), varying association patterns should become evident, and no correlation between association patterns and genetic relatedness should be found. If, in contrast, this species lives in a structured multi-level society, cluster analyses of proximity data should identify the different strata in the association patterns. Moreover, if related males form the core of the society, as assumed in hamadryas baboons (Abegglen 1984), subjects that range together should reveal a higher genetic relatedness compared to the community average.

METHODS

Field Site and Study Subjects

The study site lies close to the field station of the German Primate Center (DPZ), the CRP Simenti (13°01’34’’N, 13°17’41’’W) in the Niokolo-Koba National Park in southeastern Senegal. The climate is highly seasonal with a rainy season from July to October. The vegetation comprises grassland, dry-deciduous, evergreen and palm tree forest, and gallery forest along the Gambia and Niokolo rivers (for further details, see Maciej *et al*. 2013). With increasing habituation of the animals, it became clear that the community was split into several middle-sized subgroups (“gangs”) containing approximately 30-60 individuals. There are at least five gangs in the area. These observations focused on one gang (Mare gang) in 2010, and on the Mare and a second gang (Simenti gang) in 2011. In 2010 the Mare gang contained c.63 individuals (incl. 9 adult males) and in 2011 the Mare gang contained c.55 and the Simenti gang c.60 individuals (both incl. 8 adult males each; see Tab. SI3.1). Between the two observation periods, two of the focal males disappeared from the Mare gang and one transferred into another gang. Two males classified as subadult in 2010 were assigned to the adult category in 2011 and included in the observations.

Spatial data

GPS Data

Initially, we captured subjects because they used the same sleeping site, without knowledge about their specific association patterns. In total, we fitted 18 baboons (11 males, 7 females) with GPS collars (Tellus GPS, Televilt, Lindesberg, Sweden) to obtain data on their ranging patterns. Collars were programmed to take synchronous dyadic distance measures (fixes) every other hour between 06:00 and 18:00, and at 21:00, 00:00 and 03:00 h). GPS data were downloaded in the field using a UHF download system (RCD-04, Televilt, Lindesberg, Sweden). The error of a fix was given as 10-15 m (Televilt, Lindesberg, Sweden). However, vegetation may have affected the precision with which the positions could be determined. We therefore set the spatial resolution of our analyses to 50 m. Because of limited resources, the considerable effort to renew the collars, and restricted battery life, not all animals could be equipped with collars at the same time. The precise number of animals equipped with a GPS collar at any one point in time is shown in Tab. SI3.2.

Based on the GPS data we calculated the inter-individual Euclidian distances among all GPS-equipped animals for each temporal sampling point. In total, we obtained 110,426 dyadic distance measures from November 2009 to January 2012 (mean 1330.4 per dyad, range 13-3997). For the calculation we used the custom software "at" (programmed by Ch. Franzl; for details please contact the corresponding author). The output of the program is a matrix of dyadic frequencies of individuals remaining within a specified distance category to each other within a given time frame. We calculated dyadic association indices (AIs) as the proportion of the number of fixes two animals were found in a certain distance category divided by the number of fixes available for the respective dyad. AIs for all dyads in a 100 m-distance were calculated as an estimator for the proportion of time individuals could possibly interact. This calculation is based on the assumption that animals in neighboring subgroups may find themselves at varying distances from the subjects that carry the collars, and hence could potentially interact even when the collared individuals were 100 m apart. To avoid an overrepresentation of fixes taken at sleeping trees, only data taken between 8.00 and 21.00h were included (i.e. one fix per night). In total, we were able to estimate the dyadic distances of 83 dyads.

In order to detect different levels in the social organisation based on variation in inter-individual distances, we conducted a change point analysis (Change Point Analyzer 2.3, Taylor Enterprises, Inc., IL, USA) to uncover significant changes in the mean squared error (MSE) distribution of the data (Taylor 2000). We ran 10,000 bootstraps without replacements and set the confidence interval (CI) at 90 %. We repeated the procedure 30 times until the solution converged.

We derived home range estimates using the fixed kernel density estimation from Hawth's Tools (http://www.spatialecology.com/htools/tooldesc.php) implemented in ArcGIS 9.3 (ESRI 2008, Inc., Redlands, US). We calculated 95 % and 50 % kernel density plots (hereafter referred to as kernel home ranges (Worton 1989); using the GPS derived dataset matching with the second observation period in 2011 (see Tab. SI3.2). We used GPS-data of one representative for each of the three gangs; data for members of the same gang were highly correlated with each other.

Spatial Association Patterns Based on Observations

AP determined spatial association patterns of individuals from March to July 2010 (75 observation days) and from January to June 2011 (106 observation days). Data were collected between 6:00-12:00h and occasionally between 16:00-19:00h. During 239 scans in 2010 and 318 scans in 2011, the identity of all adult males who were seen in proximity of each other up to 20 m distance was noted. Scans were taken in the course of behavioral observations, i.e. at the beginning of each focal protocol (lasting 60 min). To obtain a sufficient sampling depth, we restricted these first observations to adult males.

We calculated dyadic association indices as (AB+BA)/2 with AB being the proportion of scans for male A seen with male B, and BA being the proportion of scans for male B seen with male A. We analyzed the datasets of 2010 and 2011 separately because of differences in the number of gangs observed as well as changes in group composition of the Mare gang, which were observed in both years (see above). To examine grouping patterns we applied hierarchical clustering using Euclidean distances in Statistica 10 (StatSoft, Inc., Tulsa, OK, USA). To determine the most appropriate clustering method, we used the cophenetic correlation coefficient (CCC), which reflects the correlation of the AIs between two individuals in the dendrogram and the actual AIs between two individuals. The CCC thus describes how correctly the real data are represented by the dendrogram (Sokal & Rohlf 1962). We obtained dendrograms using the single, complete and average linkage methods and compared them to the real data. The results obtained with the average linkage method revealed the highest correlations (CCC_{2010}=0.981 and CCC_{2011}=0.987). The other methods yielded only marginally weaker correlations (single link 0.978 (2010) and 0.965 (2011); complete link 0.979 (2010) and 0.975 (2011)). Additionally, we used an iterative clustering method (Tabu Search provided in UCInet version 6 (Borgatti *et al*. 2002)) to confirm the number of clusters in the dataset obtained from the hierarchical cluster analysis. The program uses a combinatorial optimization algorithm to assign nodes to as many clusters as hypothesized by the user and attempts to find the best fit (i.e. the highest r^2-value). For each dataset, all possible cluster solutions (i.e. up to the total number of adult males) were tested.

To assess the identity of males' neighbors in close proximity, AP additionally conducted scan samples at 10min-intervals and recorded the identity of all adult individuals within a 1m-radius of the focal male. We calculated the percentage of scans the focal males spent in close proximity to an adult female, an adult male, or both at the same time. We collected 1480 scans of 11 focal males (5 of the Mare and 6 of the Simenti gang) in 2011; (mean = 135 scans/male; range: 127-140).

Genetic Data

During the capture of the animals, we collected tissue samples (ear punch, c. 0.5 x 0.5 cm^2) from 40 adult males under anesthetic (data on subgroup affiliation see Tab. SI3.3a). Samples from females are not considered here. We stored the samples in 90 % ethanol for up to six months at ambient temperature in the field before shipping them to the German Primate Center, Germany. We extracted DNA using the QIAamp DNA Blood and Tissue Mini Kit (Qiagen, Hilden, Germany) following the manufacturer's protocol and stored the extracts at -20°C. We genotyped individuals at 25 polymorphic autosomal microsatellite loci (mean number of alleles per locus 4.08 ± 1.19 SD) using 5 multiplex PCR reactions (more details on loci in Tab. SI3.4b). We determined PCR fragment length by capillary electrophoresis on an ABI 3130xL Genetic Analyser (16 capillary sequencer, Applied Biosystems, U.S.A.). Details on loci and the protocol are given in SI3.3. Fragment length was rated relative to the size standard using PEAK SCANNER^{TM} Software v1.0 (Applied Biosystems, U.S.A.). To assure accuracy, we repeated the genotyping and two investigators called the alleles independently.

We estimated dyadic relatedness coefficients (Queller & Goodnight 1989) in COANCESTRY v 1.0 (Wang 2011) (the estimator may range from - 1.0 to + 1.0 and negative values indicate that individuals share fewer alleles than the mean level of the population). We then examined the average genetic relatedness of male-male dyads in relation to their social affiliation (see below). Dyads that could not be assigned to any category of social affiliation (i.e. they were never seen again) were excluded from the analysis (175 out of 703 dyads removed). We assessed differences in average dyadic relatedness between the pairs of social levels by bootstrapping the individuals 10,000 times using the program COANCESTRY v1.0 (Wang 2011). Because of the lack of information about known mother-offspring pairs, we refrained from parentage analyses. For more details on genetic analyses see SI3.3.

RESULTS

Spatial Data

Both GPS data and data on spatial associations collected during focal observations support the assumption that the Guinea baboon community consists of multiple levels. 14 out of 18 collared individuals belonged to the two focal gangs and three individuals belonged to a gang that we regularly encountered during focal follows (River gang). One remaining male belonged to a separate gang that we never saw during focal observations. GPS data revealed that this male came in proximity with all other collared individuals occasionally (AI range 0.01-0.04).

The change-point analysis (CPA) based on GPS data detected three structural levels in the data. Firstly, there was a change point separating AIs smaller and larger than 0.12, respectively. This corresponds to the distinction between the community and what we termed the “gang” (Fig. 3.1).

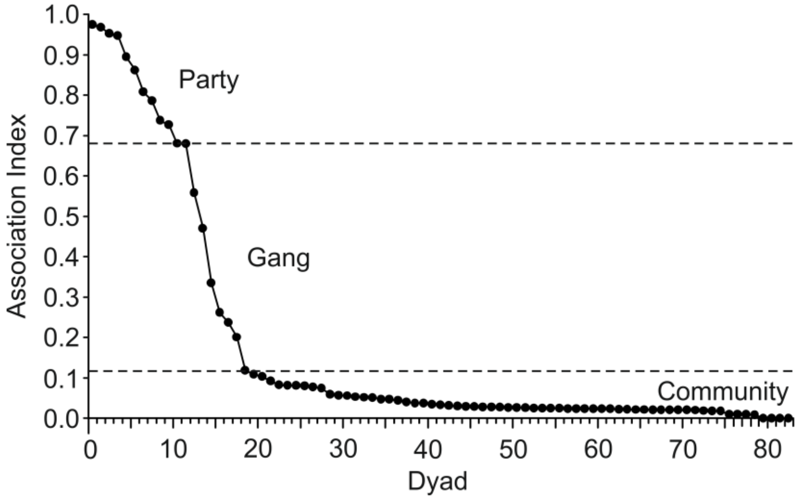

Figure 3.1 Distribution of dyadic spatial association indices of 83 dyads within the study community. The two dotted lines indicate change points in the distribution, suggesting three levels. The complete GPS data set is represented (see Table SI2).

The majority of dyads (65 out of 83) associated rarely (AI ≤ 0.12); these dyads were classified as belonging to the same community. Secondly, the algorithm detected a change point reflecting dyads with an AI ≥ 0.68 (n=12); these were classified as belonging to the same "party". The second change point is however less supported than the first one (91% vs. 100% confidence level). The community-gang split was confirmed in 28 out of 30 runs (93%) and the gang-party split in 22 out of 30 runs (73%). We include the second change point here assuming that a larger sample size would have led to a clearer result. To give an impression of the varying grouping patterns, an example of dyadic distances for the course of four days is depicted in Fig.3.2.

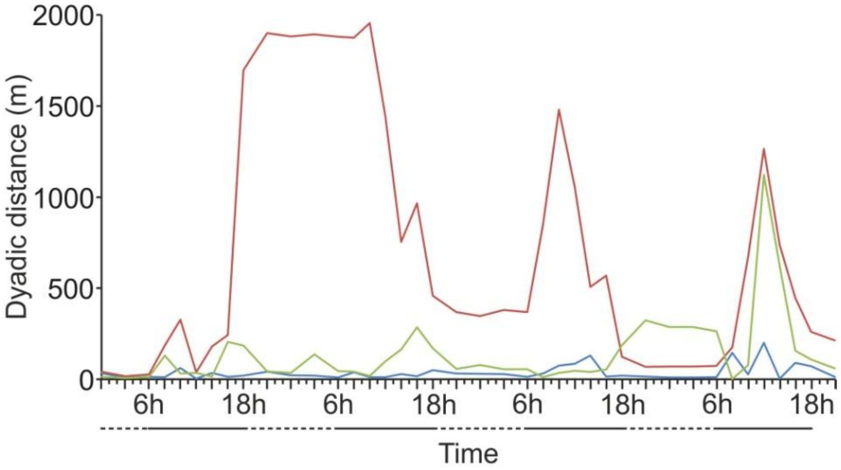

Figure 3.2 Dyadic distances during the course of four consecutive days (filled horizontal bars) and five nights (open horizontal bars; 5th through 8th of March 2010) for three dyads. The figure illustrates an example of the variable association patterns within the community (blue line= party-dyad, green line=gang-dyad, red line=community dyad).

Although the three gangs had almost identical home ranges (Fig. 3.3), they did not spend much time in close proximity. In 2011 the Mare and Simenti gangs spent only 2.7 % of their time within 100 m distance. The Mare and River gangs spent 7.2 %, and the Simenti and River gangs 2.4 % of their time within 100 m (including one fix taken after dusk, thus when animals were on sleeping trees).

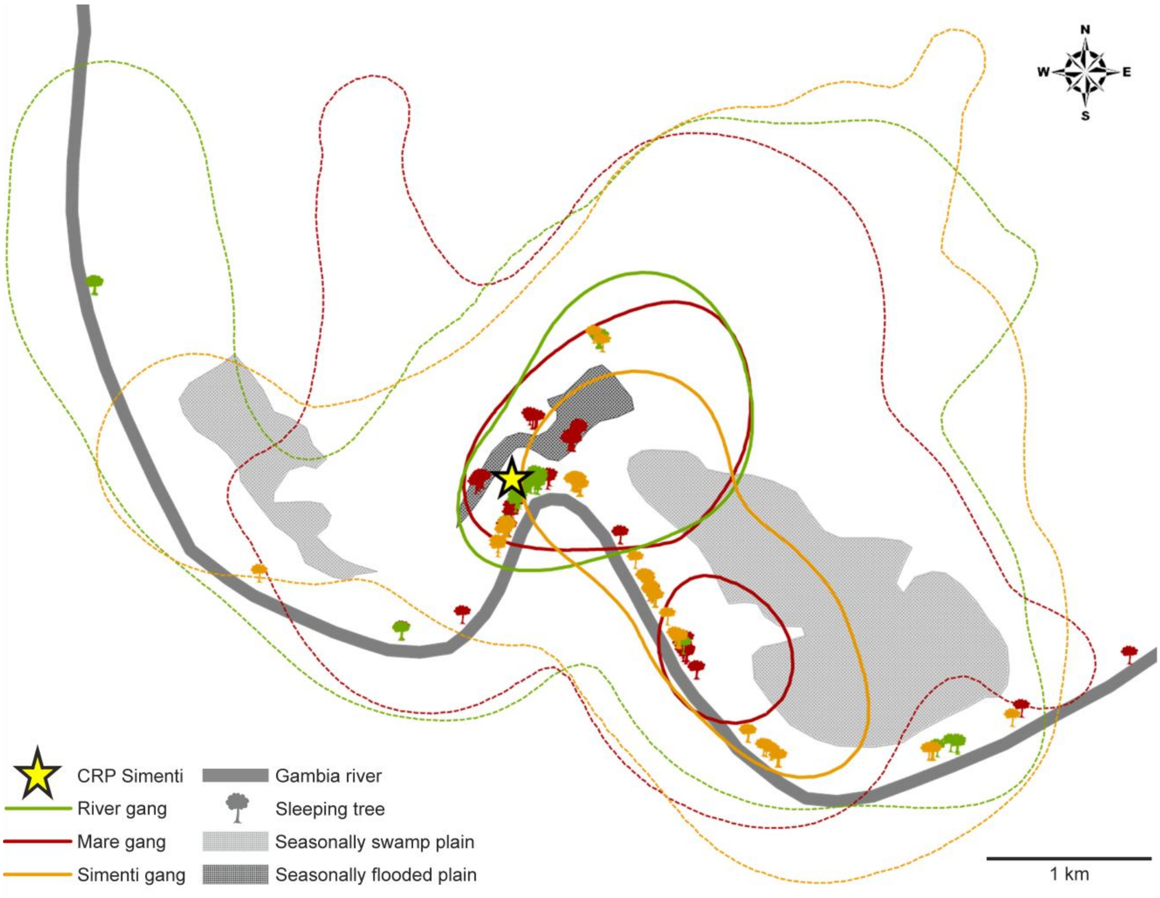

Figure 3.3 Sketch of the study area including fixed kernel home ranges and sleeping trees of three gangs based on GPS data obtained from March to June 2011. Colored lines represent the home ranges of the different gangs (dotted lines: 95% kernel home range; thick lines: 50% kernel core area). The 50 % data showed a somewhat higher differentiation, where one area was used by the Mare and Simenti, but not by the River gang.

The results of the hierarchical cluster analysis based on dyadic AIs extracted from focal observations also support the view of a multi-level organisation. Fig. 3.4 shows three clusters of 3 adult males each for the 2010 dataset. This was confirmed by Tabu Search cluster analysis resulting in a best fit for 3 clusters (r^2=0.91). In the 2011 dataset the first bifurcation reflects the split into the two gangs (8 adult males each). Within both gangs, we found two clusters (best fit 4 clusters; r^2=0.74), each including 4 males. These clusters represent different parties. In 2011 the composition of the Mare gang changed as two males disappeared (CSS, MBY), one changed into another gang (ANT), and two subadults became adult and were included in the analysis of 2011 (BAA, NDR). Thus, six males were included in the analyses of both years (HOK, SNE, SML, PTR, OSM, DTM). On average, the AIs among party dyads were 0.65 (± 0.10 SD) while those among gang dyads were 0.24 (± 0.10 SD; see Tab. SI3.4). Mean party size was 25 individuals (range 16-35).

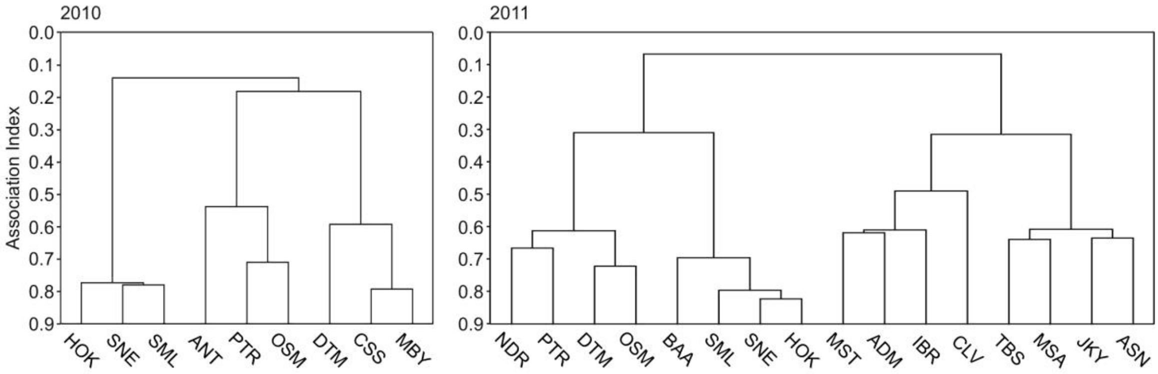

Figure 3.4 Dendrograms resulting from hierarchical cluster analysis (average linkage method) based on association indices among 9 adult males during the 2010 observation period (n=36 dyads) and among 16 adult males during the 2011 observation period (n=120 dyads). Letter codes represent individual males.

The close proximity scans (i.e. 1 m) indicated that males spent considerable time near each other: in case there was another individual within 1m of the focal animal, in 63% of scans the partner was a female, in 26% it was a male, and in 11% a male and a female. Note that the male:female ratio is about 1:2 (see Tab. SI3.1). In about one out of five cases (22.1 %), the male partner in 1 m proximity belonged to another party (of the same gang).

Genetic Data

Relatedness coefficients for within- and between-gang male-male dyads were significantly different for both the 2010 and the 2011 dataset at a 99% confidence level (Tab. 3.1). Regarding within-party and between-party dyads, we found however no difference in pairwise relatedness (Tab. 3.1). The analyses included all dyads that could be assigned to a category of social affiliation.

Within the whole dataset we detected 17 dyads among adult males that appeared to be highly related (pair-wise *r*-values ranged from 0.25-0.51). Three of the five parties we observed apparently comprise one closely related male-male dyad and additional males that were not (highly) related to any other adult male in the group. One further highly related party-dyad was not subject of our observations. Members of 5 dyads belonged to different gangs. The remaining

8 highly related dyads included males that we could not assign to any party since we did not observe them again after taking the samples for genetic analyses.

Table 3.1 Mean pair wise relatedness (*r* ±SD) of adult males at different social levels within the community for both study periods. Within-gang dyads were significantly more related than between-gang dyads (*Asterisk* =statistical significance). The number of dyads varies between years due to demographic changes.

Level	2010	n dyads		2011	n dyads	
within party	0.02 ± 0.22	29		0.01 ± 0.21	34	
between parties	0.00 ± 0.15	43		0.01 ± 0.16	30	
within gang	**0.01** ±0 .18	72	] **	**0.01** ± 0.19	64	] **
between gangs	**-0.05** ± 0.16	456		**-0.05** ± 0.15	464	

DISCUSSION

Based on the ranging patterns derived from GPS data, and the proximity data collected during focal observations, we found support for a three-level system consisting of the party, the gang, and the community. While some of the male-male dyads with highest AIs, who were classified as belonging to the same party, were highly related, there were also close spatial associations between unrelated males within parties, yielding no significant differences in average relatedness at the party and the gang level. However, on average males were more related within than between gangs. Males spent a considerable amount of time in close proximity of each other.

Spatial Data

The distribution of the GPS-based association indices revealed that most dyads spent less than 12% of their active time (AI≤0.12) within 100m, while some dyads spent ≥68% within this distance. Some remaining dyads revealed intermediate values, suggesting three levels within the society. This was generally supported by the results of the change point analysis. There were unfortunately few of the intermediate dyads in our sample, thus the statistical power is relatively low, which may have led to a lower confidence interval for the second change point (i.e. the gang-party split). However, the results of the cluster analyses of the proximity measures taken during focal observations, which complement the GPS data by including all adult males within the focal gangs, are in line with those obtained from GPS data and strongly support our assumption of the existence of three levels within this community (AIs obtained from both datasets are depicted in Tab. SI3.4).

Our results refute the assumption of a highly fluid and relatively unstructured fission-fusion system that was based on previous observations from unhabituated animals (Patzelt et al. 2011). Instead, we found evidence for three different levels in the social organisation of this species. Parties consisting of 3-4 males form the core of the society. These males appear to be highly tolerant of each other, as they spent considerable time in close proximity. This is in line with reports from captivity (Boese 1973), where strong bonds between specific males have been observed. The Guinea baboon party is not an exclusive unit though; one in five dyads sitting within 1 m distance belonged to different parties. This may explain why we earlier on found that group size and composition varied (Patzelt *et al*. 2011). Specific parties may range together as a gang. Thus, the gang composition is relatively predictable, unlike in individualistic fission-fusion societies where a high variability in association patterns can be observed (Aureli *et al*. 2008; Grueter *et al*. 2012a). In sum, our results confirm the notion that Guinea baboons live in a multi-level society and show extensive male-male interaction and tolerance based on quantitative data. This supports previous ideas expressed by Sharman (1981) who reported that his study groups temporarily split into smaller sub-groups, as well as findings from Galat- Luong and colleagues (2006), who reported 'second- and third level-groupings' among Guinea baboons. Evidence from playback experiments with males of our study groups revealed that they responded strongly to grunts from other males of the same gang, while they ignored calls recorded from either neighboring gangs or unknown animals (Maciej *et al*. 2013). These findings, together with our spatial and genetic analysis, tentatively suggest that the gang constitutes an important organisation level in this species.

Genetic Data

The genetic analyses revealed that males within a gang are more related to each other than males of different gangs. Overall, the genetic relatedness was however rather low and close genetic relationships also existed between males from different gangs, suggesting that males disperse across parties and gangs. Three of five parties comprised at least one closely related male-male dyad and two additional males who were not related to any other male in the party. This may suggest that long-term ties with related as well as unrelated subjects are more important than kinship alone. Indeed, data from captivity indicate that associations between adult and subadult Guinea baboon males already developed when they were juveniles and infants, demonstrating that such bonds may continue for several years (Boese 1975).

The observed grouping patterns indicate a relatively high tolerance among males. This could possibly be caused by male philopatry, similar to what is supposed for hamadryas baboons (Abegglen 1984). If males stayed in their natal group, the existence of some kin relations between males might promote the evolution of male-male tolerance more generally. This in turn facilitates the formation of ties among unrelated males. Long-term observations from the field as well as population-genetic studies will be needed to resolve this question.

The Comparative Perspective

The multi-level organisation of Guinea baboons superficially shares some features with the social organisation of hamadryas baboons. However, the characteristics of male-male bonds seem to differ; Guinea baboon males form stable clusters (parties) and proximity data suggests that they are highly tolerant of one another and maintain strong affiliative relationships. This observations corroborate Sharman`s findings (Sharman 1981), who frequently observed adult males grooming each other (see also Boese 1973; Galat-Loung *et al*. 2006). In contrast, affiliative contact between hamadryas leader males of different OMUs is rare (Kummer 1968; Schreier & Swedell 2009; Grueter *et al*. 2012a). The social organisation of Guinea baboons also differs from that of geladas. Most importantly, spatial associations at all levels are lower in Guinea baboons than in geladas (Snyder-Mackler *et al*. 2012) while male-male relationships seem to be more important.

The data presented here are mostly referring to males. During each observation period most of the males maintained close associations with a specific set of females. Systematic data on the persistence of these bonds are still lacking. Notably, in previous studies females were observed to move freely within groups and the aggressive herding behavior hamadryas males exhibit towards their females was not observed (Sharman 1981; Galat-Luong *et al*. 2006; Patzelt *et al*. 2011). In a previous study on spatial grouping patterns we found no support that OMUs constitute the smallest entities in the social organisation of the study community (Patzelt *et al*. 2011). In our view, the combined results of the present study and the findings from previous studies (e.g. Sharman 1981; Galat-Luong *et al*. 2006) justify the assumption that the Guinea baboon society differs substantially from that of other members of the genus *Papio*, as well as that reported for geladas. In particular the combination of pronounced male-male tolerance and female freedom within a multi-level society indicates that the Guinea baboon society might not simply represent behavioral flexibility within either of the known baboon systems. To avoid confusion with the hamadryas system, we opted for a separate terminology to label the different levels in the Guinea baboon society.

CONCLUSION AND OUTLOOK

Taken together, our results strongly support earlier assumptions (e.g. reviewed in Henzi & Barrett 2005) that the diversity of social systems in the genus *Papio* is larger than previously reported. Our observations of the Guinea baboon social organization strongly suggest that the genus *Papio* encompasses at least three, and not just two different types of social systems, the savanna and hamadryas baboon systems (see also Galat-Loung *et al*. 2006; Patzelt *et al*. 2011). More detailed observations (currently underway) on the social relationships including data on female social relationships and mating patterns, as well as paternity and population genetic analyses will be needed to fully characterize their social system, however.

Ultimately, the question arises which processes gave rise to the variation in social systems in the genus *Papio*. Socio-ecological models consider resource distribution, predation pressure and infanticide risk being major factors shaping social systems (Wrangham 1980; Sterck *et al*. 1997). Presently, evidence is accumulating that variation in the key factors considered in socio-ecological models is not sufficient to explain grouping patterns observed in extant nonhuman primates. In Old World monkeys, for instance, grouping patterns reveal a strong phylogenetic signal (di Fiore & Rendall 1994; Shultz *et al*. 2011). As a consequence, phylogenetic constraints and inertia have received increasing interest (Henzi & Barrett 2005; Chapman & Rothman 2009; Clutton-Brock & Janson 2012). Phylogenetic modeling of the transitions between different primate social systems also stressed the importance of evolutionary constraints and indicated a step-wise and directed evolution (Shultz *et al*. 2011). Notably, Jolly (2009) argued that shifts in the social organisation of baboons may be related to demographic factors acting during the range expansion of the genus during the Pleistocene. Genes predisposing for male philopatry in ‘frontier’ populations might have been accumulated, when males which stayed within their natal group might have reproduced more successfully than males dispersing into the ‘baboon-free’ territory beyond the frontier of expansion. Staying within their natal groups in turn may have led to increased male-male cooperation via kin selection. The idea that population genetic processes, such as drift and bottlenecks particularly in populations experiencing range expansion, might have an important impact on the genetic makeup of a species, and thus also on its behavior, has been supported in several studies Hallatschek *et al*. 2007; Excoffier & Ray 2008; Datta *et al*. 2013). Future research will need to integrate information on past and present resource distribution using spatially explicit models (e.g. Chan *et al*. 2011) while aiming to develop a better understanding of the phylogenetic constraints limiting the flexibility in social behavior. This will also be relevant for a deeper comprehension of human social evolution.

ACKNOWLEDGEMENTS

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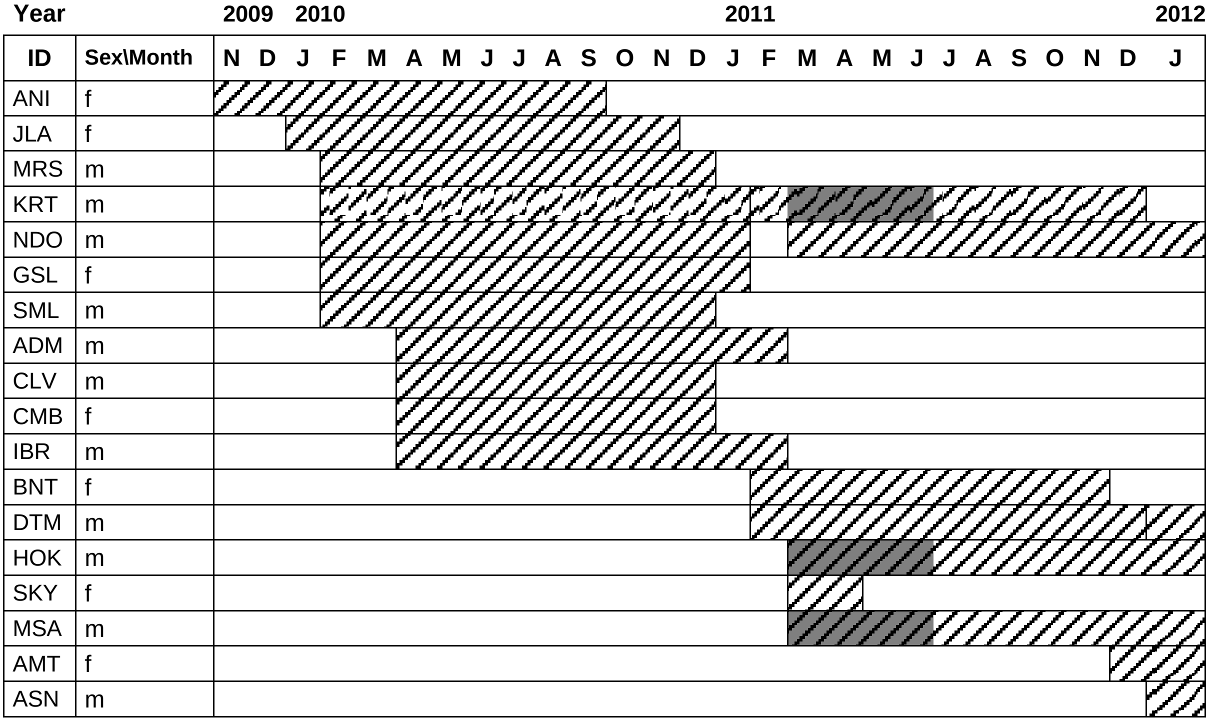
SUPPLEMENTARY MATERIAL CHAPTER 3

Table SI3.1 Gang compositions for the two study periods

Gang	Year	Number of individuals	Adult males	Adult females	Subadult males	Juveniles	Infants
Mare	2010	c.63	9	c.19	3	c.22	10
Mare	2011	c.55	8	16-17	2	19-20	9
Simenti	2011	c.60	8 (+2*)	c. 18	4	c. 20	8+

*this gang contained two older subadult/young adult males which were seen occasionally and not habituated to observers. They were thus not included as focal subjects, but as unspecified "subadult male" partners in interactions.

Table SI3.2 GPS dataset. Light grey: dataset used in CPA (Fig.3.1), dark grey: dataset used for home range calculations (Fig. 3.3).



Year		2009		2010												2011												2012
ID	**Sex\Month**	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**
ANI	f	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨																
JLA	f			▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨														
MRS	m				▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨													
KRT	m				▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨		■	■	■	■	▨	▨	▨	▨	▨	▨	
NDO	m				▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
GSL	f				▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨												
SML	m				▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨													
ADM	m						▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨											
CLV	m						▨	▨	▨	▨	▨	▨	▨	▨	▨													
CMB	f						▨	▨	▨	▨	▨	▨	▨	▨	▨													
IBR	m						▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨											
BNT	f																▨	▨	▨	▨	▨	▨	▨	▨	▨	▨		
DTM	m																▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
HOK	m																	■	■	■	■	▨	▨	▨	▨	▨	▨	▨
SKY	f																	▨	▨									
MSA	m																	■	■	■	■	▨	▨	▨	▨	▨	▨	▨
AMT	f																										▨	▨
ASN	m																											▨

SI3.3 Genetic Analyses

Table SI3.3a ID and subgroup membership of individuals used in genetic analyses

2010	ID	Party	Gang	2011	ID	Party	Gang
1	CSS	MBY-CSS	Mare				
2	MBY	MBY-CSS	Mare				
3	DTM	MBY-CSS	Mare		DTM	OSM-PTR	Mare
4	OSM	OSM-PTR	Mare		OSM	OSM-PTR	Mare
5	PTR	OSM-PTR	Mare		PTR	OSM-PTR	Mare
6					NDR	OSM-PTR	Mare
7	ANT	OSM-PTR	Mare		ANT		AMU
8	SML	SNE	Mare		SML	SNE	Mare
9	SNE	SNE	Mare		SNE	SNE	Mare
10	HOK	SNE	Mare		HOK	SNE	Mare
11					BAA	SNE	Mare
12	ADM	MST	Simenti		ADM	MST	Simenti
13	CLV	MST	Simenti		CLV	MST	Simenti
14	IBR	MST	Simenti		IBR	MST	Simenti
15	MST	MST	Simenti		MST	MST	Simenti
16	ASN	JKY	Simenti		ASN	JKY	Simenti
17	JKY	JKY	Simenti		JKY	JKY	Simenti
18	MSA	JKY	Simenti		MSA	JKY	Simenti
19	TBS	JKY	Simenti		TBS	JKY	Simenti
20	FLL	FM	?		FLL	FM	?
21	MOR	FM	?		MOR	FM	?
22	BDU	NASE	?		BDU	NASE	?
23	MDI	NASE	?		MDI	NASE	?
24	RMB	NASE	?		RMB	NASE	?
25	SNA	NASE	?		SNA	NASE	?
26	KRT	KRTNDO	River		KRT	KRTNDO	River
27	NDO	KRTNDO	River		NDO	KRTNDO	River
28	BDG	?	?		BDG	?	?
29	DVD	?	?		DVD	?	?
30	FRD	?	?		FRD	?	?
31	LDW	?	?		LDW	?	?
32	MMD	?	?		MMD	?	?
33	MRS	?	?		MRS	?	?
34	MRT	?	?		MRT	?	?
35	MTS	?	?		MTS	?	?
36	OMR	?	?		OMR	?	?
37	RMN	?	?		RMN	?	?
38	SMB	?	?		SMB	?	?
39	SNG	?	?		SNG	?	?
40	SRN	?	?		SRN	?	?

Microsatellite Amplification

We amplified the 25 microsatellite loci using human map pair primers (Table SI3b). We chose loci that have previously been used in other studies on baboons, whose fragment length and annealing temperature fit into the multiplex protocol and that proofed to amplify well in a pilotstudy (GF unpublished data). Multiplex PCR amplifications were performed on a Sensoquest labcycler in a total volume of 10µl, composed of 1.2µl DNA extract, 2.65µl H_2O, 5.0µl Qiagen Multiplex PCR Kit Mastermix (contains HotStartTaq® DNA Polymerase, Multiplex PCR Buffer (contains 6mM $MgCl_2$), dNTP Mix; Qiagen, Valencia, California, U.S.A), 1.0µl Primermix (containing 0.07-0.9µM of 4-6 primer pairs, Tab. SI3.4) and 0.15µl BT. PCR conditions comprised a pre-denaturation and polymerase activation step at 95°C for 15min, followed by 35 cycles at 94°C for 30s, optimal annealing temperature T_a for 40s, 72°C for 40s, and a single final extension step at 72°C for 30min. All sets of amplifications contained negative controls with HPLC water to monitor contamination. PCR amplification success was confirmed by visualization of 1µl of product under UV light after electrophoresis on 2.5% agarose gels containing ethidium bromide. Concentration of DNA was estimated by comparison with 1µl pUC19 DNA (Fermentas, Burlington, Ontario, Canada) with known concentration of 5, 10, 25, and 50 ng/µl respectively. 0.5µl approptiately diluted PCR product was mixed with 9.9 µl Hi-Di^{TM} (Applied Biosystems, Foster City, CA, U.S.A.) and 0.1 µl GeneScan^{TM}-400HD ROX Size® Standard (Applied Biosystems) and further analysed by capillary electrophoresis on an ABI 3130xL Genetic Analyser (16 capillary sequencer, Applied Biosystems).

We calculated summary statistics in GENEPOP 4.0.10 (Rousset 2008) and ARLEQUIN 3.5 (Excoffier & Lischer 2010; see Table SI3b). All loci were in Hardy–Weinberg equilibrium, and showed no evidence of linkage disequilibrium or null alleles. F_{IS} values were all around zero (mean 0.03; range -0.21-0.13), thus the population does not seem to be affected by inbreeding.

Table SI3.3b Multiplex-PCR relevant information (left) and summary statistics (right) for 25 microsatellite loci used for dyadic relatedness estimates

Multiplex PCR	Locus	Ta (°C)	Primer Conc.(uM)	Allele range (bp)	No. of allels	H obs.	H exp.	Fis
M1	D6s264	57	0,07	94-100	4	0,55	0,51	-0,08
57°C	D7s503	54	0,7	144-158	5	0,81	0,75	-0,08
	D12s375	57	0,1	165-181	5	0,73	0,78	0,06
	D3s1766	58	0,05	194-202	3	0,30	0,28	-0,07
	D13s765	58	0,15	197-213	5	0,42	0,46	0,10
M2	D14s306	62	0,08	157-177	4	0,57	0,55	-0,04
50°C	D1s533	55	0,05	187-203	4	0,69	0,67	-0,02
	D2s1329	50	0,9	210-226	5	0,60	0,60	0,01
	D2s1326	56	0,08	239-263	4	0,42	0,39	-0,08
M3	D10s611	60	0,1	133-141	3	0,57	0,55	-0,03
59°C	D8s1106	58	0,1	144-160	4	0,51	0,46	-0,09
	D17s791	57	0,3	164-170	4	0,46	0,50	0,07
	D6s501	58	0,3	172-192	5	0,72	0,71	-0,01
	D17s1290	56	0,25	194-206	4	0,57	0,58	0,03
	D6s311	54	0,3	226-228	2	0,36	0,37	0,02
M4	D5s1457	58	0,08	121-133	2	0,36	0,38	0,06
57°C	D8s505	57	0,1	139-151	2	0,25	0,25	-0,04
	D10s1432	56	0,3	159-171	4	0,57	0,54	-0,04
	D5s820	53	0,4	178-198	6	0,84	0,76	-0,10
	D3s1768	56	0,08	193-209	4	0,43	0,50	0,13
	D7s2204	57	0,4	232-248	5	0,72	0,76	0,06
M5	D1s207	57	0,1	133-135	2	0,55	0,46	-0,21
58°C	D4s243	60	0,1	147-171	5	0,75	0,65	-0,15
	D1s548	57	0,1	192-208	5	0,85	0,76	-0,12
	D21s1142	58	0,5	226-246	6	0,78	0,71	-0,09
	mean				**4,08**	**0,57**	**0,56**	**-0,03**
	SD				1,19	0,17	0,16	

Table SI3.4 Association indices obtained from GPS data and focal observations, respectively (mean±SD).

Group Level	**AI $_{\text{GPS data}}$**	**AI $_{\text{focal data}}$**
Party	0.83±0.11	0.65±0.10
Gang	0.34±0.14	0.24±0.10
Community	0.04 ± 0.03	0.07±0.02

CHAPTER 4

Strong Male Bonds at the Core of a Tolerant Multi-Level Primate Society

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Author contributions: All authors designed research, AP collected and analyzed data. All authors discussed the results and contributed to the final manuscript.

prepared for submission

Male relationships are generally characterized by intra-sexual competition (Trivers 1972; van Hooff & van Schaik 1994) and according to kinship theory, bonding among unrelated individuals is supposed to be rare (Hamilton 1964). Yet, human societies rely on the ability to cooperate and to form strong bonds between males, regardless of kinship (Chapais 2010). The emergence of cooperative relationships has been linked to the multi-level structure of traditional human societies (Grueter *et al*. 2012a; Silk & Boyd 2010). Due to the scarcity of archaeological evidence, attempts to understand the transition from competitive to cooperative relationships include comparisons with nonhuman primates (Grueter *et al*. 2012a; Swedell & Plummer 2012). Based on an analysis of social interaction patterns in combination with genetic networks, we here show that male Guinea baboons (*Papio papio*) living in a multi-level social organization maintain strong bonds and high tolerance among each other within and between subgroups. Bonding patterns among males were, however, not correlated with genetic relatedness. This result supports the view that bonds *per se* may be adaptive (Clutton-Brock 2009; Hill & van Hooff 1994; Langergraber *et al*. 2007; Schülke *et al*. 2010). The social relationships of male Guinea baboons differ markedly from other members of the genus, adding valuable comparative data to test hypotheses regarding social evolution. As the Guinea baboons' social organization and social relationships resemble those of traditional human societies (Chapais 2010; Foley & Gamble 2009), this also renders them an intriguing model to study the predictors of male bonds as well as the fitness benefits of cooperative relationships.

An analysis of behavioral data collected during 466 h of focal observations of adult males over a two-year period suggests that Guinea baboon males are exceptionally tolerant of one another. We found that in 17% of 591 affiliative interactions the partner was an adult male (see Tab. SI4.3 for a complete break-down of interaction frequencies and partners). This is in line with the finding that adult males were regularly observed within 1m distance to each other (37% of all instances when there was another individual nearby (Patzelt *et al*. under review). The share of affiliation between adult males was far higher than reported for other baboon taxa. In addition, morphometric data reveal that traits associated with intra-sexual selection such as relative canine and testis size (Jolly & Phillips-Conroy 2006; Plavcan & Ruff 2008; Trivers 1972) are reduced suggesting decreased direct male-male competition in comparison to other baboon species (see Tab. SI4.5). Finally, we did not observe any infanticide within the last 6 years. Our results corroborate the notion of a south-to-north gradient of a decrease in male despotism and an increase in male-male coalition formation (Henzi & Barrett 2003; Noë & Sluijter 1995). This gradient reflects the genus' dispersal pattern over the African continent (Fig. 4.1) during the Pleistocene (Jolly 2009). Thus, in the most-southern baboon species, *P. ursinus*, affiliative body contact (Saayman 1971) as well as coalitions (Henzi & Barrett 2003) between males are virtually absent, while coalitions occur frequently in olive (*P. anubis*) and yellow (*P. cynocephalus*) baboons (Noë & Sluijter 1995). Solitary hamadryas males also frequently groom each other, but become less tolerant once they acquire females (Abegglen 1984; Kummer 1968). This is not the case in Guinea baboons, where adult males still maintain bonds with other males once they establish social and mating relationships with females (personal observations). These findings further strengthen the assumption that Guinea and hamadryas baboons exhibit important differences in their social system.

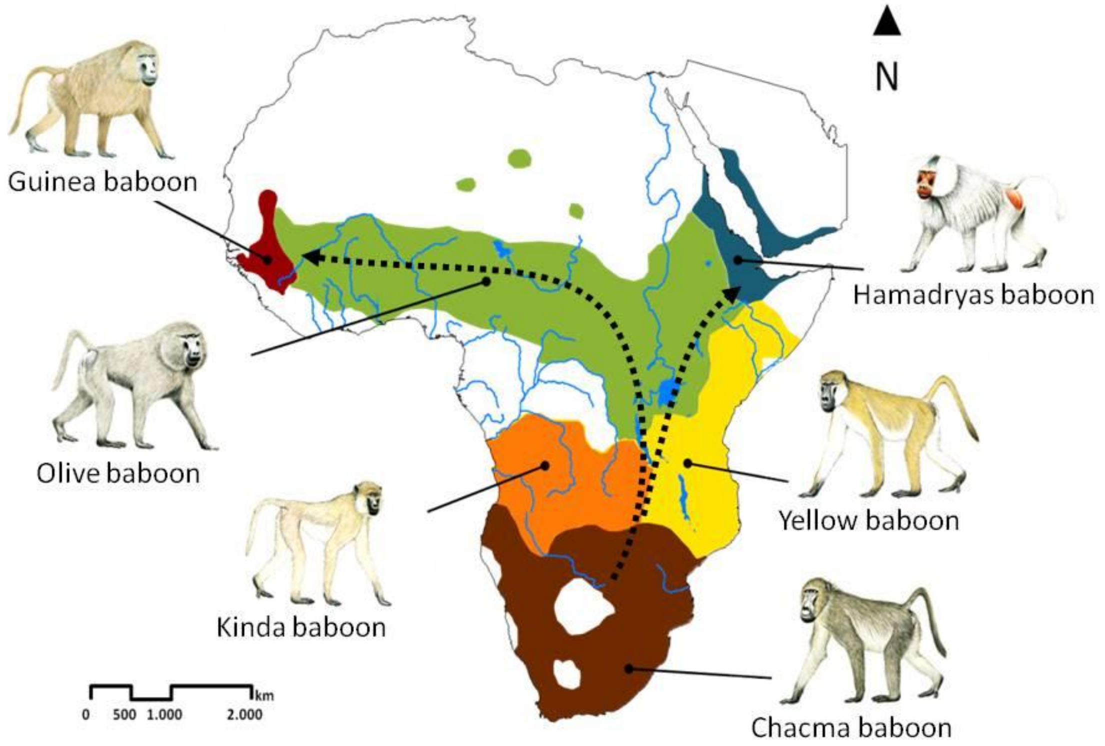

Figure 4. 1 Baboon distribution and dispersal pattern (map based on Kingdon 1997; Jolly 2007; Zinner *et al*., 2009; illustrations © 2013 Stephen D. Nash / IUCN/SSC Primate Specialist Group. Used with permission).

The social organization of Guinea baboons encompasses three levels, namely the community, the gang, and the party (Patzelt *et al*. under review). We observed the majority of male-male interactions within a male’s gang (78% of 580 interactions). The remaining male interaction partners could either not be identified or they were members of a different gang. More specifically, all social interactions except severe aggression were significantly more frequently observed within rather than between parties of the same gang (exact Wilcoxon Test, n=14; affiliative: W=-91.0, p<0.001; agonistic: W=-81.0, p=0.009; greetings: W=-105.0, p<0.001; support: W=-91.0, p=0.006; Tab.4.1 & Fig. 4.2). Severe aggression, in contrast, was more often observed between than within parties of the same gang (W=47.0, p=0.014). The proportion of available partners, which were observed as interaction partners, was higher within than between parties only for affiliative interactions, but not for agonistic interactions and greetings. These greetings involve intense manipulation of the genitals and body contact, such as mounting or hip clasping (exact Wilcoxon Test, n=14; affiliative: W=91.0, p<0.001; agonistic and greetings: p≥0.2; Tab.4.1). When we compared the proportion of available partners that were observed as interaction partners in different networks, we found that only 1/3 of all possible male-male dyads within a gang exchanged affiliative interactions, while about 80% exchanged greetings (One Way Repeated Measures ANOVA and post-hoc Bonferroni test; n=14, df=13, all p<0.001; t $_{\text{affil*greet}}$ = 9.86; $_{\text{agon *affil}}$ = 5.51; $t_{\text{greet* agon}}$ = 4.35, see Fig.4.2 and Tab.4.1).

Except for one pair of males, all dyads that maintained a close relationship (see Supplementary Methods) consisted of males of the same party (9 out of 10). Moreover, we observed the majority of coalitions (27 out of 29) between males of the same party. There was a significant positive correlation between the support and the affiliation network (QAP-correlation; Mare gang 2010: r=0.92, p=0.001; Mare gang 2011: r=0.71; p=0.002; Simenti gang 2011: r=0.52, p=0.016). Eight out of 10 dyads that maintained a close relationship supported each other at least once. Furthermore, close relationships of males within dyads observed in both years persisted over time. These results corroborate our assumption that parties are at the core of the (male) Guinea baboon society. Males seem to be highly selective in their choice of affiliation partners.

Table 4.1 Association and interaction indices for different social levels.

Level	**AI**	**Affiliation**		**Agonism**		**Greetings**	
		IF	*PP*	*IF*	*PP*	*IF*	*PP*
Party	0.65 (0.10)	0.08 (0.11)	0.47 (0.21)	0.04 (0.03)	0.58 (0.16)	0.24 (0.16)	0.70 (0.07)
Gang	0.24 (0.10)	0.01 (0.02)	0.13 (0.13)	0.01 (0.02)	0.46 (0.22)	0.04 (0.04)	0.71 (0.21)
Community[1]	0.07 (0.02)						
Average No. of Partners		2.4		4.1		5.8	

[1] only 2011

Values (i.e. mean (s.d.)) refer to exclusive categories (i.e. *Party*=dyads within parties, *Gang*=dyads between parties of the same gang, *Community*=dyads between gangs). We observed no interactions between the two focal gangs. AI = association index (i.e. the proportion of time spent in 20m proximity (Patzelt *et al*. under review) IF=dyadic hourly interaction frequency; PP= average proportion of possible partners individuals effectively interact with.

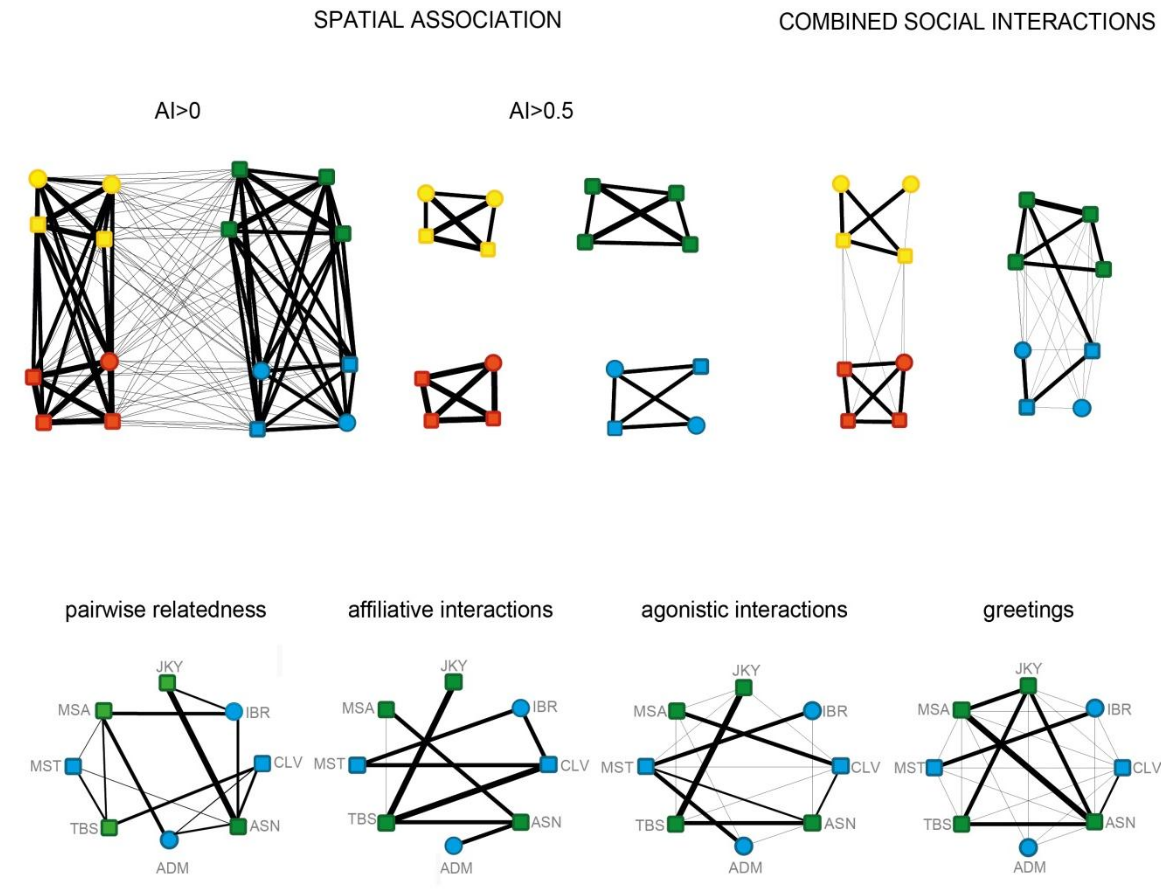

Figure 4.2 Male- male networks. Top: for the two focal gangs (left: Mare gang, right: Simenti gang) based on spatial association indices and combined interaction frequencies (no. of interactions per dyad per hour). Squares represent focal, circles non-focal males. Different colors reflect party membership. The thickness of the lines connecting nodes (=individuals) characterizes the frequency of dyadic interactions. **Bottom:** Examples of the male-male genetic and interaction networks based on pairwise relatedness estimates (Queller & Goodnight 1989) and different behaviors (affiliation, agonism and greetings). Data from 2011 for the Simenti gang are depicted. Different colors reflect party membership. Focal individuals are represented by squares, non-focal male members of their gangs by circles. Networks are based on dyadic interaction indices.

Crucially, dyads from different parties within the same gang were also observed to affiliate and support each other occasionally (association indices from (Patzelt *et al*. under review) and dyadic interaction frequencies within and between the social levels are visualized in Fig. 4.2 and summarized in Tab. 4.1). Moreover, males sometimes spent a whole day within another party of their gang, interacted with these adult males and were generally well tolerated, suggesting that the party level is not an exclusive unit. Playback experiments revealed that males only attended to calls recorded from their own gang members, while they largely ignored calls from neighboring or stranger males (Maciej *et al*. 2013). These findings support the view that the gang is an important social unit for males.

In sum, the investigation of Guinea baboon male-male networks revealed that males play an important role in the maintenance of the multi-level society they live in. Our results moreover stress the link between social organization and social structure as male-male dyads were observed to interact affiliatively and form coalitions against males from other gangs. Thus, they contribute actively to the cohesion of gangs.

Decided agonistic interactions among the males within the focal gangs were rare (total n=64). Forty-two of these occurred within parties and 22 between members of different parties. We were not able to detect a significant hierarchy (MatMan: all h´= 0.3-0.4; all p>0.386), either within or between parties, most likely due to the small sample size, as the outcomes of the agonistic interactions did mostly go into the same direction (all DCI = 0.7-0.8). Importantly, in contrast to predictions based on kin selection theory, there was no consistent correlation between the genetic and any of the social interaction networks (Tab. 4.2), although individuals had the opportunity to interact with kin.

Table 4.2 Correlations between matrices of genetic relatedness and interaction networks. Social interaction networks are based on weighted matrices (according to rates of interactions). Pearson correlation coefficients (r) derive from a Quadratic Assignment Procedure (QAP). We ran 10,000 permutations to obtain P values.

	Affiliation		**Agonism**		**Greetings**	
Gang	*r*	*P*	*r*	*P*	*r*	*P*
Mare 2010	0.11	0.29	0.24	0.14	0.01	0.48
Mare 2011	0.02	0.44	0.15	0.19	0.07	0.35
Simenti 2011	-0.34	0.04	-0.47	0.01	0.02	0.46

We do not yet have the data to test how bonds between males develop and are maintained, but data from captivity show that close relationships may develop between adolescents and persist for several years (Boese 1975). Thus, familiarity may be an important factor driving affiliation and coalition formation. Moreover, population genetic analyses suggest that Guinea baboon males are philopatric (Fickenscher 2010), similar to what is supposed for hamadryas baboons (Abegglen 1984; Hapke *et al*. 2001). If males indeed stayed in their natal group, the existence of kin-dyads in the group may favor a higher tolerance among males, which may have led to the evolution of male-male tolerance more generally, including the formation of ties among unrelated males that we observed in our study. For females, in turn, it might be beneficial to join males who form strong bonds and are thus able to defend the group more successfully from potential predators and male harassment in form of infanticide by external males than one male alone (Altmann 1990; Smuts & Smuts 1993).

While the results of this study highlight the diversity of the quality of male-male relationships across the genus *Papio*, long-term data will be needed to identify the benefits males gain from bonding with other males, and to pin down the reproductive strategies of both males and females. Future research should be aimed at understanding the processes that give rise to the transition from one type of social system to another. As population structure is closely related to tolerance and cooperation between individuals (Nowak & Sigmund 2005), our results are highly relevant for the understanding of the evolution of the unique pattern of social bonding and cooperation in human societies.

METHODS SUMMARY

We conducted this study in 2010 and 2011 in the Niokolo Koba National Park in Senegal. The analysis is based on 466 h of continuous focal observations of 14 free-ranging Guinea baboon males residing in 2 different subgroups (Mare and Simenti gang) belonging to the same community. The 2010 Mare gang dataset included 36 dyads, the 2011 Mare gang data set 25 dyads and the 2011 Simenti gang data set 27 dyads. We recorded affiliative and agonistic interactions, as well as greetings (for definitions see Tab. SI4.2). Coalitionary support and decided agonistic interactions among adult males were recorded *ad libitum*. We defined “close relationships” based on the frequency that two individuals sat in body contact ($\leq$ 10cm), embraced or groomed each other. Genetic relatedness was determined based on 25 microsatellite markers. Dyadic relatedness coefficients (Queller & Goodnight 1989) were estimated in COANCESTRY v 1.0 (Wang 2011). Correlations between the genetic and interaction networks as well as between the coalition and affiliation networks were calculated in UCInet (Borgatti *et al*. 2002). Body measurements were obtained during regular trapping sessions (for further details on methods see supplementary material).

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SUPPLEMENTARY MATERIAL CHAPTER 4

SUPPLEMENTARY METHODS

Field Site and Study Subjects

The study community comprised 350-400 individuals and ranged close to the field station of the German Primate Center (DPZ), the Centre de Recherche de Primatologie (CRP) Simenti (13°01’34’’N, 13°17’41’’W) in the Niokolo Koba National Park, SE Senegal. The community splits into several subgroups, termed “gangs”. Further details can be found in (Maciej *et al*. 2013 and Patzelt *et al*. under review). AP conducted behavioral observations on 8 adult males of one gang in 2010 and on 11 adult males of two gangs in 2011. Males were well habituated and females tolerated us nearby when following the males. Observation distances were 1 to 20 m. The study gang consisted of about 50-55 individuals in 2010, including nine adult males (“Mare gang”). In 2011 we added a second gang of c. 60 individuals (“Simenti gang”), including eight adult males (for group compositions see Supplementary Table 1.). Additionally, the Simenti gang included two young males who were only seen occasionally and could not be reliably distinguished due to their poor habituation status. They were thus not included in the dyadic analyses. Between the two observation periods (2010 and 2011), two of the focal 2010 males disappeared from the Mare gang and one moved into another gang. Two 2010 subadult males were classified as adults in 2011 according to morphological characteristics including increased body size and mass.

Morphometrical Data

During regular trapping sessions we took body measurements of 38 adult males. Animals were trapped in individual cages (1m^3). Individuals were anaesthetized with 500 mg Xylacin + 4 ml Ketamin solution [10%] applied with a blowpipe. We weighed the individuals with a hanging scale. The length of the canines as well as length and width of the testis was measured with a vernier caliper. During the treatment we regularly controlled body temperature, respiration and the corneal reflexes. The head was covered with a cloth, and the cornea was continuously wettened with medical tear supplement. For six individuals, body measurements were repeated two times in a row, revealing a rather moderate measurement error: $X = 3.7 \pm 5.1$ %. After the treatment individuals were guarded until they fully recovered and left to join their group

Behavioral Data Collection

Data were collected during two observation periods. The first period lasted from 24.03.2010–01.07.2010 (75 observation days) and the second from 19.01.–07.06.2011 (106 observation days). AP conducted a total of 466.1 h of continuous focal observations. The dataset included 188.8h of 8 adult males belonging to one gang (Mare gang) in 2010 and 277.3h of 11 adult males belonging to two gangs (Mare gang: 5 individuals; Simenti gang: 6 individuals). 5 males of the Mare gang were observed in both periods. Data were collected between 6.00-12.00h and occasionally between 16.00- 19.00h. Focal protocols were aimed to last one hour. However, due to habitat conditions that was not always possible. The average protocol duration was 50 min (SD 15min).

We recorded (1) affiliative interactions (such as sitting in body contact [≤ 10cm; “fur to fur”], grooming and embrace), (2) agonistic interactions (threat, supplant, chase, fight; chase and fight were referred to as “severe aggression”) and (3) greetings (for definitions see Supplementary Table SI4.2).

The hourly frequency of the three behavioral categories per dyad was calculated as follows: (n events observed in protocol male A+ n events observed in protocol male B)/ (n observation hours male A + n observation hours male B). Coalitionary support and decided agonistic interactions among adult males were recorded *ad libitum*. Coalitionary support was defined as conflicts where two individuals simultaneously attack the same target (parallel coalitions; [Noë 1986]) or when one or more males intervene in an ongoing conflict (interference coalitions; [Silk 1992]; [Noë 1994]), irrespective of the sex-age class of the target. Decided agonistic interactions were used for accessing a male dominance hierarchy.

Although the two focal gangs occasionally met during behavioral observations or shared the same sleeping site, we did not observe any interactions between them (Fig.4.2), but one fight (during which it was impossible to assess to recognize actors and receivers of aggression). Individuals from both gangs however occasionally interacted with members of other unidentified gangs.

Social Networks among Guinea Baboon Males

We aimed to investigate how behavioral networks are related to the genetic network. Moreover, we wanted to know if the social levels derived from spatial data are also reflected in interaction patterns. We therefore tested if individuals interacted more frequently with partners in their party and if close relationships are restricted to the party-level. We defined "close relationships" based on the frequency that two individuals sat in 10 cm proximity or groomed each other. Dyads with frequencies in the top quartile were considered to have a close relationship. Proximity and grooming are commonly used as a measure of bond strength in studies on primate behavior (e.g. Cords 1997, Smuts 1985).

Dyadic interaction frequencies and the proportion of available partners which were observed as interaction partners within and between parties were compared using exact Wilcoxon tests. To compare the proportion of available partners which were observed as interaction partners across different networks (i.e. affiliative, agonistic, greetings) we used a One Way Repeated Measures ANOVA and post-hoc Bonferroni test. Statistics were calculated in Sigma Plot 11.0 (Systat Software, Inc. SigmaPlot for Windows). All tests were two- tailed and the significance level was set at 0.05. Networks were visualized in NETDRAW (Borgatti *et al*. 2002).

The dominance rank order was calculated in MatMan for Microsoft Excel Version 1.1 (2007 Noldus Information Technology b.v., Wageningen, The Netherlands; (de Vries *et al*. 1993)), based on a giver-receiver matrix of decided agonistic interactions. We tested the presence of a linear dominance hierarchy separately for each period and gang. We used the improved linearity index h' (de Vries 1995) since not all relationships between dyads were known (i.e. no interaction took place). To assess the statistical significance of the degree of linearity a two-step randomization test (10,000 randomizations) was performed (de Vries 1995). This test was one-tailed and the significance level set at 0.05. The analysis of hierarchy characteristics included a calculation of the directional consistency index (DCI): the total number of times the behavior was performed in the main direction within each dyad minus the number of times the behavior occurred in the less frequent direction within each dyad divided by the total number of times the behavior was calculated. It ranges between 0 (completely equal exchange) and 1 (completely unidirectional) (van Hooff & Wensing 1987).

Pairwise Relatedness Estimates

We used tissue samples (ear punch, c. 5x5mm) from 40 adult males obtained during regular trapping sessions. DNA was extracted using the QIAamp DNA Blood and Tissue Mini Kit (Qiagen, Hilden, Germany) following the manufacturer's protocol, and stored at -20°C. We genotyped individuals at 25 polymorphic autosomal microsatellite loci (mean number of alleles per locus 4.08±1.19 SD) using 5 multiplex PCR reactions. We determined PCR fragment length by capillary electrophoresis on an ABI 3130xL Genetic Analyser (16 capillary sequencer, Applied Biosystems). Details on loci and the protocol are published elsewhere (Patzelt *et al*. under review). Fragment length was rated relative to the size standard using PEAK SCANNER^{TM} Software v1.0 (Applied Biosystems). Genotyping was repeated and two investigators called the alleles independently to assure accuracy. We estimated dyadic relatedness coefficients (Queller & Goodnight 1989) in COANCESTRY v 1.0 (Wang 2011).

We assessed the number of loci needed to provide consistent estimates of relatedness by simulating full-sib dyads (r=0.5) at a given number of loci based on the allele frequency distribution in the real dataset using the programm COANCESTRY (Wang 2011). We estimated dyadic relatedness for each dyad (n=2000) adding one locus in each step (range 2-25 loci). We used 10,000 bootstraps and calculated mean difference values. We plotted the obtained r-values (±MSE) as well as the changes in MSE as a function of the number of loci (Fig.SI4.1). The figure indicates that when using ≥17 microsatellite loci, there is no important change in estimates and the error surrounding it.

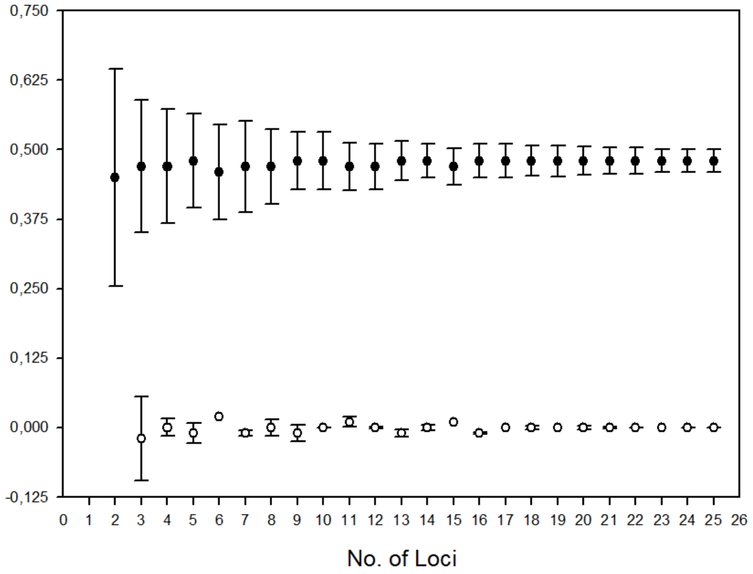

Fig.SI4.1 Relationship between the number of loci used and mean relatedness r ± MSE (full circles), and the difference between consecutive relatedness r ± MSE estimates (open circles), based on simulated relatedness of full-sib relationships with expected r=0.5 (10,000 bootstraps; COANCESTRY; Wang 2011).

Correlations Among Networks

We then tested to what extent the strength of a link in one network predicts link strength in the other networks. Here, we were particularly interested in a possible correlation of the genetic and the affiliative interaction-network (kinship hypothesis). Moreover, we were interested in a possible exchange of coalitionary support and affiliative interactions (Silk 1994, reviewed in Arnold and Whiten 2003); thus we tested whether the affiliation- and coalition-networks are correlated. Correlations were calculated using quadratic assignment procedures (*QAP*) correlation provided by UCInet (Borgatti *et al*. 2002). This program calculates measures of association between the relations in two matrices and searches for correlations between two networks with the same actors**.** Quadratic assignment procedures are used to develop standard errors to test for the significance of association. To test the hypothesis that there is an association, the program looks at the proportion of random trials that would generate a coefficient as large as (or as small as, depending on the measure) the statistic actually observed. We used 10,000 permutations and allowed for missing values. For each group, we compared undirected weighted social networks with weighted kinship networks. We used the Pearson correlation coefficient. Coefficients of correlation were considered as high loadings when greater than 0.5 or less than -0.5.

Ethical standards

All behavioral observation methods, as well as capturing and handling procedures, were conducted under permits issued by the Diréction des Parcs Nationaux du Senegal and comply with the national law of Senegal. Catching, anesthetizing and the extraction of tissue samples were conducted under supervision of veterinarians from the administration of the national park.

Table SI4.1 Group compositions for the two study periods

group	year	total group size	adult males	adult females	subadult males	juveniles	infants
Mare	2010	c.63	9	c.19	3	c.22	10
Mare	2011	c.55	8	16-17	2	19-20	9
Simenti	2011	c.60	8 (+2*)	c.18	4	c.20	8+

*this gang contained two older subadult/young adult males which were seen occasionally and not habituated to observers

Table SI4.2 List of behavioral interactions recorded

affiliative interactons

body contact

contact sitting, -lying,-standing in a distance of max. 10 cm (“fur to fur”); also dorso-ventro-ventral position (one individual hunkers over another).

embrace

an individual puts its arm around the shoulder or back of another one, mostly accompanied by grunts.

grooming

one individual inspects its partner´s fur using one or two hands and removes particles with its hand or mouth.

agonistic interactions

supplant

one animal leaves the place when another individual is coming closer. The approaching individual takes over the sitting position of the other.

threat

quick head movements, eyelid flashes, lunges, ground slaps, threat-grunt vocalizations, stares with raised eyebrows.

chase

pursuing another group member for more than 5m without body contact contact (*cf.* Kitchen *et al*. 2005).

physical fights

body contact aggression, including slaps, bites; may be accompanied by screams.

greetings

may involve manipulation of the genitals, mounting, hindquarter touch or rubbing, head bobbing, head rubbing (head to head, move up and down), hip clasping, shoulder puffing, tail wrap or lean/lying on the partners back; often accompanied by grunts.

Table SI4.3 Relative frequency (%) of male interactions by age-sex class

	Behavioral Category		
Interaction partner	*Affiliation*	*Agonism* *(severe aggression)*	*Greetings*
% adult male	17.1	33.7 (19.2)	53.0
% adult female (incl. infant)	46.2	35.4 (52.0)	45.6
% Others	36.7	29.5 (29.7)	
% unidentified	-	1.3	1.4
n	658	313(166)	1029
frequency/h	1.4	0.67	2.2

% do not always add up to 100 since there were unidentified individuals

Table SI4.4 Dyadic relatedness estimates (Queller & Goodnight 1989)

Simenti Gang

	ASN	JKY	MSA	TBS	MST	CLV	ADM	IBR
ASN								
JKY	0.51							
MSA	-0.07	-0.12						
TBS	-0.08	-0.36	0.07					
MST	*0.02*	*0.00*	*0.02*	*0.09*				
CLV	*0.13*	*-0.21*	*-0.01*	*0.17*	-0.20			
ADM	*0.09*	*0.00*	*0.20*	*-0.11*	-0.17	0.04		
IBR	*0.14*	*0.08*	*0.22*	*-0.21*	-0.41	-0.08	0.43	

Mare Gang

	OSM	PTR	NDR	DTM	SML	SNE	BAA	HOK
OSM								
PTR	0.28							
NDR	-0.25	-0.28						
DTM	-0.13	0.08	-0.19					
SML	*0.02*	*0.20*	*-0.11*	*0.13*				
SNE	*0.11*	*0.16*	*-0.13*	*-0.19*	-0.01			
BAA	*-0.26*	*-0.25*	*0.12*	*-0.24*	0.25	-0.17		
HOK	*0.24*	*-0.03*	*0.07*	*-0.21*	0.05	0.06	-0.01	

Values range from -1 to 1. Negative values reflect dyads that are less related than the average population. Between-party dyads in italics.

Table SI4.5 Traits associated with intra-sexual selection in different *Papio* taxa

	P.papio	*P.hamadryas*	*P. cynocephalus*	*P.anubis*	*P.ursinus*	source
SEX DIMORPH m/f	**1.7***	1.8	2.0/1.8	1.8/1.9	1.8/2.0	Jolly & Phillips-Conroy 2006, Thorén *et al*. 2006
REL TESTICULAR VOL **	**0.8*** **/1.4**	1.4	1.7	2.2	?	Jolly & Phillips-Conroy 2006
REL CANINE SIZE***	**1.31***	1.6	1.5	1.5	1.6	Thorén et al. 2006

*Current study, ** (mm^3/body weight), *** (height/body weight)

CHAPTER 5 - General Discussion

Baboons have traditionally served as a model in comparative studies to investigate primate social evolution. However, while most baboon taxa had been extensively studied, little was known about Guinea baboons. Conclusions of earlier studies on the species were mostly based on data from captive groups or short field stints. Although all authors almost consistently described sub-structuring of groups and tolerant behavior among adult males, there was large disagreement about the social system of Guinea baboons (reviewed in 1.4 and chapter 2 [Patzelt *et al*. 2011]). The main problem of all previous studies was that in none of them data were collected from habituated and individually recognized subjects in the wild. Therefore, the overall aim of my thesis was to collect these data from free-ranging individuals to aid in the clarification of their disputed social system.

Some authors took the view that the Guinea baboon social organization showed considerable similarities to that of the hamadryas baboon society (Galat-Luong *et al*. 2006; Jolly 2007), which is described as extremely male-dominated (Swedell 2002; Kummer 1968, 1995). In order to investigate whether Guinea baboons show a comparable behavior, I was particularly interested in the study of males. In this context, I furthermore investigated whether Guinea baboon males fit into the proposed south-to-north gradient of an increasing disposition for male philopatry and male-male tolerance, which has been related to the dispersal pattern of baboons over the African continent (Jolly 2007, 2009; see also Henzi & Barrett 2003, 2005). Because of their position at the frontier of the northwestern distribution, information on the characteristics of male-male relationships in this species is crucial for testing that assumption.

5.1 The Guinea Baboon Society

By combining spatial, behavioral and genetic data, we investigated the Guinea baboon social organization and male-male interaction patterns (i.e. part of the social structure). We were able to quantitatively confirm that Guinea baboons live in a multi-level society and exhibit considerable male-male affiliation and tolerance. While these characteristics and the general idea that Guinea baboons are "different" from other baboons had been recognized in earlier studies (e.g. Boese 1973; Sharman 1981; Galat-Luong *et al*. 2006), these assumptions had never been tested with data on individually recognized Guinea baboons in their natural habitat.

Spatial, social and genetic relationships among males

In the first part of my project (chapter 2) we documented a high frequency of fission and fusion in the study community, with varying group sizes and compositions in terms of age- and sex-classes according to season and daytime. But, we could not yet recognize individuals at that time and, consequently, were unable to investigate whether the individual composition of subgroups remained stable. In the second part (chapter 3), data on individually recognized animals revealed that subgroups do not form randomly. Analyses of spatial association and social interaction patterns among adult males indicated a three-level social organization with different nested levels labeled as party, gang, and community (see Fig.5.1). The smallest subgroups (i.e. parties) appeared to be stable over time and consisted of 3 or 4 adult males plus several females and immatures. Most of the males maintained close associations with a particular set of females within the party, at least through one observation period. Specific parties form a gang, and several such gangs form larger aggregations, which we refer to as community. Parties seem to be the unit where most of the social interactions occur and where close bonds and coalitions among males are usually observed (chapter 4).

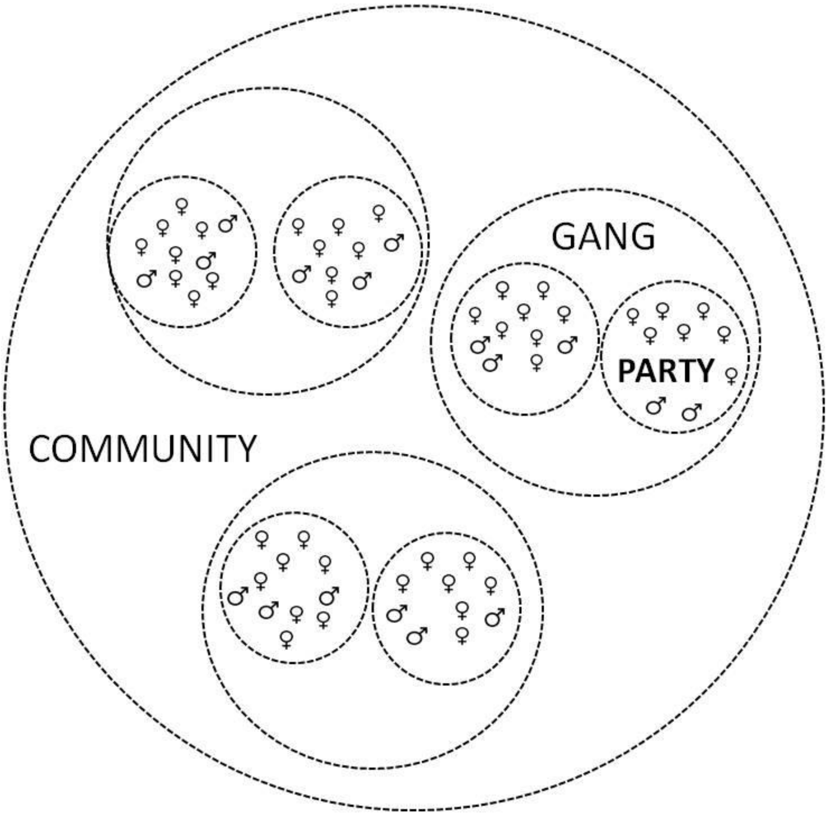

Figure 5.1 Sketch of the three-level Guinea baboon society. The *community* is made up of *gangs*, which further split into *parties*, which most likely constitute the core unit within the society.

Our genetic analysis revealed that male-male dyads within parties in Guinea baboons are not necessarily more closely related than male-male dyads consisting of males of different parties. Yet, males within gangs were more closely related to each other than males belonging to different gangs. Overall, however, the genetic relatedness was rather low and close genetic relationships also existed between males from different gangs, indicating that males disperse across parties and gangs.

Characteristics of different social levels

Parties most likely represent the core units of the Guinea baboon society, as suggested by the high frequency of social interactions. Particularly the high frequency of affiliative interactions, as well as the formation of coalitions, suggests that males maintain strong bonds within parties in contrast to males of different parties. Similarly to male Guinea baboons belonging to one party, male clan members in hamadryas baboons are also more strongly bonded among each other than with other males (Abegglen 1984). Moreover, under captive conditions hamadryas males belonging to a clan were more successful in the defense and takeover of females (Colmenares *et al*. 2006) than leader males who led single OMUs not belonging to a clan (Colmenares 1997). These observations suggest that coalitions among males within a clan may facilitate access to females (see also Schreier & Swedell 2009). Moreover, in the same study, clan males supplanted single male units from food resources (Colmenares *et al*. 2006). In my study, Guinea baboon males from the same party were also observed to engage in coalitions against males from other parties or against females within their own party, suggesting that the Guinea baboon party has a similar function as the hamadryas clan.

Overall, social interactions were largely restricted to the gang-level, i.e. interactions among males of different gangs were rarely observed (chapter 4). Moreover, results from playback experiments conducted with males of the same community revealed that males respond strongly to grunts from other males of the same gang, while they ignore those recorded from either other gangs ranging in the same area or unknown animals (Maciej *et al*. 2013). All these findings, including the fact that males within gangs are more related to each other than males between gangs, suggest that the gang constitutes an important organizational level within the Guinea baboon society. At various occasions, we observed males of different parties, but from the same gang, forming coalitions against males from other gangs, suggesting that the formation of gangs may provide benefits in terms of the defense of important resources, such as females and feeding sites. On one occasion I observed several adult males belonging to one gang chasing a leopard (*Panthera pardus*) up a tree, indicating that males also cooperate in predator defense. It therefore appears that the function of Guinea baboon gangs is comparable to that suggested for bands in hamadryas baboons, in that they share similar travel patterns and defend common resources (Abegglen 1984; Kummer 1968). Such bands are supposed to be homologous to the group or troop of other baboon species (Dunbar 1988; Schreier & Swedell 2011). The ability to fission into parties may provide an extra level of flexibility during periods of relative resource scarcity (discussion chapter 2; see also Galat–Luong *et al*. 2006, Schreier & Swedell 2009). My data collection was restricted to the dry season and, presently, we still lack the data to test whether gangs split into parties in response to varying ecological conditions.

Regular affiliative and cooperative interactions between males of different parties might strengthen the cohesion of gangs. While only a few individuals interacted affiliatively with member of other parties (chapter 4), males generally tolerated the close proximity of other males. These results are in line with earlier observations. For example, Galat-Loung and colleagues suggested that the multi-level system was “rooted in male-male tolerance” (Galat-Loung *et al*. 2006, p.117; see Boese 1975 and Sharman 1981 for similar conclusions).

Aggregations at the community level are probably formed in response to ecological factors rather than as a consequence of social preferences, as indicated by the observation that individuals use the same home range but that members of different gangs do not spend much time in close proximity (chapter 3) and usually do not interact. Therefore, it is not clear whether the community can be defined as an organizational level at all. Maybe the large aggregations of 300 or more individuals simply arise due to spatial overlap of home ranges in combination with high tolerance among adult males. The formation of large troops in hamadryas baboons is related to the scarcity of sleeping sites. However, this assumption was derived from particular habitat conditions with a scarcity of safe sleeping cliffs (Kummer 1968). It remains to be investigated whether this also applies to other hamadryas habitats, such as the more mountaneous habitats in other parts of the hamadryas range (Zinner *et al*. 2001). In our study area, safe sleeping sites such as high trees may be also rare since they can mainly be found in the gallery forest along the Gambia River. Moreover, water becomes a limited resource in the dry season and thus subgroups regularly meet at water places (the baboons usually do not rely on the Gambia River for drinking, most likely due to the presence of crocodiles). Notably, the largest groups can be observed in the rainy season. This may be a response to decreased visibility when the habitat becomes very dense, hampering the detection of predators, and / or the fact that at this time sufficient food is available to support large aggregations (discussed in chapter 2). Data on resource distribution and predation risk in relation to fission-fusion dynamics in the community are needed to test these assumptions. A study concerning this subject is currently under way.

5.2 Intersexual Relationships

Multi-level societies in primates usually constitute OMUs as the smallest entities (Kummer 1968; Dunbar 1988, Grueter & Zinner 2004; Grueter *et al*. 2012b). Indeed, the Guinea baboon system superficially resembles that of hamadryas baboons, inevitably raising the question of whether it also consists of OMUs, as indicated by the observation that males maintained close associations with a particular set of females throughout the study periods (see 5.1). When considering this question, it is important to distinguish between (I) OMUs as an organizational level (i.e. as part of the social organization) and (II) as a reproductive unit, i.e. whether they represent the mating system (*sensu* Kappeler & van Schaik 2002; see 1.2).

One-male-units as organizational entities?

Based on observed spatial interaction patterns, most authors concluded that OMUs were the smallest organizational entity in Guinea baboons (Anderson & McGrew 1984; Boese 1973; Dunbar & Nathan 1972; Galat-Loung *et al*. 2006; Maestripieri *et al*. 2007; but see Sharman 1981), yet only studies conducted in captivity reported a rigid structure with males herding females aggressively (Boese 1973; Maestripieri *et al*. 2007). Based on our data on spatial association patterns (chapter 2 and 3) we concluded that Guinea baboons do not show distinct OMUs comparable to hamadryas baboons (Grueter & Zinner 2004; Kummer 1968; Stammbach 1987). The different sex ratios in OMUs and multi male-multi female units (MMUs) suggest that MMUs do not simply reflect a temporary association of several OMUs (chapter2). Moreover, we only rarely (i.e. occasionally in group encounters) observed the typical herding behavior described for hamadryas baboons where leader males routinely herd females to establish and maintain the cohesion of OMUs (Kummer 1968; Swedell & Schreier 2009). Boese (1973) also reported that he did not observe the strict herding behavior in wild Guinea baboons that he knew from his captive study group. Furthermore, we observed females countering aggression of males mostly in coalition with other females or juveniles (data not presented, but see also Petit *et al*. 1997). Finally, some males may forage alone or within another party for minutes or even hours, leaving the females that were usually observed to be attached to them behind, thus taking the risk that the females would interact with other males (personal observation). Such a situation has not been observed in hamadryas baboons while it happened quite frequently in our study groups. Summarizing the arguments listed above, OMUs seem unlikely to be an organizational unit in Guinea baboons.

One-male-units as reproductive units?

On the assumption that reproduction in this species may be monandrous, OMUs would constitute the core of the society at the level of reproduction. During my focal observations in 2011, 8 of 11 focal males were observed predominantly in close proximity to a stable set of females (1-6 per male) and only copulating with them. While social interactions between the sexes did not necessarily predict the mating partners, copulation partners were not shared among males (personal observation). The assumption that females mainly copulate with one specific male is also supported by morphological data (chapter 4): in primates (as in other mammals), the intensity of sperm competition imposed by their mating system may be reflected in testicular size with larger testis sizes in species with stronger sperm competition (Harcourt *et al*. 1981; Jolly & Philips-Conroy 2006). Accordingly, savanna and hamadryas baboons show pronounced differences. A single hamadryas male monopolizes a group of females. Consequently, males in this species do not engage in sperm competition like the promiscuously mating savanna baboons. Therefore, savanna baboons have relatively larger testes than those of hamadryas. Guinea Baboons have very small testes relative to body mass (chapter 4, see also Jolly & Phillips-Conroy 2006), suggesting that sperm competition does not play a crucial role (Jolly & Phillips-Conroy 2006). Thus, testis size in Guinea baboons suggests a polygynous rather than a promiscuous mating system.

In sum, my conclusions on OMUs as an organizational unit are in accordance with those of Sharman (1981) who summarized “nearest neighbor data suggest that the baboon females did not interact socially within the constraints of one-male groups similar to those of either *T. gelada* or *P. hamadryas*. The close association between adult males in *P. papio* makes their segregation into one-male groups improbable” (Sharman 1981; chapter 10.13). While OMUs indeed do not seem to be an organizational part of the Guinea baboon society, strong bonds between males and specific females were observed. These observations, combined with the relatively small testis size, suggest that OMUs exist as a characteristic of the mating system. It remains to be investigated, however, if these units are stable over time.

5.3 Male-Male Relationships

Social relationships among adult Guinea baboon males were characterized by a high level of tolerance, coalition formation, as well as frequent affiliation and differentiated relationships. Some males did not interact affiliatively, while others did so frequently. Likewise, Galat-Loung and colleagues (2006) described adult males as highly tolerant and observed male-male grooming. Similar patterns have also been observed in hamadryas baboons and geladas, however only in males that are not sexually active (Sharman 1981), such as followers and males in all-male units, which stands in stark contrast to observations on adult savanna baboon males (Harding 1980; Hausfater 1975; Noë & Sluijter 1995; Saayman 1971; Smuts 1985). Even in hamadryas baboons, which are supposed to be the most tolerant non-Guinea baboons, "there is an almost complete lack of interactions among leader males" (Kummer 1968, p. 89/90). Thus, while the social organization seems superficially similar to that of hamadryas baboons, regarding the quality of male-male relationships, Guinea baboons are unique.

A south-to-north gradient in aggressiveness and coalition formation

In order to systematically investigate the variation in coalition formation among adult males, Henzi and Barrett (2003, 2005) introduced the idea of a south-to-north gradient in male baboon behavior (although they never explicitly named it like this), which was advanced later by Jolly (2007, 2009). This gradient is characterized by decreasingly rigid and aggressive relationships among males from south to north, while tolerance and coalition formation among adult males increases in more northern species. Simultaneously, there is a shift from multi-male multi-female social organization with promiscuous mating as observed in the savanna-species (*P. ursinus*, *P. cynocephalus*, *P. anubis*) to male philopatry within a multi-level social organization in species in the northeast and northwest (observed in *P. hamadryas*, and suggested for *P. papio* [Jolly 2007; Swedell 2011]). The results of my thesis corroborate this assumption for Guinea baboons; as the most northwestern species living at the edge of the baboon distribution they seem to represent the extreme in terms of tolerance and affiliation among adult males. In line with this, direct male-male competition seems to be reduced in Guinea baboons, as indicated by our morphometric data (e.g. sexual dimorphism and relative canine size) and the lack of an apparent dominance hierarchy (compared to that seen in ´savanna´ baboon species; chapter 4).

The observed high frequency of greeting interactions (chapter 4), however, may indicate that relationships among Guinea baboon males are not as relaxed as it would seem according to the low rates of severe aggression. This is because greeting behavior has been suggested to function as tension reduction in aggressive contexts (Colmenares 1991; Hall & de Vore, 1965, Pelaez 1982). Greetings are also the most frequently observed interactions among adult males in other baboon species (Colmenares 1991; Smuts & Watanabe 1990). They involve an intense treatment of the genitals, representing a high potential risk of injury. In hamadryas baboons, greetings occur mainly in the context of negotiation over females (Abegglen 1984; Kummer *et al*. 1974), and thus in highly competitive situations, and are thought to replace dominance interactions seen in species exhibiting hierarchies (Jolly 2007).

The function of greetings, however, is still debated. Other authors suggested that they serve as a bond-testing mechanism, as indicated by the observation that dyads with strong social bonds exchanged a higher frequency of intense greetings than did pairs with poor relationships (Whitham & Maestripieri 2003). I have not systematically analyzed the greeting behavior of male Guinea baboons, but greetings mainly occurred within parties (chapter 4). Here, the highest interaction frequencies occurred between potential "rivals", firstly between males that interacted affiliatively among each other vs. those that never interacted affiliatively with other males of their party (hourly rate/dyad: 0.37 vs. 0.20) and, secondly, between the older adult males and the younger adult males that recently started to engage in reproductive interactions (i.e. that were observed to copulate and to gather females around them (hourly rate/dyad 0.33 vs. 0.16; dyadic interaction frequencies see Appendix II). Thus, while bond-testing among party members may be one possible function of greetings in Guinea baboons, the increased frequency among potential rivals also suggests that greetings play a crucial role as a mechanism in regulating tension, most likely in the context of competition over females. An ongoing study being conducted at our field site will provide further information on the function of greetings in the near future.

The role of kinship

According to *kin selection theory* (Hamilton 1964), affiliative interactions among individuals are often related to benefits that come along with genetic relatedness. For kin selection to operate, individuals have to be able to recognize their kin (Chapais 2001). This can work, for example, by *phenotype matching* where individuals compare phenotypic cues (such as visual similarity or odor) of others with their own phenotype or phenotypes of their relatives to determine their kin relations (Langergraber *et al*. 2007, Langergraber 2012). Although phenotype matching is frequently studied in primates, particularly with regard to visual similarity, this mechanism is highly complex and is still not well understood (Langergraber 2012). A more simple mechanism is *familiarity*, such that individuals that grow up together will recognize each other as kin (Kappeler 2006). Accordingly, in matrilinear species, females will become familiar with each other due to the common attachment to their mother (Langergraber 2012) and, in contrast to males, they stay in their natal group and will therefore still be familiar as adults. If bonds are more likely to develop among relatives, strong bonds between males are expected to develop in male philopatric species (e.g. van Hoof & van Schaik 1994). Indeed, in male muriquis (*Brachyteles* spp.; Strier 1994; Strier *et al*. 2002) or chimpanzees, for example, the closest bonds are those among males (Muller & Mitani 2005).

Preliminary results of a population genetic study at and around our field site indicate that the observed high tolerance among males could be caused by male philopatry (chapter 4). According to that study, gene flow between communities is mediated by females as (I) genetic sub-structuring between different sites in the Niokolo-Koba National Park is significantly higher in males compared to females, and (II) females of different communities are more closely related than males (Fickenscher 2010).

Despite these indications, our data do not confirm a correlation between kinship and affiliation frequencies on the dyadic level. Nevertheless, if males tend to stay in their natal group, generally tolerant relationships may develop based on familiarity, irrespective of the specific kinship relation between interacting individuals (chapter 4). As mentioned above, the results presented in chapter 3 suggest that males disperse across parties and gangs (subgroups), while they tend to stay within the community (Fickenscher 2010). Consequently, males of different subgroups are sometimes more closely related than males within subgroups. Such kin-relations across subgroups may enhance tolerance between subgroups as it has been proposed for lion prides (Spong *et al.* 2002).

Several studies have demonstrated that kin-biased altruism becomes less common if the degree of relatedness between individuals declines. For example, macaque females do not consistently discriminate between kin and non-kin when the degree of relatedness is lower than 0.125 (e.g. aunt-nephew) (Chapais *et al*. 2001; Kapsalis & Berman 1996). Whether this reflects a lack of kin recognition or unprofitable altruism is still unclear (Chapais *et al*. 2001). Kin recognition may be further complicated in species with male philopatry compared to species with female philopatry. In groups where males stay in their natal group, they may not have much close maternal kin (only additional infants of their own mothers, while other adult females are not related to them) and they are possibly not able to recognize their paternal relatives depending on the degree of paternal care. Furthermore, reproductive skew may affect kin recognition, as in species with high skew age-cohorts are likely to have the same father (Chapais 2001; Langergraber *et al*. 2007, Langergraber 2012, Schülke & Ostner 2008). Finally, long-term data from our Guinea baboon community are needed to supplement the relatedness information gained from molecular markers with pedigrees (e.g. known parent-offspring, maternal and paternal sibling-pairs) and demographic information to complete the picture of genetic patterns within the study community (Harris *et al*. 2009; van Horn *et al*. 2008). The distinction between maternal and paternal siblings could help to explain why some highly related individuals do not interact while others do.

Alternative explanations for male tolerance

As kinship does not appear to explain the affiliation patterns of Guinea baboons, other potential factors driving the tolerant behavior observed among potential competitors must considered. Reproductive skew models may serve as an alternative explanation. Such models try to explain the evolution of shared reproduction in multi-male groups (reviewed e.g. in Clutton-Brock 1998, Port & Kappeler 2010). The *limited control model* assumes that males cannot completely control all females in their group and thus lose some reproduction to subordinates. This could be shown in several studies on different mammals, including primates (Clutton-Brock 1998; Ostner *et al*. 2008). The *concession model* in contrast, presumes that dominants are able to control reproduction by subordinates and suggests that dominants who benefit from the presence of additional males should tolerate some reproduction of subordinates (=concession) to give them an incentive to stay (Clutton-Brock 1998). Recently, Snyder-Mackler and colleagues (2012) found support for the concession model in a study on geladas. They observed that males with followers had a longer tenure because these additional males helped to defend their group (females). In turn, followers sired some offspring in the group, suggesting benefits for both leaders and followers (Snyder-Mackler *et al*. 2012). The amount of concessions in favor of subordinates may depend on factors such as the chance of the latter to reproduce elsewhere, the probability of being defeated, and the degree of genetic relatedness, while the incentive should decrease as relatedness increases since individuals already gain indirect fitness benefits via kin selection (Pereira *et al*. 2000).

As mentioned earlier in this section, the reduced sexual dimorphism in Guinea baboons indicates reduced direct sexual competition among males in comparison to savanna baboon species. Moreover, sperm competition does not seem to be prevalent in Guinea baboons, as indicated by their small relative testis size. Males, however, do form coalitions against males from other parties or gangs, most probably to defend the females within their party. Hence, male cooperation might indeed result in reproductive benefits and it might pay for dominants to tolerate additional males in their group. We do not have data on either the reproductive skew or the history of the group to identify potentially reproducing males or males that formerly reproduced but were defeated by new males, respectively. However, since the distribution of copulations may indicate a skew in reproductive success (as shown for baboons: Alberts *et al*. 2006, Moscovice *et al*. 2010; but see Berard *et al*. 1994 and Port & Kappeler 2010 and references therein for other species), and some of the focal males had more copulations than others (copulation data see Appendix IV), it is indeed possible that some males reproduce more successfully. In order to study male strategies in the future, the most essential question to investigate will be how paternities are distributed among different males.

The role of female reproductive tactics

When discussing possible reproductive strategies adopted by males it has to be noted that these are, to a certain extent, responses to female strategies (Pereira *et al*. 2000; van Hooff 2000). Females may prefer males who cooperate with other males in order to defend the group more effectively from potential predators and infanticidal males than one male alone (Altmann 1990, Smuts & Smuts 1993). The present dataset is insufficient to derive any explanation for the observed high degree of tolerance among adult male Guinea baboons, but can be used to generate hypotheses. More data are needed to investigate the role of (I) the common defense of females and associated reproductive benefits and (II) female choice in shaping the observed behavior. Upcoming results of a study on female behavior currently underway will help to resolve the latter question.

5.4 The Broader Perspective

Diversity in baboon societies

So far baboons have been divided into two types, separating the hamadryas (or ´desert´) from all the remaining (´savanna´) baboon species (Barton 2000, Smuts *et al*. 1987). The results of my thesis add to a growing body of evidence that baboon social systems are more diverse than previously acknowledged. Recent results from an intensive study of Kinda baboons (Wehyer & Chiou 2013) add further evidence suggesting that the dichotomic view needs to be abandoned. As indicated earlier (see 1.4.), Kinda baboons also show some features that clearly distinguish them from all other baboon species. They exhibit strong male-female bonds which seem to be maintained by grooming interactions mostly initiated by males. In contrast, the strong intersexual bonds in hamadryas baboons are maintained via strict herding by males, while females initiate grooming. The male-female bonds in Kinda baboons are also not comparable to bonds in savanna baboons as they last even if the female is not in estrus or lactating. Finally, Kinda baboons show a very restricted sexual dimorphism (Weyher & Chiou 2013). It also has been evident for a long time that Guinea baboon societies are different from either of the two known systems (e.g. Boese 1973, 1975; Sharman 1981), especially with regard to the exceptionally relaxed male-male relationships, and a multi-level social organization. At least for the male-male perspective, the results of my thesis quantitatively confirm these earlier views, which had mostly been based on anectodal observations.

The term savanna baboon was already critized earlier, since it neither represents the ecology nor the phylogeny of the included species (Jolly 2007; Newman *et al*. 2004; Swedell 2011; Zinner *et al*. 2001, 2009, 2013). There are, for example, hamadryas baboons living in more ‘savanna’ (and not desert)-like habitats (Zinner *et al*. 2001) and chacma baboons (classified as savanna baboons) living under ´desert´ conditions (Barton *et al*. 1996; Whiten *et al*. 1987). More importantly, phylogenetic analyses revealed that the savanna baboons are polyphyletic, and hamadryas baboons are more closely related to some savanna-baboon species than certain savanna species among each other (Zinner *et al*. 2009, 2013b).

Causes for variation in baboon societies

According to socio-ecological models, variation in food-distribution, predation pressure and infanticide risk are thought to have driven the evolution of social systems. Furthermore, most former studies assumed that behavioral patterns were stable within species, and the variability found was somehow discounted as “noise” (Henzi & Barrett 2005). However, the observation that in primates ecological diversity within species was almost as large as variation between species (Chapman & Rothman 2009) indicated that the current ecological conditions might not fully explain variation in baboon social systems. Phylogenetic inertia has been a persistent issue in the study of primate social evolution (Chapman & Rothman 2009; Clutton Brock & Harvey 1977; Clutton-Brock & Janson 2012; di Fiore & Rendall 1994; Janson 2000; Kappeler *et al*. 2013; Rowell 1979; Strier 1994; Struhsaker 1969; see discussion chapter 3). But also in other animal species individuals show traits that do not reflect adaptations to their current habitats (e.g. wild sheep, *Ovis gmelini*: Bon *et al*. 1995; Trinidadian guppies, *Poecilia reticulata*: Magurran 1998, reviews in Foster 1999, Lott 1991).

With regard to baboons, Henzi and Barrett (2003, 2005) introduced the idea that the evolutionary history (including historical ecologies) has to be considered when explaining the behavioral diversity observed in baboons. Traditionally, hamadryas baboons have been set apart from all other baboon species according to their multi-level social organization and male-dominated society. These traits have been attributed to ecological conditions that would favor the formation of OMUs and ultimately lead to the extensive herding behavior of females (Kummer 1995, Jolly 2007). However, the typical OMU-organization and -structure persists in captivity (Colmenares 1992). Moreover, differences in social behavior between hamadryas and olive baboons found at the same site (in Awash, Ethiopia; e.g. Jolly & Phillips-Conroy 1992; Kummer 1968) show that current ecological conditions cannot account for the difference in social systems (Henzi & Barrett 2005), suggesting that the underlying behaviors have a genetic basis. Later it was recognized that not only hamadryas but also chacma baboons seem to be very restricted in their behavior (Henzi & Barrett 2003, 2005). This assumption refers to the fact that chacma baboon males are not observed to form coalitions like other baboon species, even if current conditions would favor it. It is assumed that the historical habitat conditions, favoring small groups with only one male, did not require the need to cooperate. Although today chacma groups often contain multiple males, they still do not engage in coalitions, leading to the assumption that they are constrained in their ´reaction norm´ (Henzi & Barrett 2003). Moreover, studies on hybrids stress that phylogenetic inertia plays an important role in baboons (Nagel 1973). For instance, hybrid *P. hamadryas* x *P. anubis* show intermediate behavioral characteristics and an intermediate social organization (Bergmann & Beehner 2004; Nagel 1973).

Interestingly, the major haplogroups of *Papio* species found in the phylogenetic analysis of Zinner and colleagues (see above) reflect geographic populations rather than morphology (Zinner *et al*. 2009, 2013b), supporting the idea that local conditions in historical environments have influenced their evolution. Therefore, it is essential to integrate information on past and current resource distribution to better understand the phylogenetic constraints limiting the flexibility in social behavior (Henzi & Barrett 2003).

Clifford Jolly proposed an alternative scenario leading from the savanna- to the hamadryas system that is based on the observation that Guinea baboons, in contrast to hamadryas baboons, occupy a variety of different habitats, ranging from humid and secondary high forests in Guinea to arid Sahelian steppe in Mauretania (Galat-Luong *et al*. 2006). This indicates that ecological factors alone, which have been invoked to explain the evolution of the hamadryas multi-level system, cannot account for the multi-level structure of Guinea baboons. Jolly (2007, 2009) therefore proposed that demographic factors during the range expansion of the genus *Papio* from south to north may have led to the formation of large groups, organized in a multi-level manner, and – most importantly - an increased probability of male philopatry. This means that, while in previous considerations ecological factors were seen as the most important aspects in the formation of OMUs and, hence, in the evolution of diversity in baboon societies, the major point for Jolly was the change in the dispersal pattern that ultimately led to multi-level group structure. The suggested scenario can be summarized as follows: During the northward expansion of the genus *Papio*, populations entered new baboon-free areas. A group at the frontier of an expanding range had access to uncontested resources leading to increased population growth. The expansion into unoccupied territory would have occurred in a "fanning out" fashion (Jolly 2009; p. 195), i.e. in different directions. The increasing distance between troops would allow only one main direction, in which dispersing males could find fertile females i.e., backwards. Assuming that individuals in this frontier population vary in their disposition to disperse from their natal troop at a moving frontier, dispersing males would have lower reproductive success than males who stayed in their natal group, particularly at high population densities when inbreeding depression is relaxed. These conditions would select for male philopatry (Jolly 2009) and, accordingly, genes predisposing to philopatry would accumulate at the frontier (Roff & Fairbairn 2004). When groups became too large they might have split for foraging, but bonds between related males would maintain the cohesion between groups. Jolly considered this scenario possible only in the case of rapid expansion, for example if a founder population passed through a narrow gap in a barrier. This could have been possible during times when dense forests disappeared and savanna corridors opened during the Pleistocene, providing ideal dispersal possibilities for baboons (Zinner *et al*. 2011).

5.5 Implications for Baboons as a Model for Human Social Evolution

Baboons have served as an important model in the study of human social evolution (e.g. de Vore & Washburn 1963; Jolly 2001). A multi-level structure with fission-fusion dynamics has been suggested to be a pivotal precondition for the emergence of the unique cooperative relationships within human societies (Grueter *et al*. 2012a; Hill 2002; Rodseth *et al*. 1991; Silk & Boyd 2010) and the emergence of affiliative bonds between men was a significant step towards tolerance between groups (Chapais 2010; Foley & Lee 1989; see also chapter 4). The Guinea baboon society appears to resemble those of traditional human societies in terms of a fluid multi-level structure (chapter 2+3) and strong male-male bonds across subgroups (chapter 3+4). These characteristics render them a valuable taxon within the baboon model to study multi-level evolution as well as the causes of male-male tolerance and the adaptive value of male-male cooperative bonds. There is more and more evidence suggesting that “the universal human tendency to engage in close social bonds may have evolutionary origins outside the context of the extended family“ (Schülke *et al*. 2010, p.2208). In chimpanzees both sexes maintain differentiated social bonds regardless of kinship (Langergraber *et al*. 2007, 2009), while Assamese macaque males form “political” coalitions (Schülke *et al*. 2010). My study adds an additional species where this may apply.

Guinea baboons also provide a good model to investigate the cognitive adaptations to complex societies (chapter 4). During human evolution fission-fusion dynamics increased with the advent of new technologies such as hunting. These dynamics are supposed to have been a driving force for increases in cognitive skills as an adaption to maintain social relationships in a large dispersed group (Foley and Gamble 2009). Interestingly, however, the playback study conducted in our study community (Maciej *et al*. 2013) (see 5.1.), as well as a comparable study on geladas, which exhibit a superficially similar social system (see chapter 3), revealed that animals were either unable or unmotivated to keep track of individuals outside their social interaction unit (Bergman 2010; Maciej *et al*. 2013). These results suggest that a complex social organization does not necessarily translate into the need for more elaborate social knowledge (Maciej *et al*. 2013).

5.6 Conclusion & Outlook

Based on an analysis of spatial association and social interaction patterns in combination with genetic networks, we found evidence that male Guinea baboons (*Papio papio*) live in a multi-level social organization and maintain strong social bonds and high tolerance among each other within and between subgroups. Bonding patterns among males, however, were not correlated with genetic relatedness. Thus, the social relationships of male Guinea baboons differ strikingly from other members of the genus. The results of my thesis quantitatively confirmed the assumption from earlier studies that the Guinea baboon society is different from all other baboon systems. These findings highlight that the diversity of social systems in the genus *Papio* is larger than previously recognized. My study has important implications for the use of baboons as a model in order to investigate social evolution, as it strongly supports the idea that ecological factors, which have traditionally been considered to shape the differences in baboon social systems, are insufficient to explain the observed variation. Inter-specific differences among societies may be driven by other factors than ecology alone. In particular, phylogeny and historical environments are an important issue that must be included in the study of social evolution (Henzi & Barrett 2003, 2005).

While my thesis is a first important step in a project to resolve the discordances about the Guinea baboon social system, it mainly covers one of three particularly important classes of relationships, those among adult males. To fully understand the social system of this species and its evolution comparable quantitative analyses of the other two classes, female-female as well as intersexual relationships, are the other two important remaining issues to resolve in order to derive final conclusions about the Guinea baboon society.

In addition, it will remain unclear how costs and benefits of strong bonds are distributed among different males as long as the distribution of paternities (i.e. reproductive skew) remains unknown. Further, a detailed study on cooperative interactions (i.e. affiliation and coalitionary support), including the directionality of interactions, is needed to investigate whether the established social network at the core of the Guinea baboon society (i.e. the party), that gives individuals the chance to interact repeatedly, favors the development of social bonds maintained by reciprocated interactions. An understanding of the mechanisms that lead to the ability of males to establish and maintain affiliative bonds can help to further understand the evolution of sociality (van Hoof & van Schaik 1994). In the future it will be important to investigate the processes that may have given rise to the transition from one type of baboon society to another.

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APPENDIX

Appendix I. Individual genotypes of 40 adult Guinea baboon males (chapter 3 and 4)

Cpt Nr	ID	D6s264		D7s503		D12s375		D3s1766		D13s765		D5s1457		D8s505		D10s1432		D5s820		D3s1768		D7s2204		D14s306		D1s533	
1	MST	94	96	156	158	173	177	194	194	201	201	129	129	147	151	163	163	186	194	205	205	236	240	169	173	191	195
2	JKY	94	94	154	156	169	173	194	194	201	201	125	129	147	147	159	167	186	186	197	209	232	240	169	177	195	195
4	MBY	96	96	148	154	169	169	194	194	205	213	125	129	147	147	159	167	190	194	205	205	240	240	169	169	195	195
5	PTR	94	94	148	156	169	169	194	194	201	201	125	129	147	151	163	167	190	194	197	209	236	240	169	169	191	199
6	DVD	94	94	144	156	173	177	194	202	201	205	125	125	147	147	163	167	186	194	205	205	232	236	173	173	191	195
7	OSM	94	96	144	148	169	173	194	194	201	201	125	125	147	147	159	163	182	194	197	197	236	236	169	173	195	199
10	CSS	94	94	144	156	169	169	194	194	201	201	125	129	147	147	163	167	186	194	197	205	232	240	169	173	191	195
12	MRS	96	100	156	158	177	177	194	194	201	201	125	125	147	151	159	163	190	194	205	205	236	236	169	173	191	195
15	SNE	94	96	148	158	169	177	194	194	205	205	125	129	147	147	163	167	186	186	197	197	244	244	169	169	195	199
16	NDO	94	96	154	158	165	181	194	194	201	205	125	125	147	151	163	163	178	186	197	205	248	248	169	173	191	199
17	KRT	96	96	144	158	177	181	194	194	201	205	125	129	147	147	163	163	186	190	205	205	236	240	169	169	191	195
20	SML	94	96	148	154	169	169	194	194	201	201	125	125	147	151	163	167	186	186	205	209	236	244	169	173	191	195
22	FLL	96	96	156	158	173	177	194	194	201	201	125	129	147	151	159	159	178	190	205	205	240	240	169	173	195	195
23	MOR	96	96	144	158	165	177	194	194	201	201	125	125	147	147	159	163	190	194	197	205	232	244	169	169	187	195
24	SRN	94	96	158	158	169	181	194	194	201	205	125	129	147	147	159	163	190	190	205	205	236	240	169	169	191	195
25	OMR	94	96	156	158	165	169	194	198	201	205	125	129	147	147	159	163	178	194	205	209	244	248	169	169	191	199
26	BDG	94	96	144	156	169	181	194	194	205	205	125	125	147	147	159	163	178	190	205	205	240	240	173	173	195	195
27	BAA	94	96	154	158	165	173	194	194	201	205	125	125	147	147	167	167	190	194	205	205	232	236	169	169	191	195
28	DTM	96	96	144	156	165	169	194	194	201	201	125	129	147	151	163	167	186	194	205	205	236	240	169	173	191	199
32	NDR	96	96	154	158	169	181	194	202	201	209	125	129	147	151	163	163	186	194	205	205	232	236	169	169	195	199
35	SNG	94	96	156	158	177	177	194	194	197	201	125	125	147	147	163	163	190	194	201	205	236	244	169	173	187	191
36	MTS	94	98	144	156	165	177	194	202	201	205	125	125	151	151	163	163	182	190	205	205	232	240	169	177	195	199
38	MRT	94	94	144	156	169	169	194	194	201	205	125	125	147	147	163	167	186	190	205	205	232	244	165	169	191	191
47	HOK	96	96	144	154	169	173	194	202	201	205	125	125	147	147	163	163	178	190	197	197	240	244	169	173	191	195
48	SNA	94	96	156	158	165	177	194	194	201	201	125	129	147	147	163	163	190	190	205	205	236	240	173	173	191	199
49	BDU	94	96	156	156	177	181	194	194	201	209	125	129	147	147	163	163	194	198	201	201	232	236	169	173	191	199
50	RMB	94	96	156	158	177	177	194	202	201	201	129	129	147	147	163	167	186	194	197	205	236	240	173	177	195	195
52	MDI	96	96	156	156	177	181	194	202	201	205	125	129	147	147	163	163	186	194	205	205	236	244	169	177	191	199
53	ANT	94	94	156	158	173	177	194	202	201	213	125	125	147	147	163	163	178	190	205	205	236	244	169	177	195	199
54	LDW	94	96	156	158	173	177	202	202	201	205	125	129	147	147	163	167	186	194	205	205	236	248	169	177	195	199
55	RMN	94	96	156	156	177	181	194	194	205	205	125	125	147	147	163	167	186	194	205	205	232	240	169	177	191	199
57	FRD	96	96	156	158	169	173	194	194	201	205	125	125	147	147	163	167	190	194	205	205	240	240	169	173	195	199
59	MMD	96	96	156	158	169	169	194	194	205	205	129	129	147	147	159	163	194	198	205	205	236	236	169	169	199	199
60	SMB	94	96	156	158	169	169	194	202	201	205	129	129	147	147	163	167	186	190	197	205	232	236	173	173	191	195
61	ADM	94	96	144	156	181	181	194	202	201	201	125	125	147	151	159	163	186	190	205	205	232	232	169	173	191	195
64	CLV	96	98	156	156	177	177	194	194	201	205	125	125	147	151	163	167	190	194	197	205	236	236	169	169	191	199
65	IBR	94	96	154	156	177	181	194	202	201	205	125	125	147	147	159	167	186	190	205	209	232	232	169	173	191	195
66	TBS	96	96	148	156	169	177	194	194	201	201	125	125	147	151	163	171	190	194	205	205	236	240	169	169	199	199
68	ASN	94	96	156	156	169	177	194	194	201	201	125	125	147	147	159	159	186	194	197	205	236	240	169	177	195	195
69	MSA	96	96	144	154	173	177	194	202	201	201	125	125	147	147	163	167	194	198	197	205	232	232	169	173	191	191

Appendix I. Individual genotypes of 40 adult Guinea baboon males (chapter 3 and 4), continuation.

CptNr	ID	D2s1329		D2s1326		D10s611		D8s1106		D17s791		D6s501		D17s1290		D6s311		D1s207		D4s243		D1s548		D21s1142	
1	MST	214	214	251	255	137	141	152	156	166	170	184	184	198	202	226	226	133	135	159	163	192	204	230	230
2	JKY	210	214	255	255	141	141	152	152	166	168	176	188	198	202	226	226	133	135	155	163	192	196	230	238
4	MBY	210	218	251	255	137	137	152	160	164	164	176	180	198	198	226	226	135	135	159	163	192	200	238	238
5	PTR	214	218	251	255	137	137	152	156	164	170	176	184	198	198	226	226	135	135	155	163	192	200	230	234
6	DVD	210	214	255	255	137	141	152	156	164	166	180	184	198	202	226	228	133	135	159	163	192	208	238	238
7	OSM	214	222	255	255	133	137	152	156	164	164	176	184	198	198	226	228	133	135	155	163	192	208	230	242
10	CSS	218	222	255	259	137	137	152	156	166	166	176	180	194	202	226	226	133	133	155	159	192	200	230	242
12	MRS	218	218	243	255	137	137	152	152	166	166	176	184	194	198	226	228	135	135	155	159	192	204	226	242
15	SNE	214	218	255	255	137	137	152	156	164	166	184	188	198	202	226	226	133	135	155	159	192	192	230	234
16	NDO	214	218	255	255	141	141	152	152	166	166	176	180	194	206	226	228	133	135	155	159	192	200	230	234
17	KRT	218	222	251	255	137	141	152	152	164	166	184	184	194	198	226	226	133	135	159	159	192	204	238	238
20	SML	214	218	251	251	137	141	152	152	164	168	180	180	198	198	226	226	133	135	159	163	192	208	230	238
22	FLL	214	218	251	251	137	141	152	152	166	168	176	184	202	202	228	228	135	135	155	159	192	200	230	238
23	MOR	214	214	251	255	137	141	152	152	164	166	180	180	198	202	226	228	133	135	159	159	192	196	230	238
24	SRN	214	218	255	255	137	141	148	152	166	166	184	188	198	198	226	228	133	135	155	159	192	200	238	242
25	OMR	214	222	251	255	141	141	152	152	166	168	180	184	198	198	226	226	135	135	159	163	200	204	226	230
26	BDG	214	214	251	251	137	137	156	156	166	166	180	188	198	202	226	228	135	135	159	163	192	192	230	238
27	BAA	218	218	251	255	141	141	152	152	166	168	180	180	198	198	226	228	133	135	159	159	192	196	230	238
28	DTM	214	218	251	255	137	137	152	152	164	166	184	188	194	194	226	226	133	135	163	163	200	204	238	238
32	NDR	214	218	255	255	137	141	152	156	166	166	180	180	198	202	228	228	135	135	159	159	200	204	230	230
35	SNG	214	218	255	255	137	141	152	152	164	166	176	180	194	198	226	226	135	135	155	163	192	200	230	238
36	MTS	218	218	255	255	137	137	152	156	166	166	180	180	194	198	226	228	135	135	159	163	192	192	230	238
38	MRT	218	218	251	255	137	141	152	156	164	166	176	180	198	198	226	226	133	135	159	159	204	208	234	242
47	HOK	214	218	251	255	137	141	152	152	164	166	184	184	198	198	228	228	135	135	159	163	192	208	230	230
48	SNA	214	214	251	255	141	141	152	156	166	166	176	184	194	198	226	228	135	135	163	167	192	196	234	238
49	BDU	218	218	255	255	137	141	152	156	166	166	180	184	198	206	226	226	135	135	155	159	196	200	234	238
50	RMB	214	214	255	255	137	141	152	156	166	166	180	188	198	206	226	226	133	135	159	163	196	196	226	242
52	MDI	214	214	255	255	133	137	152	156	166	166	180	184	202	206	226	226	133	135	159	159	196	200	230	238
53	ANT	210	218	255	255	137	141	152	152	166	166	180	184	194	202	228	228	133	135	159	163	200	200	230	238
54	LDW	214	214	255	255	137	137	152	152	166	166	180	188	194	206	226	226	133	135	155	159	192	196	230	230
55	RMN	218	222	255	255	137	137	152	152	166	166	180	184	198	206	226	226	133	135	163	163	192	200	230	238
57	FRD	214	218	255	255	137	141	148	152	164	166	180	184	198	198	226	226	133	135	155	159	196	200	230	238
59	MMD	218	218	251	255	133	141	152	152	166	168	180	180	198	198	226	228	133	135	159	163	200	204	238	242
60	SMB	214	214	251	255	133	137	152	156	166	166	180	184	198	206	226	228	135	135	155	159	192	192	230	246
61	ADM	218	222	255	255	137	141	152	152	164	166	188	188	194	198	226	226	133	133	159	159	196	200	230	242
64	CLV	218	222	255	255	133	141	152	152	164	166	176	180	198	202	226	226	133	135	155	159	200	204	242	242
65	IBR	218	218	251	255	137	141	148	152	164	166	180	188	198	198	226	226	133	133	155	159	196	208	230	238
66	TBS	214	218	251	255	137	137	152	152	164	164	180	184	198	202	226	228	133	135	159	163	192	204	230	238
68	ASN	214	218	255	255	141	141	152	152	166	166	184	188	198	198	226	226	133	135	155	155	192	200	230	238
69	MSA	214	218	255	255	137	141	148	152	164	164	184	184	198	198	226	226	133	135	159	163	192	196	230	242

Appendix II. Dyadic hourly interaction frequencies used in QAP correlation (chapter 4)

MARE GANG 2010

affiliation 2010

	ANT	CSS	HOK	MBY	OSM	PTR	SML	SNE	DTM
ANT		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CSS	0.00		0.00	0.40	0.04	0.00	0.00	0.02	0.00
HOK	0.00	0.00		0.00	0.00	0.00	0.23	0.16	0.00
MBY	0.00	0.40	0.00		0.04	0.00	0.00	0.00	0.00
OSM	0.00	0.04	0.00	0.04		0.08	0.00	0.00	0.00
PTR	0.00	0.00	0.00	0.00	0.08		0.00	0.00	0.00
SML	0.00	0.00	0.23	0.00	0.00	0.00		0.15	0.00
SNE	0.00	0.02	0.16	0.00	0.00	0.00	0.15		0.00
DTM	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	

agonism 2010

	ANT	CSS	HOK	MBY	OSM	PTR	SML	SNE	DTM
ANT		0.06	0.00	0.00	0.02	0.02	0.00	0.02	0.00
CSS	0.06		0.00	0.04	0.02	0.00	0.02	0.02	0.12
HOK	0.00	0.00		0.04	0.00	0.00	0.04	0.02	0.00
MBY	0.00	0.04	0.04		0.00	0.02	0.00	0.00	0.04
OSM	0.02	0.02	0.00	0.00		0.04	0.00	0.00	0.00
PTR	0.02	0.00	0.00	0.02	0.04		0.00	0.00	0.00
SML	0.00	0.02	0.04	0.00	0.00	0.00		0.04	0.08
SNE	0.02	0.02	0.02	0.00	0.00	0.00	0.04		0.00
DTM	0.00	0.12	0.00	0.04	0.00	0.00	0.08	0.00	

greetings 2010

	ANT	CSS	HOK	MBY	OSM	PTR	SML	SNE	DTM
ANT		0.06	0.02	0.04	0.27	0.28	0.06	0.02	0.00
CSS	0.06		0.00	0.25	0.00	0.04	0.00	0.09	0.57
HOK	0.02	0.00		0.04	0.02	0.00	0.10	0.11	0.00
MBY	0.04	0.25	0.04		0.06	0.06	0.02	0.07	0.35
OSM	0.27	0.00	0.02	0.06		0.14	0.04	0.04	0.00
PTR	0.28	0.04	0.00	0.06	0.14		0.02	0.04	0.00
SML	0.06	0.00	0.10	0.02	0.04	0.02		0.11	0.08
SNE	0.02	0.09	0.11	0.07	0.04	0.04	0.11		0.00
DTM	0.00	0.57	0.00	0.35	0.00	0.00	0.08	0.00	

coalitions 2010

	ANT	CSS	HOK	MBY	OSM	PTR	SML	SNE	DTM
ANT		0	0	0	0	0	0	0	0
CSS	0		0	3	0	0	0	0	0
HOK	0	0		0	0	0	1	1	0
MBY	0	3	0		0	0	0	0	0
OSM	0	0	0	0		0	0	0	0
PTR	0	0	0	0	0		0	0	0
SML	0	0	1	0	0	0		2	0
SNE	0	0	1	0	0	0	2		0
DTM	0	0	0	0	0	0	0	0	

Appendix II. Dyadic hourly interaction frequencies used in QAP correlation (chapter 4), continuation.

SIMENTI GANG 2011

affiliation 2011

	ASN	CLV	JKY	MSA	MST	TBS	ADM	IBR
ASN		0	0	0.04	0	0.06	0.04	0
CLV	0		0	0	0.06	0.08	0	0.04
JKY	0	0		0	0	0.08	0	0
MSA	0.04	0	0		0	0.02	0	0
MST	0	0.06	0	0		0	0	0.04
TBS	0.06	0.08	0.08	0.02	0		0	0
ADM	0.04	0	0	0	0	0		
IBR	0	0.04	0	0	0.04	0		

agonism 2011

	ASN	CLV	JKY	MSA	MST	TBS	ADM	IBR
ASN		0.02	0.00	0.00	0.04	0.06	0.04	0.04
CLV	0.02		0.02	0.06	0.02	0.02	0.00	0.00
JKY	0.00	0.02		0.04	0.02	0.10	0.00	0.00
MSA	0.00	0.06	0.04		0.00	0.02	0.04	0.00
MST	0.04	0.02	0.02	0.00		0.00	0.04	0.08
TBS	0.06	0.02	0.10	0.02	0.00		0.00	0.00
ADM	0.04	0.00	0.00	0.04	0.04	0.00		
IBR	0.04	0.00	0.00	0.00	0.08	0.00		

greetings 2011

	ASN	CLV	JKY	MSA	MST	TBS	ADM	IBR
ASN		0.18	0.52	0.77	0.16	0.26	0.08	0.04
CLV	0.18		0.08	0.16	0.18	0.04	0.08	0.12
JKY	0.52	0.08		0.32	0.00	0.3	0.04	0.04
MSA	0.77	0.16	0.32		0.10	0.16	0.04	0.08
MST	0.16	0.18	0.00	0.10		0.04	0	0.24
TBS	0.26	0.04	0.30	0.16	0.04		0	0
ADM	0.08	0.08	0.04	0.04	0.00	0		
IBR	0.04	0.12	0.04	0.08	0.24	0		

coalitions 2011

	ASN	CLV	JKY	MSA	MST	TBS	ADM	IBR
ASN		0	0	0	0	3	0	0
CLV	0		0	0	0	0	0	0
JKY	0	0		0	0	3	0	0
MSA	0	0	0		0	1	0	0
MST	0	0	0	0		0	1	0
TBS	3	0	3	1	0		0	0
ADM	0	0	0	0	1	0		
IBR	0	0	0	0	0	0		

MARE GANG 2011

affiliation 2011

	HOK	OSM	PTR	SML	SNE	BAA	NDR	DTM
HOK		0	0.02	0.2	0.32	0.04	0	0
OSM	0		0.08	0	0	0.04	0.04	0
PTR	0.02	0.08		0	0.04	0	0	0
SML	0.2	0	0		0.32	0.04	0	0
SNE	0.32	0	0.04	0.32		0.12	0	0
BAA	0.04	0.04	0	0.04	0.12			
NDR	0	0.04	0	0	0			
DTM	0	0	0	0	0			

agonism 2011

	HOK	OSM	PTR	SML	SNE	BAA	NDR	DTM
HOK		0.00	0.02	0.00	0.04	0.08	0.00	0.00
OSM	0.00		0.06	0.00	0.04	0.04	0.04	0.08
PTR	0.02	0.06		0.02	0.06	0.00	0.00	0.04
SML	0.00	0.00	0.02		0.02	0.04	0.00	0.00
SNE	0.04	0.04	0.06	0.02		0.00	0.00	0.00
BAA	0.08	0.04	0.00	0.04	0.00			
NDR	0.00	0.04	0.00	0.00	0.00			
DTM	0.00	0.08	0.04	0.00	0.00			

greetings 2011

	HOK	OSM	PTR	SML	SNE	BAA	NDR	DTM
HOK		0.02	0.00	0.2	0.18	0.16	0.00	0.00
OSM	0.02		0.20	0	0.04	0.00	0.04	0.20
PTR	0.00	0.20		0.06	0.08	0.00	0.27	0.19
SML	0.20	0.00	0.06		0.14	0.20	0.00	0.00
SNE	0.18	0.04	0.08	0.14		0.39	0.00	0.00
BAA	0.16	0.00	0.00	0.2	0.39			
NDR	0.00	0.04	0.27	0	0			
DTM	0.00	0.20	0.19	0	0			

coalitions 2011

	HOK	OSM	PTR	SML	SNE	BAA	NDR	DTM
HOK		0	0	1	4	0	0	0
OSM	0		5	0	0	0	0	0
PTR	0	5		0	1	0	0	0
SML	1	0	0		2	0	0	0
SNE	4	0	1	2		4	0	0
BAA	0	0	0	0	4			
NDR	0	0	0	0	0			
DTM	0	0	0	0	0			

Appendix III. Copulation data during focal protocols and *ad libitum*-data

2010 MARE GANG

PTR-OSM Party

PTR	23
ANT	12
OSM	3

SNE Party

SML	4
SNE	2
HOK	1

MBY-CSS Party

CSS	16
MBY	2

2011 MARE GANG

PTR-OSM Party

PTR	8
OSM	7

SNE Party

SNE	7
HOK	0
SML	2

2011 SIMENTI GANG

MST-Party

CLV	3
MST	11

JKY-Party

TBS	25
MSA	10
JKY	5
ASN	30

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2006	Diploma thesis at Georg-August-University Göttingen and German Primate Center (DPZ), Goettingen, Cognitive Ethology Laboratory: "Reconciliation in Barbary macaques (*Macaca sylvanus*)".
2000-2006	Studies of Biology at Georg-August-University Goettingen, Germany
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Practical Experience

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2006	Volunteer at "Gibbon Conservation Center", Santa Clarita, CA, USA (3 months)
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2007 -2012	Four longer and two shorter stays at DPZ field site Simenti, Senegal (total of 30 month; project coordination and data collection for PhD thesis)

Conference contributions (1st author)

2007	Patzelt, A. and Fischer, J. Reconciliation in female Barbary macaques. Poster presentation, *GfP Wintermeeting*, Leipzig.
2009	Patzelt, A. and Fischer, J. Post-conflict affiliation increases the chances of short term renewed aggression in Barbary macaques. Poster presentation, 2nd *Congress of the EFP,* Zurich, Switzerland.
2010	Patzelt, A., Fickenscher, G., Diedhiou, S., Camara, B., Zinner, D., Fischer, J. Group composition of Guinea baboons (*Papio papio*) suggests a fluid social organization. Invited

talk within symposium “Where Next? Group Coordination and Decision-Making in Primates”, *23rd Congress of the IPS*, Kyoto, Japan.

2010 Patzelt, A. and P. Maciej, P. Baboon research in Senegal - The social system & vocal communication of Guinea baboons. Talk at *CRC PhD-Workshop*, Goettingen.

2011 Patzelt, A., Zinner, D., Maciej, P., Fischer, J. Male-male relationships in Guinea baboons (*Papio papio)* suggest a tolerant social style. Poster presentations at the *4th Congress of the EFP,* Almada, Portugal & *8th Göttinger Freilandtage* , Goettingen.

2012 Patzelt, A., Maciej, P., Ndao, I., Zinner, D., Fischer, J. Spatial and social association patterns of Guinea baboons (*Papio papio*) reveal strong male bonds within a multi-level society. Oral presentations at the *ECBB* Essen and at *CRC PhD-workshop*, Goettingen.

2012 Patzelt, A. Insights into the Guinea baboon society – Combining spatial, social and genetic data. Oral presentation at the *CRC Summerschool,* Goettingen.

Publications

Patzelt, A., Pirow, R., Fischer, J. (2009) Post-conflict affiliation in Barbary macaques is influenced by conflict characteristics and relationship quality, but does not diminish short term renewed aggression. *Ethology* 115: 658-670.

Fischer, J., Teufel, C.R., Drolet, M., Patzelt, A., von Cramon, D.Y., Rübsamen, R., Schubotz, R.I. (2009) Orienting asymmetries and lateralized processing of sounds in humans. *BMC Neuroscience* 10: 14.

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Maciej, P., Patzelt, A., Ndao, I., Hammerschmidt, K., Fischer, J. (2013) Social monitoring in a multilevel society: a playback study with male Guinea baboons. *Behavioral Ecology and Sociobiology 67*, 61–68.

Patzelt, A., Maciej, P., Kopp, G.H., Ndao, I., Kalbitzer, U., Zinner, D., Fischer, J. (under review) Spatial, social and genetic relationships of Guinea baboons (*Papio papio*) suggest a new dimension in primate social diversity.

Prices

2006 GfP-prize for best diploma thesis

2011 1st poster prize in the student competition at the *4th Congress of the EFP*, Almada, Portugal.

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Ausbildung

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2006	Diplomarbeit an der Georg- August-Universität Göttingen und dem Deutschen Primatenzentrum (DPZ), Göttingen, Abteilung Kognitive Ethologie: “Versöhnungsverhalten bei Berberaffen (*Macaca sylvanus*)”
2000-2006	Studium der Biologie an der Georg-August-Universität Göttingen
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Praktische Erfahrungen

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Konferenzbeiträge (Erstauthorin)

2008	Patzelt, A. und Fischer, J. Reconciliation in female Barbary macaques. Posterpräsentation, *GfP Wintermeeting*, Leipzig.
2009	Patzelt, A. und Fischer, J. Post-conflict affiliation increases the chances of short term renewed aggression in Barbary macaques. Posterpräsentation, *2nd Congress of the EFP,* Zürich, Schweiz.
2010	Patzelt, A., Fickenscher, G., Diedhiou, S., Camara, B., Zinner, D., Fischer, J. Group composition of Guinea baboons (*Papio papio*) suggests a fluid social organization. Eingeladener Vortrag im Rahmen des Symposiums "Where Next? Group Coordination and Decision-Making in Primates", *23rd Congress of the International Primatological Society*, Kyoto, Japan.
2010	Patzelt, A. und P. Maciej, P. Baboon research in Senegal - The social system & vocal communication of Guinea baboons. Vortrag, *CRC PhD-Workshop*, Göttingen.
2011	Patzelt, A., Zinner, D., Maciej, P., Fischer, J. Male-male relationships in Guinea baboons (*Papio papio)* suggest a tolerant social style. Posterpräsentationen beim *4th Congress of the EFP,* Almada, Portugal & *8. Göttinger Freilandtage,* Göttingen.
2012	Patzelt, A., Maciej, P., Ndao, I., Zinner, D., Fischer, J. Spatial and social association patterns of Guinea baboons (*Papio papio*) reveal strong male bonds within a multi-level society. Vortrag, *ECBB,* Essen und *CRC PhD-workshop*, Göttingen.
2012	Patzelt, A. Insights into the Guinea baboon society - Combining spatial, social and genetic data. Vortrag, *CRC Summerscool*, Göttingen.

Publikationen

Patzelt, A., Pirow, R., Fischer, J. (2009) Post-conflict affiliation in Barbary macaques is influenced by conflict characteristics and relationship quality, but does not diminish short term renewed aggression. *Ethology* 115: 658-670.

Fischer, J., Teufel, CR, Drolet, M., Patzelt, A., von Cramon, D.Y., Rübsamen, R., Schubotz, R.I. (2009) Orienting asymmetries and lateralized processing of sounds in humans. *BMC Neuroscience* 10: 14.

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Preise

2006	GfP-Preis für die beste Diplomarbeit
2011	1. Posterpreis im Studentenwettbewerb beim *4th Congress of the EFP*, Almada, Portugal

EIDESSTATTLICHE ERKLÄRUNG

Hiermit erkläre ich, dass ich diese Dissertation selbstständig ohne unerlaubte Hilfe angefertigt habe. Ich habe keine anderen als die angegebenen Quellen benutzt. Alle den benutzten Quellen wörtlich oder sinngemäß entnommenen Stellen sind als solche einzeln kenntlich gemacht.

Das gesamte Promotionsvorhaben wurde gemeinsam mit Julia Fischer und Dietmar Zinner geplant. Die Freilandforschung habe ich in Rücksprache mit Julia Fischer und Dietmar Zinner durchgeführt. Die Daten habe ich unter Betreuung von Julia Fischer und Dietmar Zinner ausgewertet. Die (vorbereiteten) Publikationen in den Kapiteln 2-4 wurden im Wesentlichen von mir verfasst und von Julia Fischer und Dietmar Zinner betreut. Alle Koautoren haben zur finalen Version der Manuskripte beigetragen.

Des Weiteren erkläre ich, dass ich mich nicht an einer anderen Universität um einen Doktortitel beworben habe und dass diese Arbeit in gleicher oder ähnlicher Form noch keiner anderen Prüfungsbehörde vorgelegen hat.

Göttingen, den 30.05.2013

Annika Patzelt