Achievement and maintenance of dominance in male crested macaques (*Macaca nigra*)

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Erzielen und Erhalten von Dominanz bei männlichen Schopfmakaken (*Macaca nigra*)

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Dominance rank often determines the share of reproduction an individual male can secure in group-living animals (i.e. dominance rank-based reproductive skew). However, our knowledge of the interplay between individual and social factors in determining rank trajectories of males is still limited. The overall aim of this thesis was therefore to investigate mechanisms that underlie individual dominance rank trajectories in male crested macaques (*Macaca nigra*) and to highlight potential individual and social determinants of how males can achieve and maintain the highest rank possible. Data for this thesis were collected on 37 males during a field study on a natural population of crested macaques living in the Tangkoko-Batuangus Nature Reserve in Indonesia. In study 1, I validate Elo-rating as a particularly well suited method to quantify dominance hierarchies in animal species with dynamic dominance relationships. In studies 2 and 3, I suggest a personality structure for crested macaque males consisting of five distinct factors and further demonstrate that two personality factors determine whether males will rise or fall in rank. Finally, in study 4, I present results on how males utilize coalitions to increase their future rank. Together, these results shed light on how individual attributes and social environment both can impact male careers. Ultimately, in order to understand what determines rank-based reproductive skew, we need to consider the complexity and likely diversity of the mechanisms underlying rank trajectories of individual males which are likely to differ across different species.

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Summary

Competition for access to females is the major principle governing the differential reproductive success observed among males in most animal species. Dominance hierarchies arise from differences in competitive abilities between individual males and often translate into reproductive benefits for high-ranking males (i.e. rank-based reproductive skew). Frequently, dominance hierarchies correspond to relatively simple variables that describe general physical abilities of individuals, such as body size or development of weaponry. In many species, however, the determinants of dominance status are more complex than that, and represent interactions between a variety of individual attributes, which collectively determine the ability to become dominant. Primates represent an interesting taxon to study this phenomenon because they live in complex social systems and further display elaborate cognitive abilities. Thus, the makeup of traits that determine which individuals will achieve high status is expected to be particularly complex in primates.

For several reasons, crested macaques (*Macaca nigra*) are a well suited taxon to study the mechanisms that underlie differential dominance achievement and maintenance between individual males. First, high dominance rank is associated with high mating and reproductive success, highlighting the importance of becoming as high-ranking as possible with regard to fitness. Second, male dominance hierarchies in crested macaques can be described as very dynamic in both, the level of males commonly migrating in and out of groups, and rank changes within the group that frequently occur outside the context of migration.

The overall aim of this thesis was therefore to investigate mechanisms underlying individual dominance rank trajectories in male crested macaques and to highlight possible, individual and social, determinants of how males can achieve and maintain the highest rank possible. In study 1, I address the problem of how dominance hierarchies can be reliably estimated even when conditions such as frequent migration events and changes within the hierarchy make the application of traditional approaches difficult, if not impossible. Studies 2 and 3 describe how male personality as an example of an intrinsic property can contribute to rank trajectories. Finally, in study 4, I investigate how coalitions, as an example for influences of the social environment, impact rank dynamics.

The data for this study were collected between 2009 and 2011 in the Tangkoko-Batuangus Nature Reserve in the north of Sulawesi, Indonesia. Study subjects were the 37 adult males residing in two social groups during this time. During *focal animal sampling* on these males, continuous data were recorded on social, aggressive and self-directed behaviour. In addition, the identities of adult individuals in spatial proximity were noted at regular intervals, as well as the focal animals' position with respect to the core of the social group. In total, more than 2,000 hours of focal animal data were collected (mean = 66.1h, range = 0.6 – 130.0h per male, total = 2447.2h). Finally, two playback experiments were conducted to supplement the observational study of personality. With the presentation of dog bark bouts, I tested whether males differ in boldness, while neophilia was measured as the response to donkey brays. Statistical methods employed during data analysis include non-parametric tests, factor analysis and linear mixed models.

In study 1, I validate Elo-rating as a useful method to quantify dominance hierarchies. Elo-rating is rooted in the rating of competitive chess players and has a range of hitherto overlooked advantages over more commonly used methods of measuring dominance hierarchies in animals. These advantages are particularly important with respect to obtaining dominance measures in the context of overly dynamic relations between individuals. The applicability of standard ranking algorithms is limited to situations in which group composition is relatively stable and in which the majority of relationships between any pair of individuals are known. Elo-rating, in contrast, uses a relatively simple algorithm, during which an individual's Elo-rating is updated after each single interaction this individual was involved in. The underlying principle of how ratings change reflects the expected as compared to the observed outcome of single dominance interactions. In this way, Elo-rating allows the estimation of dominance status on a very fine-grained time scale, without the need to aggregate dominance data over substantial periods of time. In addition, Elo-rating results in dominance hierarchies that closely match those derived from commonly used methods – given the data allow the application of these methods. Elo-rating therefore provides the necessary tool for reliable assessment of dominance status in dynamic systems, such as male crested macaque hierarchies. Furthermore, it allows to address conveniently questions related to individual rank trajectories.

In study 2, I suggest a personality structure for crested macaque males that consists of five personality factors: connectedness, sociability, anxiety, aggressiveness, and boldness. Connected males spent their time with a high diversity of female and male group members in spatial proximity. Sociable males spent more time grooming and had more diverse grooming partners. Anxious males were inactive, approached females rarely and showed high frequencies of self-directed behaviors. Aggressive males exhibited high rates of aggressive and threat behaviors towards other group members, with the notable exception of other adult males. Finally, bold males showed consistently stronger responses to the playback of dogs. The general makeup of crested macaque personality resembles to a high degree that of other macaque species. Yet, a notable difference to other macaques is the presence of connectedness, which covers aspects of social network diversity. These results not only contribute to our understanding of the evolution of personality structure in primates, they further set the grounds to investigate the possible adaptive value of differential expression of specific personality factors with regards to dominance rank – the topic of the subsequent study.

In study 3, I tested the relationships between the five personality factors determined in study 2 and dominance rank as determined with Elo-ratings. For this, I divided the study period into two-month blocks (necessary to obtain repeated personality scores for each male), for which I gathered corresponding current rank (Elo-rating), past rank

trajectory (i.e. the difference between current Elo-rating and the Elo-rating corresponding to the preceding time block), and future rank trajectory (i.e. the difference between Elo-rating of the time block after and current Elo-rating). The first set of results revealed that four personality factors (connectedness, aggressiveness, anxiety and boldness) co-varied with concurrent dominance rank. However, none of the personality factors was predicted by past rank trajectory. The second set of results indicated that future rank trajectory was predicted by connectedness and anxiety, independent of the co-variation between current rank and personality scores. More connected and less anxious males were more likely to rise in rank as compared to less connected and more anxious males. These results indicate that personality can affect social careers and not vice versa. On the one hand, connectedness might reflect the ability of males to optimize their access to social partners in a dynamic environment. Here, the ability to diversify, rather than to concentrate, relationships might be crucial given the frequent changes among males caused by migration and rank changes. On the other hand, anxiety as correlate of future success might relate to physiological adaptions in male ability to cope with environmental and social stress. In sum, the results of study 3 highlight the salience of personality as an individual feature with potential impact on male dominance careers.

In the final study 4, I investigate the consequences of coalitions with regard to future rank of males. Overall, coalitions were relatively infrequent (0.03 events per hour), and the majority (about 65% of events) was composed of only males, while about 35% of coalitions included at least one female participant. All coalitions observed were targeted at single adult males. Although rare, coalitions had pronounced effects on individual ranks in the future. As could have been expected, a male's role in a given coalition (participant or target) had the most pronounced effect, i.e. participating males generally rose in rank while targeted males dropped. However, these effects interacted with other important coalition characteristics. For example, coalitions in all-up configuration (all participants rank below the target) resulted in greater changes in both participants and targets as compared to bridging and all-down coalitions (target ranks between and below all participants, respectively). Additional results indicated that coalitions acted in an additive way to age-predicted patterns of rank trajectories, for example, while old males generally dropped in rank, they dropped less if they participated in coalitions. Further characteristics that influenced rank consequences of coalitions include the degree of feasibility (difference in rank between target and the combination of participants) and whether coalitions were composed of males only, or included females. These results contribute to our understanding of how coalitions impact dominance rank trajectories by highlighting the importance of several coalition characteristics with respect to the consequences of coalitions. Coalitions can therefore be regarded as an effective strategy employed by males to maximize their dominance rank, which in turn is associated with advantages regarding access to females.

This thesis provides evidence for the complex interplay between factors and their collective impact on dominance rank trajectories of male crested macaques. Two general classes of such factors can be distinguished: individual attributes and social environment. This thesis suggests that both, individual attributes (e.g. personality) and social environment (e.g. coalitions), have important consequences regarding the rank a male can achieve and whether he can maintain it once he reached it. In addition, individual characteristics and social environment are likely to interact with each other, for example by personalities that facilitate the formation of bonds and/or coalitions. Ultimately, if we want to understand what determines rank-based reproductive skew, we need to consider the complexity of mechanisms that govern rank trajectories that individual males will follow and we further have to take into account the likely diversity and cross-species differences of these mechanisms.

Zusammenfassung

Der Wettkampf um Zugang zu Weibchen ist eines der wichtigsten Prinzipien um die Variation im individuellen Reproduktionserfolg von Männchen in vielen Tierarten zu erklären. Durch inter-individuelle Unterschiede in kompetitiven Fähigkeiten zwischen Individuen entstehen Dominanzhierarchien, in denen hochrangige Männchen oft Vorteile im Hinblick auf Reproduktion haben (rang-basierter *reproductive skew*). Häufig korrespondieren solche Hierarchien mit relativ einfachen individuellen Merkmalen, welche die allgemeine physische Erscheinung beschreiben, wie beispielsweise Körpergröße oder die Ausbildung von Waffen. Allerdings sind die Determinanten von Dominanzstatus oft komplexer und können als Interaktionen zwischen verschiedenen individuellen und sozialen Merkmalen betrachtet werden, die in ihrer Gesamtheit die Fähigkeit eines Individuums beschreiben dominant zu werden. Primaten stellen ein geeignetes Taxon dar um dieses Phänomen zu untersuchen, da sie in komplexen Sozialsystemen leben und ihre kognitiven Fähigkeiten den Einfluss von sozialen Komponenten auf Dominanzstatus wahrscheinlich machen. Es kann daher erwartet werden, dass die Zusammensetzung der Merkmale, die in ihrere Kombination bestimmen welches Männchen einen hohen Rang erreicht, in Primaten äußerst komplex ist.

Zwei Gründe machen Schopfmakaken (*Macaca nigra*) zu einer sehr geeigneten Art die Mechanismen zu untersuchen, die dem zwischen individuellen Männchen variierenden Erreichen und Erhalten von Dominanz zugrunde liegen. Zum einen ist hoher Dominanzrang mit hohem Paarungs- und Fortpflanzungserfolg assoziiert, was die Wichtigkeit, so hochrangig wie möglich zu werden, in Hinblick auf Fitnessvorteile unterstreicht. Zum anderen sind die Dominanzhierarchien männlicher Schopfmakaken äußerst dynamisch; sowohl mit Blick auf immigrierende und emigrierende Männchen, als auch durch regelmäßige Rangwechsel während stabiler Gruppenzusammensetzung.

Ziel dieser Arbeit war daher, jene Mechanismen zu untersuchen, die individuellen Rangdynamiken männlicher Schopfmakaken zugrunde liegen und dabei mögliche individuelle und soziale Determinanten zu identifizieren, die Erreichen und Erhalten des höchstmöglichen Ranges der Männchen bestimmen. In Studie 1 untersuche ich die Problematik der zuverlässigen Quantifizierung von Dominanzhierarchien im Angesicht häufiger Migration und Rangwechsel, welche die Anwendung herkömmlicher Methoden erschweren. In Studien 2 und 3 beschreibe ich, als Beispiel für individuelle Merkmale, wie die Persönlichkeit von Männchen Rangdynamiken beeinflussen kann. In der abschließenden Studie 4 untersuche ich Koalitionen, als Beispiel für soziale Faktoren, auf ihre Auswirkungen auf Dominanzrang.

Für diese Studie wurden zwischen 2009 und 2011 im Tangkoko-Batuangus Naturreservat in Nordsulawesi, Indonesien, Daten von jenen 37 Männchen gesammelt, die

während dieser Zeit in zwei sozialen Gruppen lebten. Mittels Fokustierbeobachtungen wurden kontinuierliche Daten über soziales, aggressives und selbst-gerichtetes Verhalten aufgenommen. Zusätzlich wurde regelmäßig notiert welche anderen adulten Tiere sich in der Nähe des Fokustieres aufhielten, und wo sich das Fokustier in Relation zum räumlichen Kern der Gruppe befand. Auf diese Weise wurden mehr als 2.000 Stunden Fokustierdaten aufgenommen (Mittelwert pro Männchen = 66,1h, min = 0,6h, max = 130,0h, total = 2.447,2h). Um die Persönlichkeitsstudie zu ergänzen, wurden zudem zwei Vorspielexperimente durchgeführt. Mittels Hundegebell wurde getestet, inwiefern Männchen unterschiedlich mutig sind, und der Schrei eines Esels diente dem Test ob Schopfmakaken einen Persönlichkeitsfaktor Neugierde besitzen. Die wichtigsten statistischen Methoden die in dieser Arbeit angewendet wurden, umfassen nichtparametrische Tests, Faktoranalyse und gemischte Regressionsmodelle.

In Studie 1 validiere ich Elo-rating als zuverlässige Methode um Dominanzhierarchien zu bestimmen. Elo-rating hat seine Wurzeln in der Bewertung von Schachspielern und besitzt eine Reihe von Vorteilen gegenüber herkömmlichen Methoden, die eingesetzt werden um Dominanzhierarchien zu messen. Diese Vorteile kommen vor allem dann zum Tragen wenn das System, für das eine Dominanzhierarchie bestimmt werden soll, sehr dynamisch ist. Traditionell verwendete Methoden setzen voraus, dass die Beziehungen zwischen den meisten Paaren von Tieren bekannt sein müssen und dass die Gruppenzusammensetzung stabil ist. Im Gegensatz dazu verwendet Elo-rating einen relativ simplen Algorithmus, in dem nach jeder einzelnen Interaktion, in die ein Tier verwickelt war, die Elo-rating Punktzahl der involvierten Tiere neu berechnet wird. Das Prinzip, nach dem eine Änderung in der individuellen Punktzahl berechnet wird, basiert auf dem Vergleich von zu erwartendem und tatsächlichem Ausgang der jeweiligen Interaktion. Dies erlaubt die Bestimmung von Dominanz mit sehr feiner Zeitauflösung. Darüber hinaus stimmen mit Elo-rating berechnete Hierarchien sehr gut überein mit den Ergebnissen von herkömmlichen Algorithmen – sofern die Bedingungen für deren Anwendungen gegeben sind. Elo-rating kann daher als das notwendige Werkzeug dienen um in dynamischen Systemen, wie den Hierarchien männlicher Schopfmakaken, Dominanz verlässlich zu quantifizieren.

In Studie 2 schlage ich eine Persönlichkeitsstruktur für Schopfmakaken vor, die aus 5 Faktoren besteht: Vernetztheit, Sozialität, Ängstlichkeit, Aggressivität und Mut. Vernetzte Männchen besaßen ein diverses Netzwerk von anderen Männchen und Weibchen in deren Nähe sie sich aufhielten. Soziale Männchen verbrachten mehr Zeit mit sozialer Fellpflege und besaßen ein diverses Netzwerk von Partnern für diese. Ängstliche Männchen waren inaktiv, näherten sich selten Weibchen an und verbrachten viel Zeit mit selbst-gerichtetem Verhalten. Aggressive Männchen zeigten anderen Gruppenmitgliedern gegenüber häufig aggressives Verhalten, mit der Ausnahme anderer adulter Männchen. Mutige Männchen zeigten gegenüber dem Vorspielexperiment konsistent stärkere Reaktionen. Damit entspricht die Persönlichkeitsstruktur von Schopfmakaken im Allgemeinen der anderer Arten der Gattung, mit der Ausnahme des Faktors Vernetztheit. Die Ergebnisse dieser Studie tragen nicht nur zum Verständnis der Evolution von Persönlichkeitsstrukturen innerhalb der Primaten bei, sondern sind darüber hinaus auch die notwendige Grundlage für Studien zum adaptiven Wert von Persönlichkeit bei Schopfmakaken – dem Thema der folgenden Studie.

Der Zusammenhang zwischen Persönlichkeitsfaktoren und Dominanzrang ist Inhalt von Studie 3. Um wiederholte Messwerte innerhalb eines Männchens für die fünf in Studie 2 beschriebenen Persönlichkeitsfaktoren zu erhalten, unterteilte ich die Gesamtstudienzeit in Blöcke zu je zwei Monaten. Für jeden dieser Blöcke und für jedes anwesende Männchen wurden ebenfalls (1) der gegenwärtige Rang (Elo-rating Punktzahl innerhalb des Blocks), (2) die vergangene Rangentwicklung (Differenz zwischen gegenwärtiger Elo-rating Punktzahl und der Punktzahl im vorausgehenden Block), und (3) die zukünftige Rangentwicklung (Differenz zwischen der Punktzahl im nachfolgenden Block und gegenwärtiger Punktzahl) berechnet. Ein erstes Ergebnisset zeigte, dass vier Persönlichkeitsfaktoren mit gegenwärtigem Dominanzrang kovariierten: Vernetztheit, Aggressivität, Ängstlichkeit und Mut. Im Gegensatz dazu gab es keinen Zusammenhang zwischen vergangener Rangentwicklung und Persönlichkeitsfaktoren. Im zweiten Ergebnisset konnte gezeigt werden, dass Vernetztheit und Ängstlichkeit die zukünftige Rangentwicklung voraussagen – unabhängig von der eben genannten Kovarianz zwischen Persönlichkeit und gegenwärtigem Rang. Vernetztere und weniger ängstliche Männchen stiegen eher im Rang, verglichen mit weniger vernetzten und ängstlicheren Männchen. Diese Ergebnisse zeigen, dass es wahrscheinlicher ist, dass Persönlichkeit Rangentwicklung beeinflusst, und nicht umgekehrt, nämlich dass Persönlichkeit von Rangentwicklung abhängt. Die Vorteile von Vernetztheit könnten mit der Fähigkeit im Zusammenhang stehen, den Zugang zu sozialen Partnern in einer dynamischen Umgebung zu optimieren. Ängstlichkeit könnte eine physiologische Anpassung im Umgang mit (sozialem) Stress widerspiegeln. Insgesamt unterstreichen die Ergebnisse dieser Studie die potentielle Wichtigkeit, die Persönlichkeit, als individuelles Attribut, auf Rangentwicklung haben kann.

In der abschließenden Studie 4 untersuchte ich die Konsequenzen von Koalitionen auf Rangentwicklung. Insgesamt waren Koalitionen relativ seltene Ereignisse (0.03 Ereignisse pro Stunde), wobei die Mehrheit der beobachteten Koalitionen nur aus Männchen bestand (etwa 65% aller Ereignisse), während an 35% aller Koalitionen mindestens ein Weibchen beteiligt war. Alle Koalitionen waren gegen einzelne Männchen gerichtet. Trotz ihrer Seltenheit hatten Koalitionen deutliche Konsequenzen für den Dominanzrang. Allem Voran hatte die Rolle, die ein Männchen in einer Koalition hatte, den größten Einfluss auf zukünftigen Rang, d.h. Teilnehmer profitierten von Koalitionen während Opfer im Rang sanken. Der Einfluss von Rolle interagierte jedoch mit einer Reihe weiterer Charakteristika von Koalitionen. Beispielsweise waren Rangänderungen am stärksten ausgeprägt nach revolutionären Koalitionen (alle Teilnehmer sind niedriger im Rang als das Opfer), verglichen mit konservativen und überbrückenden Koalitionen (Opfer ist im Rang unter, beziehungsweise zwischen den Teilnehmern). Weitere Ergebnisse zeigten, dass Koalitionen einen additiven Effekt auf altersbedingte Rangänderungen hatten. Beispielsweise sanken alte Männchen im Allgemeinen im Rang, allerdings weniger, nachdem sie Teilnehmer einer Koalition waren. Weitere Eigenschaften von Koalitionen mit Rangeinfluss beinhalten die „Machbarkeit“ (*feasibility*, der Unterschied zwischen Rang des Opfers und der Summe der Ränge aller Teilnehmer) und die Geschlechterzusammensetzung der Koalitionen. Diese Ergebnisse tragen zu unserem Verständnis bei wie Koalitionen Rangentwicklung beeinflussen können, indem sie aufzeigen, dass eine Reihe von Koalitionsparametern in ihrem Einfluss auf Rangentwicklung interagieren. Insgesamt können Koalitionen als effektive Strategie betrachtet werden, die von Männchen verfolgt wird um ihren Dominanzrang zu optimieren, was wiederum mit Vorteilen in Bezug auf Zugang zu Weibchen verbunden ist.

Insgesamt demonstriert diese Arbeit das komplexe Zusammenspiel zwischen einzelnen Faktoren und deren gemeinsamen Einfluss auf Rangentwicklung bei männlichen Schopfmakaken. Generell kann zwischen zwei Typen von Faktoren unterschieden werden: individuellen und sozialen. In dieser Arbeit zeige ich, dass sowohl individuelle Faktoren (bspw. Persönlichkeit), als auch soziale Faktoren (bspw. Koalitionen) wichtige Folgen haben können, wenn es darum geht, den höchst-möglichen Rang zu erreichen und diesen dann zu erhalten. Weiterhin ist es wahrscheinlich, dass individuelle und soziale Faktoren miteinander interagieren, beispielsweise durch Persönlichkeitsprofile die das Formen von engen Sozialbeziehungen und/oder Koalitionen erleichtern. Um letztendlich die Varianz im individuellen Reproduktionserfolg zu verstehen, sollten wir zuerst die komplexen Mechanismen untersuchen, die die Grundlage für die Rangentwicklung einzelner Männchen bilden. Dabei ist es sicher auch hilfreich die Diversität der Mechanismen zu betrachten die sehr wahrscheinlich zwischen Arten auftritt.

Chapter 1

General Introduction

1.1 The relationship between dominance and fitness

"The vigorous, the healthy, and the happy survive and multiply."
Charles Darwin, On the Origin of Species, Darwin 1859, p. 73

The investigation of differential fitness in individual animals is probably one of the most studied topics in biology. The framework in which we address questions to explain this variance was initially provided by Darwin (1859), who theorized that traits are selected for if they lead to higher survival of the carrying individual (natural selection). Later on, with the introduction of sexual selection, he extended his theory aiming to explain not only variability in survival but also differences in reproductive performance (Darwin 1871). An additional and crucial distinction between natural and sexual selection is that sexual selection provides a framework to explain competition for reproduction within one sex and within the same species (see Clutton-Brock 2004). Two types of such competition exist. Intra-sexual selection comprises the selection of traits that are advantageous in preventing other same-sex individuals from access to mates, while inter-sexual selection refers to the advantages of traits that are attractive to the opposite sex. Generally, the sex that invests less in offspring is the one in which competition for mates is greater while the sex that invests more in offspring production is the one expected to exert mate choice (Trivers 1972). Given this, the reproductive potential and variability is greater in the sex with smaller parental investment (e.g., Bateman 1948).

Among mammals, males usually fit the description of the sex with smaller investment (e.g., no gestation and lactation costs, little or no contribution to parental care) and therefore compete for access to females. The assessment of sexual dimorphism in body weight, body size and canine size represents a commonly used measure to quantify the presence and intensity of intra-sexual selection pressures within a given species, including its potential effects on competition among males for access to females (Clutton-Brock et al. 1977; Mitani et al. 1996; Plavcan and van Schaik 1997; Plavcan 2004; see also Weckerly 1998). For example, in social species (i.e. those living in permanent mixed sex groups), we generally observe greater dimorphism in multi-male/multi-female organizations as compared to monogamous species (Plavcan 2004). This reflects the fact that in multi-male/multi-female systems, males permanently face competition from rivals for access to females. Although overt fighting is costly and therefore likely rare, differential competitive abilities usually manifest themselves through dominance hierarchies. Consequently, in many species of diverse taxa, dominance in both sexes is directly linked to physical characteristics such as body size and mass, i.e. larger or heavier individuals dominate smaller or lighter ones (e.g., zebrafish, *Danio rerio*: Paull et al. 2010, copperhead, *Agkistrodon contortrix*: Schuett 1997, willow tit, *Poecile montanus*: Hogstad 1987, bighorn sheep, *Ovis Canadensis*: Pelletier and Festa-Bianchet 2006). However, for species with complex social systems and elaborate cognitive abilities, such as many primate species, the determinants of dominance can be expected to go beyond the mere physical domain (e.g., Bernstein 1981; Boehm 1999).

In the light of sexual selection theory, it is not surprising that we observe variance in reproductive performance among males with regards to the ability to exclude rivals from reproducing (e.g., Setchell et al. 2005). Variation between individuals in mating and reproductive success is one of the most studied topics in behavioural biology, with hundreds of studies having been published on primates alone (Dewsbury 1982; Ellis 1995; Alberts 2012). One of the major determinants of this observed variance is individual dominance rank (see below for the definition of dominance). One major model to explain the link between dominance rank and variance in mating success (skew) is the priority of access model (PoA, Altmann 1962; Alberts et al. 2003). This PoA model posits that if there is exactly one fertile female present, an alpha male will be able to monopolize mating with her by preventing all other males present from mating and therefore secure paternity of that female's offspring. Obviously, the ability of a male to monopolize matings with fertile females is constrained by the number of females being fertile at the same time. Accordingly, if there are two fertile females present, the beta male will be able to secure access to this second female. Summarized, the PoA model predicts male mating, and implicitly reproductive success, dependent on male dominance rank and synchrony in fertility of females (i.e. how many females are fertile at the same time). Though the PoA model generally fits well with observed mating distributions, some considerable amount of variance in the mating distribution usually remains unexplained by male dominance rank (e.g., Kutsukake and Nunn 2006; Ostner et al. 2008; Dubuc et al. 2011; see also Gogarten and Koenig 2013).

Nevertheless, the overall consensus is that dominance rank and mating/reproductive success correlate positively with each other in male primates. That being said, there is substantial evidence that this relationship is quite variable. A number of reviews identified overall positive relationships (e.g., Fedigan 1983; Berenstain and Wade 1983; Cowlishaw and Dunbar 1991; Bulger 1993; Ellis 1995; Rodriguez-Llanes et al. 2009; Majolo et al. 2012), though evidence for variation can be found across species, but also within genus and species, and even within groups of the same species across time (Smith 1994; Altmann and Alberts 2003; Alberts et al. 2003; Alberts 2012).

This led to identifying additional factors, other than male rank and its consequences of monopolizing access to females, to affect reproductive skew and more generally, reproductive and life-history decisions (e.g., Altmann and Alberts 2003; van Noordwijk and van Schaik 2004). For instance, males might try to circumvent direct competition with each other by seeking out sneak copulations that can occur with or without the cooperation of females (e.g., Berard et al. 1994; Crockford et al. 2007). Likewise, females might have preferences for specific mating partners, but this preference does not necessarily need to be synonymous with male rank (e.g., Dubuc et al. 2011). An additional alternative strategy might be for males to form coalitions. In such cases, two or more males aggressively displace a male from a female that the target of the coalition is monopolizing (Pandit and van Schaik 2003). Finally, paternities can also be determined on a post-copulatory level (e.g., Harcourt et al. 1981; Birkhead and Kappeler 2004). Males might face sperm competition if a female mated with more than one male during her fertile period (regardless of how this came about), so the sperm of the males are competing for the actual fertilization of the female's egg. At the same time, females might (also) exhibit choice after copulations with multiple males have occurred, i.e. females might have a preference for the sperm of a specific male (cryptic female choice, e.g., Thornhill 1983).

1.2 What is dominance (rank)?

Despite such alternative strategies available to males, dominance is an overall useful concept to explain a great portion of the variance in reproductive success among male primates. So far though, I used the terms dominance and dominance rank without defining them. As Seyfarth (1981, p. 447) stated, one might consider the attempt to find a universal definition for dominance “a fairly sterile intellectual exercise”, yet it is important to point out that dominance and dominance rank are relational properties (within dyads or groups of individuals) that have no meaning as absolute individual properties when seen outside the context of interactions with other individuals (Bernstein 1981; Barrette 1993; Drews 1993). I therefore follow Drews (1993, p. 283) and consider *dominance* as “an attribute of the pattern of repeated, agonistic interactions between two individuals, characterized by a consistent outcome in favour of the same dyad member and a default yielding response of its opponent rather than escalation”. An individual is not dominant per se; rather it is dominant over another individual within a dyad in which the other individual is subordinate (Bernstein 1981; Drews 1993). *Dominance rank* extends the concept of dyadic dominance into groups of animals, where an individual that is dominant over many others is considered to have a high rank, and an individual that is dominant over few or no others is considered to be low-ranking. The resulting order of individuals in descending rank is then referred to as *dominance hierarchy.* As with dyadic dominance, dominance rank in a hierarchy is only meaningful as an individual property with respect to the other individuals (and their ranks) that are included in the hierarchy.

Given the reproductive benefits of dominance or high dominance rank, the question arises whether dominance (rank) as defined above and in the sense it is generally used in behavioural biology can be under (sexual) selection pressure. The simple answer is: no, dominance cannot be selected. As outlined above, dominance is an attribute of a relationship between two individuals and as such is not heritable and therefore not selectable. This discussion has received a lot of attention (Bernstein 1981 and comments therein; Barrette 1987, 1993; Drews 1993, see also Dewsbury 1990; Moore 1990), and starting with Hinde and Datta’s (1981, see also Hinde 1978) stance of considering dominance as an intervening variable, a general understanding emerged that not dominance itself but the ability to become dominant is the trait that can be selected. The idea here being that a variety of individual traits (e.g. body size, personality, experience) interact with each other and result in a theoretically quantifiable propensity to become dominant over another individual whose trait combination amounts to a smaller ability to become dominant (Figure 1.1). This argument is not new and has already been hinted at by Kawai (1958), who distinguished between an individual’s basic rank which is a purely dyadic measure based on the individual differences between two opponents and an individual’s dependent rank in which the dyadic relationship is influenced by the social situation. It is these individual traits which collectively determine dominance, or rather the ability to dominate, and which should be the focus of trying to understand rank-based reproductive skew. Overall, most of these individual traits are heritable and can therefore be selected for.

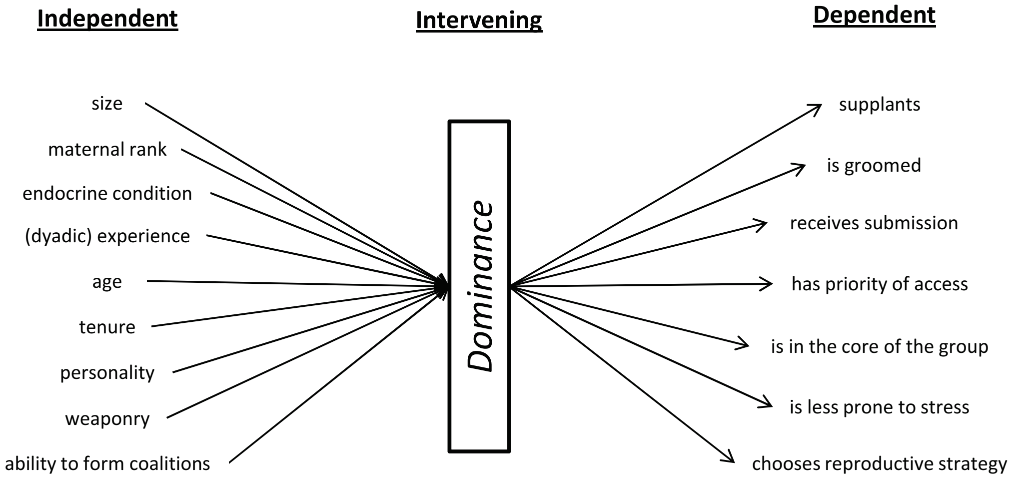

Figure 1.1: Dominance as intervening variable. Individual traits listed under independent interact with each other to form the ability to become dominant or subordinate given the opponent's expressions of the same traits. Traits that follow from becoming dominant in a given dyad are listed under dependent. Note that the traits listed under dependent are from the perspective of the dominant individual. Redrawn and modified from Hinde and Datta (1981).

1.3 Determinants of dominance (rank): the interplay between individual traits and social environment

A variety of factors influences the ability of an individual to achieve the highest rank possible (see Figure 1.1 for a non-exhaustive selection of such factors). Perhaps the most obvious trait that determines which individual will win a fight is weaponry. There is evidence from a wide range of taxa, that individuals with bigger weapons are more likely to win contests (e.g., dung beetles, *Euoniticellus intermedius*: Pomfret and Knell 2006; red deer, *Cervus elaphus*: Clutton-Brock et al. 1979). Similarly, body size and weight often determine contest outcome in favour of the larger and/or heavier individual (e.g., Anolis lizard, *Anolis aeneus*: Stamps and Krishnan 1994; red deer: Clutton-Brock et al. 1979). What determines the outcome of dyadic contests among primates, however, is less clear. For example, to my knowledge, there is no evidence in primates for the often stated assumption that males with larger canines (primates' primary weapons) are more likely to win fights. One reason for this lack of data might be that experiments, i.e. staged conflicts, are difficult to conduct in primates due to ethical concerns (though see, for example, Bissonnette et al. (2009b) for a mild experimental approach, and Alexander and Hughes (1971) for a quasi-experiment involving removal of canines).

In contrast, numerous studies on primates looked at the relationship between dominance rank as measure of contest outcome and various individual traits. For example, age is a very important predictor of dominance rank in various species. This reflects the relationship between general physical prowess and age, i.e. males reach their prime physical condition at some point after becoming adult, after which it declines with age (Setchell and Lee 2004). Age is therefore often considered as an indirect measure of general male fighting ability (e.g., long-tailed macaques, *Macaca fascicularis*: van Noordwijk and van Schaik 2001; rhesus macaques, *Macaca mulatta*: Bercovitch et al. 2003; Widdig et al. 2004; mandrill, *Mandrillus sphinx*: Setchell et al. 2005; yellow baboons, *Papio cynocephalus*: Alberts et al. 2006; for a counter example: Assamese macaques, *Macaca assamensis*: Schülke et al. 2010). Complicating the relationship between age and rank is the observation that sometimes tenure in the group confounds this link. In Japanese (*Macaca fuscata*) and rhesus macaques, males often attain a very low rank upon immigration into a new group, and rise passively as other male above them in the hierarchy emigrate or die (Drickamer and Vessey 1973; Hill 1987; Sprague et al. 1996; Sprague 1998). It was argued, however, that the relationship between tenure and rank stems from the fact that the populations in which this pattern was observed were provisioned and contained very large groups with high number of males (Manson 1998). Whether such tenure-based mechanisms of rank achievement exist in nature remains to be seen.

Following from this it appears that age as proxy for general physical condition and prowess is a very important determinant of rank for male primates because rank often follows fairly predictable trajectories of a male's life. The question that follows from this is, what determines rank among males of similar age, or in other words, what are the predictors of residual rank (e.g., Schülke et al. 2010)? This question can only be answered with analyses that test relationships between individual variables and rank, while controlling for age. A study nicely demonstrating such an approach comes from chacma baboons (*Papio ursinus*). Male rank was related to faecal testosterone levels, but after controlling for age this relationship disappeared (Beehner et al. 2006). However, testosterone levels predicted rank changes in the future, and this relationship was independent of age, suggesting that testosterone production can be regarded as an individual trait, that explains some of the remaining variation between age and dominance rank (Beehner et al. 2006). In contrast, many other studies that report simply relationships between individual traits and rank while not controlling for age as the most likely confounding variable provide us with little information about the determinants of male rank (e.g., canine size: Bercovitch 1993; body weight/size: Kitchen et al. 2003; Neumann et al. 2010; personality factors: Konečná et al. 2012).

In addition to the individual properties that I have mentioned so far, the social environment is likely to play a prominent role in rank achievement and maintenance (Harcourt 1989). Already in 1958, Kawai realized that among female Japanese macaques the continued support of other individuals is crucial for females to maintain their ranks. The importance of such alliances that preferentially occur among kin has since been confirmed for females in many primate species (e.g., Datta 1983; Chapais 1988; reviewed in Chapais 1992, see also Silk 2007). In contrast, our knowledge about the consequences of alliances (or coalitions) occurring between male primates is much more limited. In general, the preferential coalitionary support often occurring between related females is less likely to explain coalition formation among adult males, given that in many primate species males are the dispersing sex (Pusey and Packer 1987). However, there is some evidence that coalitions between males influence the rank of the participants, and therefore serve a similar function as coalitions between females (e.g., Schülke et al. 2010; Gilby et al. 2013; see Silk (1993) for the absence of such an effect). Models of coalition formation among males support the idea that coalitions can serve functions related to dominance rank trajectories, though other important functions are also possible (Noë 1994; Pandit and van Schaik 2003; van Schaik et al. 2004, 2006).

As becomes clear from the arguments above, the determinants of dominance rank in male primates are particularly complex. A variety of individual properties, such as age, and social influences, such as coalitions, are likely to interact in varying magnitude with regard to their ultimate contribution to a male's ability to achieve the highest rank possible and thereby maximizing his reproductive success and fitness.

1.4 Dynamics in rank relationships

Dominance relationships and the resulting hierarchies among females in many, particularly cercopithecine, primate species have been shown to be very stable over extended periods of time, due to the matrilineal organization in which females usually attain ranks just below their mothers (e.g., Hausfater et al. 1982; Samuels et al. 1987; Datta 1989). Rank changes in females therefore mostly occur only as females are born and mature or die. In contrast, hierarchies of male primates are much more dynamic. Not only do males in cercopithecines usually migrate between groups repeatedly over their lifetime and upon successful immigration into a new group attain a rank in the existing hierarchy, but rank changes also occur among males within groups (e.g., Samuels et al. 1984; Zhao 1994; van Noordwijk and van Schaik 2001; Kutsukake and Hasegawa 2005; Setchell et al. 2006; Beehner et al. 2006; reviewed in van Noordwijk and van Schaik 2004). Though differences between and within species exist regarding to what the degree of stability in a hierarchy is, such dynamics are the prerequisite to study mechanisms of how males achieve and maintain their ranks.

It is here that a general methodological issue arises. A myriad of methods is available to quantify dominance hierarchies (e.g., Boyd and Silk 1983; Martin and Bateson 1993; de Vries 1998; Gammell et al. 2003; reviewed in de Vries 1998; Whitehead 2008), yet they all present researchers with substantial challenges when aiming at measuring dynamics in dominance relationships. All commonly used methods rely on dyadic interactions as the initial data. The spectrum of interaction types usually considered ranges from physical fights, threat-and-leave interactions, displacements (also, make room or supplant) to signals of submission (e.g., the silent-bared teeth display of many macaque species, e.g., de Waal and Luttrell 1985; Preuschoft and van Schaik 2000). Though the latter is strictly speaking not a dyadic interaction (though the signal is considered to be directed at another individual), all have in common that the dominance relationship between the dyad members can be inferred if a "winner" and a "loser" can be identified. Here, a problematic issue with regards to dynamics arises because dyadic interactions are aggregated over time and arranged in a matrix, on which the currently most important methods considered by primatologists work. A concern resulting from this method is that the obtained dominance ranks will be an aggregate over the applied time period. As such, with these static methods, dynamics (changes in ranks of individuals) cannot readily be detected as they might disappear in data noise, and it is up to the investigator as to whether rank changes are recognized as such. A method that is able to adequately deal with issues of dynamics in rank relationships is therefore greatly needed if we want to understand the mechanisms underlying rank dynamics in more detail.

1.5 Crested macaques as study species

A suitable taxon in which to study the determinants and dynamics of male dominance rank ideally meets two expectations. First, high dominance rank translates into high fitness, and second, the hierarchy is dynamic enough so that observations of rank changes are possible. Crested macaques (*Macaca nigra*) meet both criteria in as much as male dominance rank is positively correlated to mating success during the periods in which females are most likely to conceive (Engelhardt et al. in prep; see also Reed et al. 1997) and male reproductive success is skewed towards high-ranking males (Engelhardt et al., unpublished data). At the same time, males frequently migrate and rank changes within groups occur on a regular basis (Neumann et al. 2010; Marty and Engelhardt, in prep).

The crested macaque is one of seven species of macaques endemic to the Indonesian island of Sulawesi (Riley 2010, see also Abegg and Thierry (2002) and Ziegler et al. (2007) for information on phylo-geography and phylogenetic history of macaques with special reference to the Sulawesi species). Crested macaques follow the typical social organization found in cercopithecine monkeys, i.e. they live in permanent multi-male/multi-female groups, comprising up to 90 individuals (Thierry 2011; Cords 2012; Duboscq et al. 2013), in which adults of both sexes form linear dominance hierarchies (e.g., Reed et al. 1997; Duboscq et al. 2013). Most of our knowledge on crested macaque behavior comes from studies in captivity (e.g., Hadidian 1980; Bernstein and Baker 1988; Petit et al. 1997; see O'Brien and Kinnaird (1997) and Reed et al. (1997) for the only field-based study on their behaviour and ecology up until recently). In 2006, the Macaca-Nigra-Project was initiated in the Tangkoko-Batuangus Nature Reserve (`www.macaca-nigra.org`) to study the behavior, ecology and reproductive biology of crested macaques. Given that there is only one small viable population left in their natural range (Palacios et al. 2012), fundamental data on their biology are crucial not only from a purely scientific point of view, but perhaps even more so to ensure that appropriate conservation efforts can be undertaken to facilitate the species' survival in the wild.

1.6 Aims of this thesis

The overall aim of this thesis is to investigate mechanisms that underlie individual dominance rank trajectories in male crested macaques and to highlight different possible, individual and social, determinants of how males can achieve and maintain the highest rank available to them. In Chapter 2, I address the problem of how dominance hierarchies can be reliably estimated even when conditions such as frequent migration events and changes within the hierarchy make the application of traditional approaches difficult, if not impossible. Chapter 3 and 4 describe how male personality as an example of an intrinsic property can contribute to rank trajectories. One particular personality factor is highlighted, given that it bridges an individual property with sociality more generally. Finally, in Chapter 5, I investigate how coalitions, as an example for influences of the social environment, impact rank dynamics.

Chapter 2

Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating

with

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2.1 Abstract

Whereas dominance hierarchies are used in a wide range of behavioural studies, their assessment with commonly used methods is often impeded by several factors such as sparse data sets or dynamics in rank relationships and unit composition. In this study we validate Elo-rating as a tool to reliably assess dominance hierarchies. In contrast to methods commonly used, Elo-ratings are calculated based on the sequence in which dominance interactions occur without tabulating these interactions in matrix form. Using data on dominance interactions from five groups of free-ranging crested and rhesus macaques (*Macaca nigra* and *M. mulatta*, respectively), we show that Elo-rating results in rankings that are in strong agreement with commonly used methods. We further demonstrate that Elo-rating provides several advantages over matrix-based methods since it is capable of tracking dynamics in dominance relationships, it is less affected by the negative effects of sparse data, and it can comfortably deal with changes in group composition. This, in combination with a straight-forward way to visualize dominance relationships, makes Elo-rating a very promising alternative to methods commonly used to assess dominance hierarchies, particularly in dynamic animal societies.

2.2 Introduction

Dominance is one of the most important concepts in the study of animal social behaviour. Dominance hierarchies in groups arise from dyadic relationships between dominant and subordinate individuals present in a social group (Drews 1993). High hierarchical rank or social status is often associated with fitness benefits for individuals (e.g., Côté and Festa-Bianchet 2001; von Holst et al. 2002; Widdig et al. 2004; Engelhardt et al. 2006), and hierarchies can be found in most animal taxa including insects (e.g., Kolmer and Heinze 2000), birds (e.g., Kurvers et al. 2009) and mammals (e.g., Keiper and Receveur 1992).

The analysis of dominance has a long-standing history (Schjelderup-Ebbe 1922; Landau 1951), and a great number of methods to assess hierarchies in animal societies are currently available (reviewed in de Vries 1998; Bayly et al. 2006; Whitehead 2008). Though differing in calculation complexity, all ranking methods presently used in studies of behavioural ecology are based on interaction matrices. For this, a specific type of behaviour or interaction, from which the dominance/subordinance relationship of a given dyad can be deduced, is tabulated across all individuals (see for example, Vervaecke et al. 2007). This matrix can either be reorganized as a whole in order to optimize a numerical criterion (e.g., I&SI: de Vries 1998; minimizing entries below the matrix diagonal: Martin and Bateson 1993), or alternatively, an individual measure of success calculated for each animal present (e.g., David's score: David 1987; CBI: Clutton-Brock et al. 1979). In the latter case, a ranking can be generated by ordering the obtained individual scores.

Although calculations of dominance hierarchies are routinely undertaken in many studies of behavioural ecology, and although there have been numerous methodological developments in this area (e.g. Clutton-Brock et al. 1979; David 1987; de Vries 1998), there are still a number of obstacles and limitations scientists have to tackle when analysing dominance relationships. This is mainly due to the fact that the methods commonly used can often not be applied to highly dynamic animal societies, or to sparse data sets, and because methods based on interaction matrices need to fulfil certain criteria in order to generate reliable results. Generally, many researchers may not be aware of some of the problems that are associated with the application of such methods to their data sets, which may in the worst case lead to the misinterpretation of results.

An alternative method that can overcome the shortcomings of matrix-based methods is Elo-rating. Developed by and named after Arpad Elo (Elo 1978), it is used for ratings in chess and other sports (e.g., Hvattum and Arntzen 2010), but has been rarely used in behavioural ecology (but see Rusu and Krackow 2004; Pörschmann et al. 2010). The major difference to commonly used ranking methods is that Elo-rating is based on the sequence in which interactions occur, and continuously updates ratings by looking at interactions sequentially. As a consequence, there is no need to build up complete interaction matrices and to restrict analysis to defined time periods. Ratings (after a given start-up time) can be obtained at any point in time, thus allowing monitoring of dominance ranks on the desired time scale.

The major aim of this paper is to promote Elo-rating amongst behavioural ecologists by illustrating its advantages over common methods, and by validating its reliability for assessing dominance rank orders, particularly in highly dynamic social systems. By providing the necessary computational tools along with an example (Appendices D - E), we also make Elo-rating user-friendly. In the following, we start with an introduction into the procedures of Elo-rating. We then show that with Elo-rating it is easy to track changes in social hierarchies, which may be overlooked with matrix based methods, and point out several general advantages of Elo-rating over matrix based methods. In order to demonstrate the benefits of Elo-rating empirically, we present the results of a reanalysis of one of our own previously published datasets. Finally, we validate the reliability and robustness of Elo-rating by comparing the performance of this method with those of two currently widely used ranking methods, the I&SI method and the David's score, using empirical data and reduced data sets that mimic sparse data.

2.3 Elo-Rating Procedure

Elo-rating, in contrast to commonly used methods, is not based on an interaction matrix, but on the sequence in which interactions occur. At the beginning of the rating process, each individual starts with a predefined rating, for example a value of 1000. The amount chosen here has no effect on the differences in ratings later: the relative distances between individual ratings will remain identical (Albers and de Vries 2001). After each interaction, the ratings of the two participants are updated according to the outcome of the interaction: the winner gains points, the loser loses points. The amount of points gained and lost during one interaction depends on the expectation of the outcome (i.e., the probability that the higher rated individual wins, Elo 1978) prior to this interaction. Expected outcomes lead to smaller changes in ratings than unexpected outcomes (Figure 2.1). Depending on whether the higher rated individual wins or loses an interaction, ratings are updated according to the following formulae:

Higher-rated individual wins:

$$WinnerRating_{new} = WinnerRating_{old} + (1 - p) \times k \qquad (2.1)$$

$$LoserRating_{new} = LoserRating_{old} - (1 - p) \times k \tag{2.2}$$

Lower-rated individual wins (against the expectation):

$$WinnerRating_{new} = WinnerRating_{old} + p \times k \tag{2.3}$$

$$LoserRating_{new} = LoserRating_{old} - p \times k \tag{2.4}$$

where p is the expectation of winning for the higher-rated individual, which is a function of the absolute difference in the ratings of the two interaction partners before the interaction (Figure 2.1; see also Elo 1978; Albers and de Vries 2001). k is a constant and determines the number of rating points that an individual gains or loses after a single encounter. Its value is usually set between 16 and 200 and, once chosen, remains at this value throughout the rating process. In the short term, k influences the speed with which Elo-ratings increase or decrease. In the long term, however, k appears to have only minor influence on the rankings obtained (Albers and de Vries 2001; C. Neumann et al., unpublished data). For the latter reason, we used an arbitrary fixed $k = 100$ throughout our analyses, even though the choice of k can have interesting implications (see section 2.4.5.

As Elo-rating estimates competitive abilities by continuously updating an individual's success, it reflects a cardinal score of success. As such, the differences between ratings are on an interval scale and may thus allow the application of parametric statistics in further analyses. An example, illustrating the process of Elo-rating in more detail, can be found in Appendix A (see also Albers and de Vries 2001).

2.4 Advantages of Elo-Rating over Matrix Based Methods

2.4.1 No minimum number of individuals

Scientists often face the problem of small sample sizes when it comes to determining dominance hierarchies. In many group living species, age-sex classes or even complete groups contain less than six individuals. Problems with matrix-based methods therefore start with the calculation of linearity (i.e., if A is dominant over B and B is dominant over C, then A is dominant over C). The commonly used index to assess the degree and statistical significance of linearity (Landau 1951; de Vries 1995), will only yield significant results if the number of individuals in the matrix exceeds five individuals (Appleby 1983), thus preventing, for example, the application of the widely used I&SI method (de Vries 1998) to small groups. Elo-rating, however, can be applied to groups of any size with only two individuals required for the calculation of Elo-ratings (see Figure 2.1).

2.4.2 Independence of Demographic Changes

Biological systems are often very dynamic in regard to group composition. New offspring is born, maturing animals migrate, individuals become the victim of predation, floating individuals may join groups temporarily, or entire groups fission and fusion regularly. An advantage of Elo-rating is the incorporation of demographic changes such as migration events without interruption of the rating process itself. Whereas matrix based methods need to discontinue rating and to build up new matrices (which

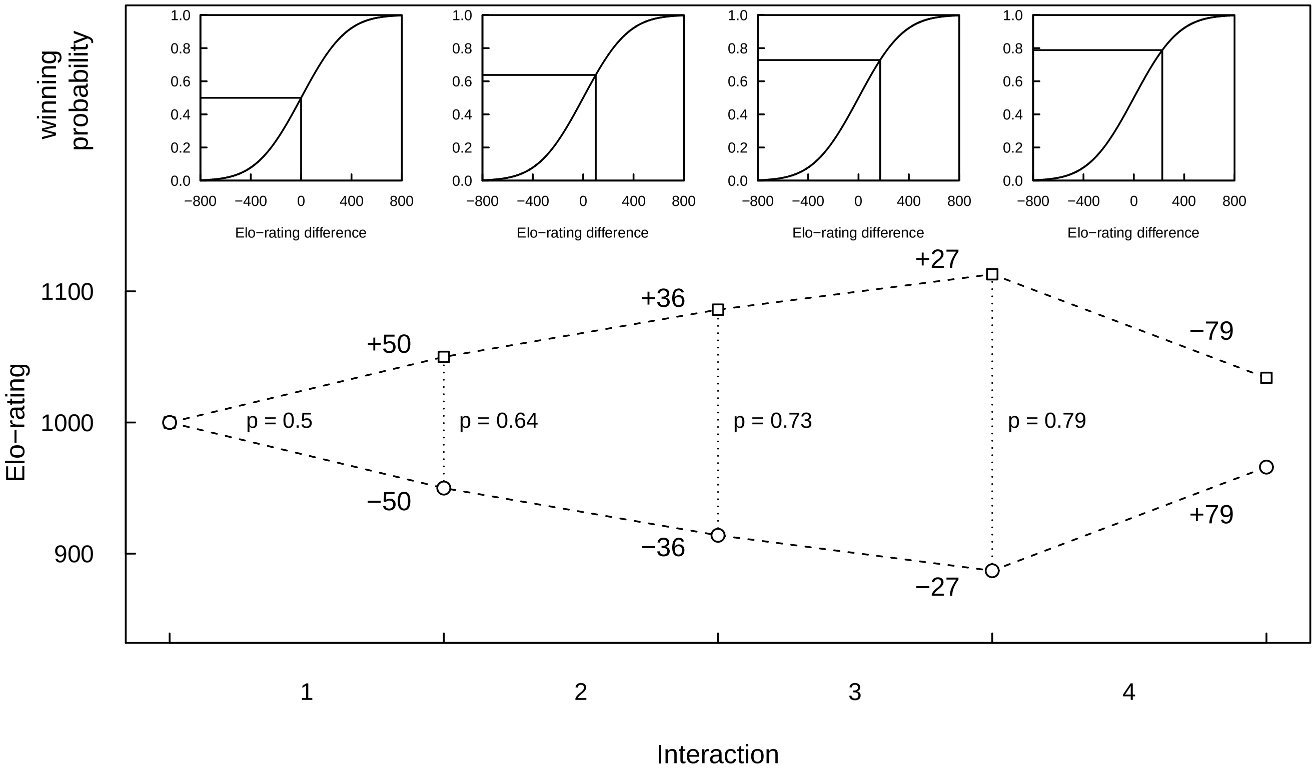

Figure 2.1: Graphical illustration of Elo-rating principles. Two individuals A (squares) and B (circles) interact four times of which the first three interactions are won by A and the fourth is won by B. The number of points gained/lost depends on the probability that the higher-rated individual wins the interaction (see text for details). The winning probability (p) is a function of the difference in Elo-ratings before the interaction (dotted vertical lines). As the difference in ratings increases with each interaction so does the chance of A winning. A graphical way to obtain the winning chance is depicted in the inset figures. A detailed description of this example can be found in Appendix A.

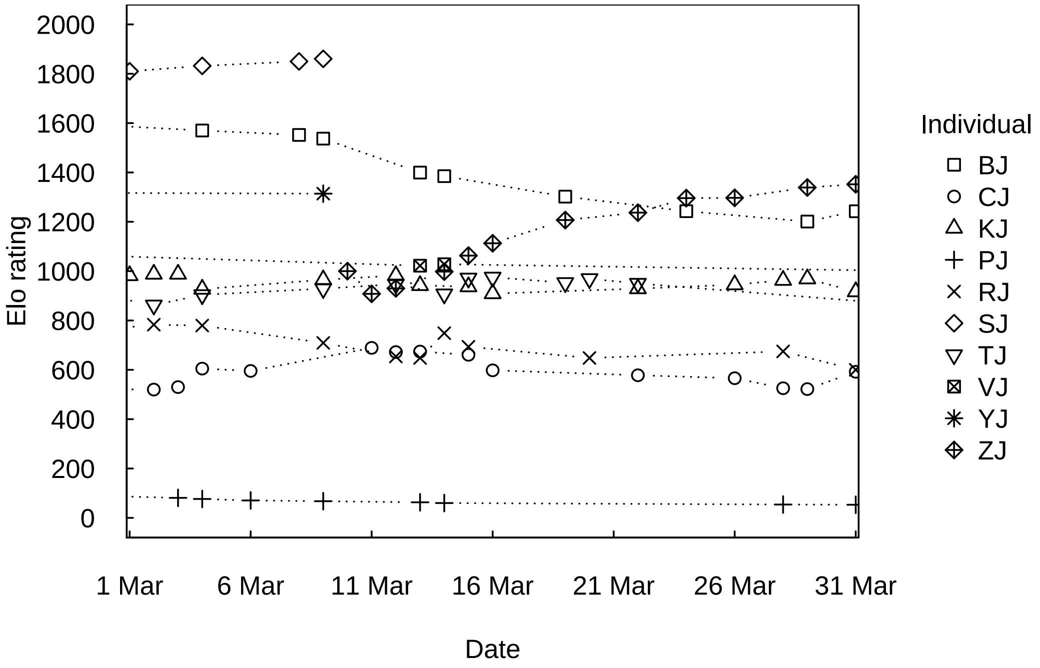

Figure 2.2: Elo-ratings of 10 male crested macaques during March 2007 (group R2). Each line represents one male. Each symbol represents Elo-ratings after they were updated following an interaction of the depicted individual. Note that on 10 March, the residing top-ranking male (SJ) and another high-ranking male (YJ) emigrated from the group and a new male (ZJ) joined the group on 11 March, becoming the group's new alpha male (see text for details).

then need a sufficient number of interactions between individuals in order to produce reliable rankings) after each demographic change, hierarchy determination can be continued despite demographic changes. This is achieved by giving a new individual the predefined starting value (as defined for all individuals before they are rated for the first time) before the first interaction with another individual. After a few interactions this individual can be ranked in the existing hierarchy (see below). This feature may be particularly advantageous for studies on species that live in large social groups with high reproductive rate, high migration rate and/or high predation rate.

To illustrate this, we plotted the development of Elo-ratings of adult males in a group of crested macaques over the course of a month during which three migration events took place (Figure 2.2, see below for details on the study population and data collection). In our example, male ZJ migrated into group R2 on 11 March 2007. To include him in the dominance hierarchy, he was assigned the initial score of 1000, and even though he lost his first observed interaction, Elo-rating made it possible to recognize him quickly as the new alpha male. Likewise, individuals that emigrate (or die) (like males SJ and YJ in this example) are simply excluded from the rating process from the date of their disappearance without causing any interruption to the rating procedure.

Since Elo-rating does not stop the rating process as a consequence of changes in group composition it circumvents a further drawback of matrix-based methods. Techniques such as I&SI and David's score result in values that directly depend on the number of individuals present, thus an observed change in calculated dominance rank or score across two time periods may in fact be a consequence of changes in the number of animals in the group rather than changes in competitive abilities, thus making a comparison invalid. For example, in the case of the normalized David's score (c.f. de Vries et al. 2006), values can range between 0 and $N - 1$, where N is the number of individuals present in the social group. Elo-rating, in contrast, results in ratings that do not depend on the number of individuals present. Given that k is fixed for the entire rating process, the current opponent's strength is the only variable that influences an individual's future rating. Hence, the Elo-rating of an individual is independent of the number of individuals, and time periods that need to be created as a consequence of changes in the number of individuals. This feature allows Elo-rating to be used in a longitudinal manner which is crucial for a wide array of studies, e.g., those on mechanisms of rank acquisition and maintenance, determinants of life-time reproductive success, and so on.

However, as in the other methods, true ratings of individuals are only known after a minimum amount of interactions involving these individuals occurred (see also Albers and de Vries 2001). For example (Figure 2.2), rank orders that would have been obtained through Elo-rating within the first two weeks of ZJ's group membership would have placed him as ranking below BJ. After 13 days (i.e., eight observed interactions), ZJ reached the top-ranked position in the Elo-ratings. Using all observed interactions from these two weeks it was not possible to construct a linear hierarchy, and only after 45 days did we obtain a matrix with a sufficient amount of interactions permitting the use of I&SI. However, it is likely that ZJ became alpha male directly upon his arrival in the group even though he lost his very first observed interaction (top entry: see e.g., Sprague et al. 1998) rather than constantly rising through the hierarchy. Albers and de Vries (2001) suggest waiting for at least two interactions before assessing a dominance hierarchy through Elo-rating whenever a new member joins the hierarchy: one against a stronger and one against a weaker opponent. In the case of ZJ, however, we observed him interacting with six out of the seven other males present. In our case it thus seems more appropriate to follow Glickman and Doan's (2010, rating chess players) suggestion to treat ratings based on less than nine interactions as 'provisional' and exclude such ratings from rankings. Therefore in general, Elo-rating still needs a short start-up time before creating reliable dominance hierarchies when group composition changes. This start-up time is however much shorter than the time needed to build up sufficiently filled interaction matrices for dominance hierarchies.

2.4.3 Visualization and Monitoring of Hierarchy Dynamics

Even if group composition is stable, matrices do not allow dynamics to be tracked within social hierarchies, especially if study periods are very short and data insufficient to obtain reliable rankings. In the worst case, a researcher may overlook rank changes when analysing hierarchies at some fixed interval (e.g., monthly).

One of the great advantages of Elo-rating is its ability to visualise dominance relationships on a time scale, thus allowing monitoring of rank relationship dynamics. As the information about the sequence of interactions is a prerequisite for applying Elo-rating, one can easily create graphs that depict the time scale on the x-axis and plot the development of each individual's ratings on the y-axis. This approach can demonstrate a fundamental feature of Elo-rating, i.e., the possibility to obtain a rank order

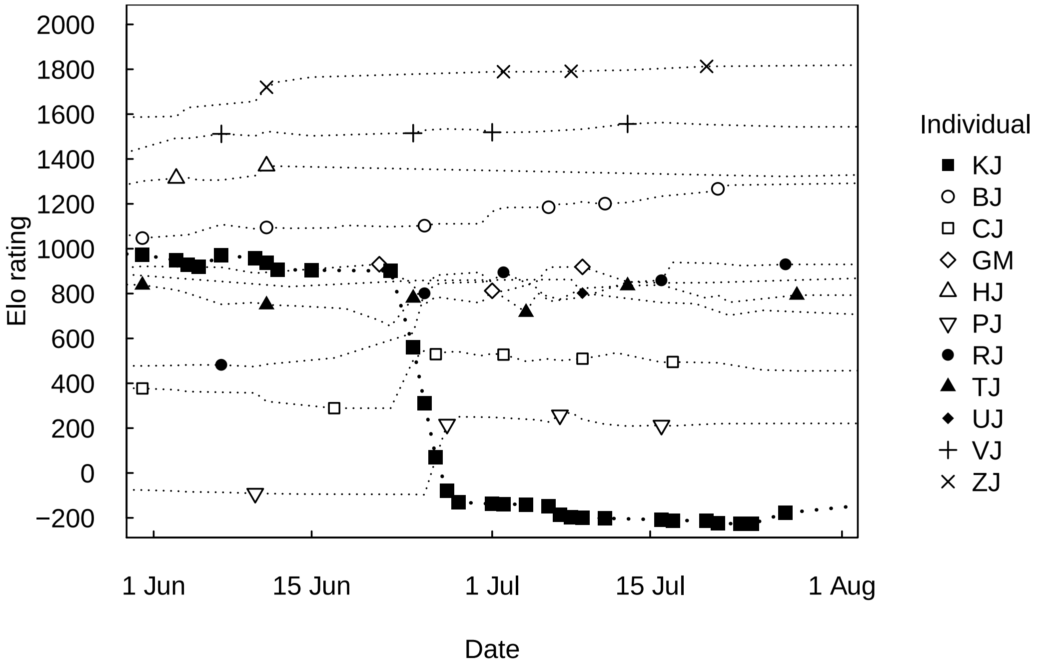

Figure 2.3: Elo-ratings of 11 male crested macaques between June and August 2007 (group R2). Note that the timescale differs from Figure 2.2 and for all males except KJ, symbols represent every fifth interaction (see text for details).

at any given point in time by ordering the most recently updated ratings for a given set of individuals. For example (Figure 2.2), the ordinal rank order among the present individuals on 1 March based on Elo-ratings was SJ (1810 Elo points), BJ (1592), YJ (1317), VJ (1068), KJ (982), TJ (942), RJ (703), CJ (526), PJ (90). By 31 March, however, the ordinal rank order had changed into ZJ (1355), BJ (1262), VJ (994), TJ (950), KJ (892), RJ (600), CJ (592), PJ (53).

Figure 2.3 gives an example illustrating how Elo-rating can reflect dynamics in rank relationships. In late June 2007, medium ranked male KJ started losing interactions against several lower ranked males and dropped to rank eleven. As such, his drop to the lowest rank among group males is reflected by a quick decrease in his Elo-rating by several hundred points in only a few days (Figure 2.3). Such dynamics are difficult to track with both I&SI and David's score since a new matrix would need to be created after such a conspicuous event, requiring a sufficient amount of data to obtain reliable rankings.

At the same time, it is common practice to calculate dominance hierarchies based on rather arbitrary time period definitions (e.g., monthly: Silk 1993; Setchell et al. 2008). This might lead to blurring or in the most extreme case even to overlooking dynamics in rank relationships. Elo-rating, with its capacity to visualize dominance relationships graphically, allows identification of such dynamics in rank relationships in great detail. Hierarchies for the example month June 2007 (Figure 2.3) obtained with matrix based methods lead to illogical rankings: the I&SI algorithm assigns KJ rank 11, whereas David's score ranks KJ 10th (note that linearity is statistically significant during this month: $h' = 0.50$, $p = 0.043$, total of 205 interactions, 24% unknown relationships).

Elo-rating, in contrast, shows that KJ held a medium rank almost throughout the entire month and dropped in rank only during the last week of June.

In Old World monkeys and many other group living mammals, it is sometimes observed that young males rise in rank before they eventually leave their natal group (e.g., Hamilton and Bulger 1990). A common approach to quantify this phenomenon would be to calculate monthly ranks and correlate them with the time to departure. Doing so for 16 natal male crested macaques (see below for details on the study population and data collection) using David's score, however, lends only little support to this phenomenon (Spearman's rank correlation: $r_s = 0.642$, $p = 0.139$, $N = 7$, Figure 2.4a). As described below, this may be the consequence of high proportions of unknown relationships leading to less reliable scores. It could also be due to the fact that David's scores directly depend on the number of individuals incorporated in the matrix. In contrast, when using Elo-rating, the hypothesis that natal males rise in rank before emigration is strongly supported ($r_s = 1$, $p < 0.001$, $N = 7$, Figure 2.4b). We observe an almost linear increase in ratings before the migration date. It appears that males went through a noticeable surge about three months before emigration, and kept rising before their departure. This is, however, a preliminary result and further investigation is warranted. Since Elo-ratings can be obtained at any desired date, even an analysis with higher time resolution (e.g., weekly) is possible (Figure 2.4c).

In addition, Elo-rating also allows objective identification and quantitative characterization of hierarchical stability. Again, the graphical features of Elo-rating provide very useful assistance in this respect. Figure 2.2, for example, shows that individuals KJ and TJ changed their ordinal rank relative to each other five times within one month, suggesting some degree of rank instability (see also individuals RJ, TJ and GM in Figure 2.3).

To quantify the degree of hierarchy stability, we propose to use the ratio of rank changes per individuals present over a given time period. Formally, the index is expressed as

$$S = \frac{\sum_{i=1}^{d}(C_i \times w_i)}{\sum_{i=1}^{d}(N_i)} \tag{2.5}$$

where C_i is the sum of absolute differences between rankings of two consecutive days, w_i is a weighing factor determined as the standardized Elo-rating of the highest ranked individual involved in a rank change, and N_i is the number of individuals present on both days (see appendix 2 for further details). Before division, values are summed over the desired time period, i.e. n days. S can take values between 0, indicating a stable hierarchy with identical rankings on each day of the analyzed time period, and $2 / \max(N_i)$, indicating that the hierarchy is reversing every other day, i.e. total instability. Our data suggest that S typically ranges between 0 and 0.5.

To test the validity of this approach we calculated S before and after the immigration of male macaques that subsequently achieved high ranks (among the top three, see below for details on the study population and data collection). We expected such events to induce instability (e.g., Lange and Leimar 2004; Beehner et al. 2005), thus leading to higher S values when compared to periods before such incidents. We found

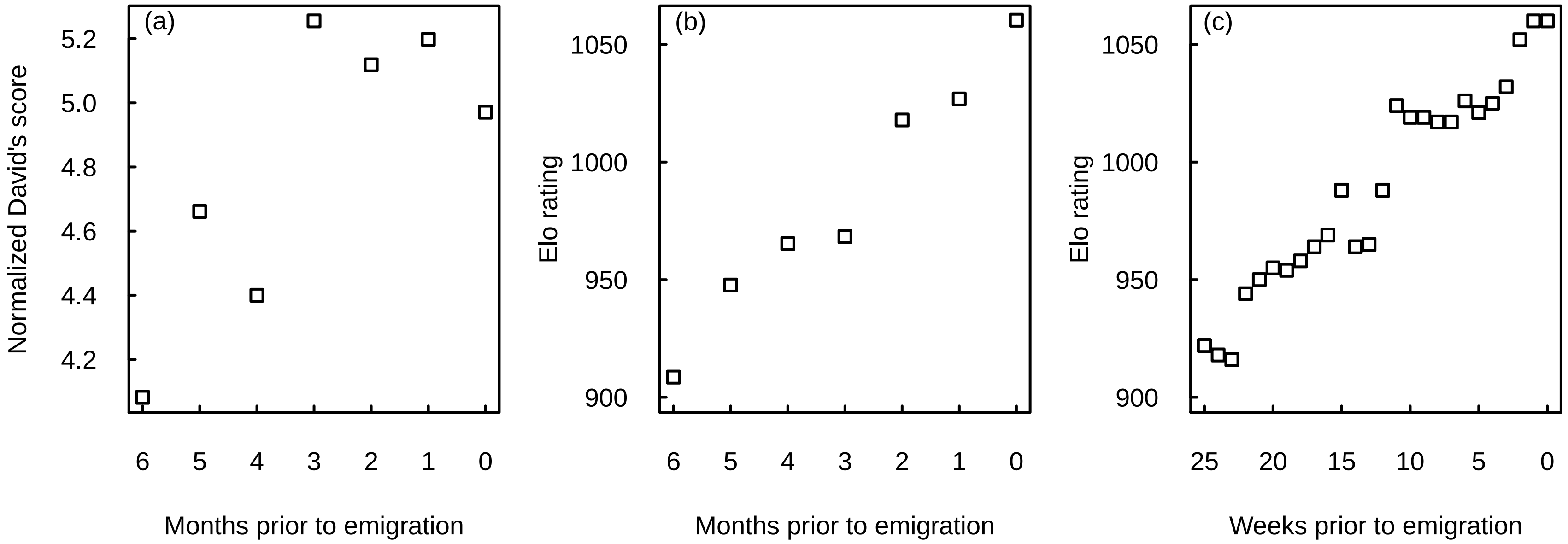

Figure 2.4: The development of dominance status of 16 natal male crested macaques during the 6 months before their emigration. Whereas using David's score only suggests an increase in status over time (a), Elo-rating indicates a clear linear increase (b). Elo-rating in addition allows a refinement of the time resolution, thereby suggesting a noticeable surge in ratings about 3 months before emigration (c, see text for details)

less stability, i.e. greater S values, during four-week periods after the immigration of males that achieved high rank compared to the four-week periods before (Wilcoxon signed rank test: $V = 87$, $N = 14$, $p = 0.030$), indicating that hierarchies were less stable after the immigration of a high ranking male. In contrast, after the immigration of males that subsequently held low ranks, we observed no such difference in stability ($V = 14$, $N = 7$, $p = 1.000$).

Such a quantitative approach may be advantageous since, so far, hierarchical instability has been identified in a non-consistent manner. Sapolsky (1983) for example, studying baboons, identified periods of instability in male dominance hierarchies through high rates of ambiguously ending agonistic interactions and through high rates of interactions that ended with the subordinate winning. In a different study of baboons, Engh et al. (2006) assessed instability in female dominance hierarchies in a mere descriptive way. On a long-term basis, stability has also been characterised by comparison of rankings in consecutive seasons using regression or correlation analysis (e.g., in mountain goats, Côté 2000). By objectively defining stability, Elo-rating may become an important tool for studies on social instability and its consequences, for example on individual stress levels and health (e.g., Sapolsky 2005), territory acquisition (e.g., Beletsky 1992) or group transfer (e.g., Smith 1987; van Noordwijk and van Schaik 2001). In addition, the objective quantification of stability may make comparisons across studies possible.

2.4.4 Independence of Time Periods

It is common practice to obtain hierarchies at some arbitrary fixed time interval (e.g. monthly). Given the dynamics of animal societies, both in group composition and rankings (see above), such an approach is prone to misjudgement of hierarchies for two reasons. First, all individuals incorporated in a dominance matrix must have the possibility to interact with each other at all times. If group composition changes within the studied interval, for example in fission/fusion societies or when individuals leave and join frequently (floaters), applying matrix based methods is unjustified. Second, rank changes that occur will be blurred (see the example above, Figure 2.3).

With Elo-rating it is possible to pinpoint rankings to a specific day. This is of particular importance when studying events, such as a male's rank at the day his offspring was conceived or born, or tracking the rank development of individuals before and after they migrate.

A related problem to the creation of time periods is the proportion of unknown relationships. When creating relatively short time periods to account for the above mentioned dynamics, one often faces a high percentage of pairs of individuals that were not observed interacting in a given period. Like any statistical test, ranking methods suffer from decreased power or precision when sample size is low (Appleby 1983; de Vries 1995; Koenig and Borries 2006; Wittemyer and Getz 2006), even though attempts have been made to counter this problem (see de Vries 1995, 1998; de Vries et al. 2006; Wittemyer and Getz 2006). As we will show below, Elo-rating seems less affected by unknown relationships than matrix based methods, and is therefore also operational on very sparse data sets.

2.4.5 Integrity of Power Assessment

Without demonstrating their application, we finally mention three further advantages of Elo-rating that may refine the precision of power assessment of individuals: a) integration of undecided interactions into the rating process, b) discrimination of agonistic interactions of differing quality, and c) choosing k according to the study species.

Undecided interactions

Though some matrix-based methods (e.g., David's score or Boyd and Silk's (1983) index) explicitly allow interactions without unambiguous winners and losers, i.e., draws or ties, to be taken into account when establishing dominance orders, researchers (including us) usually choose to discard such observations. Clearly, agonistic interactions that end without unambiguous winners and losers contain information about competitive abilities of the involved individuals and should therefore not be disregarded. When using Elo-rating, an undecided interaction can be incorporated into the rating process to the disadvantage of the higher rated individual whose rating will decrease, even though the decrease will be smaller than had the higher rated individual lost the interaction (Albers and de Vries 2001). After a draw the rating for the higher rated individual is reduced to $\text{Rating}_{new} = \text{Rating}_{old} - k\ (p - 0.5)$, whereas the rating for the lower rated individual increases to $\text{Rating}_{new} = \text{Rating}_{old} + k\ (p - 0.5)$. Hence, a draw between two individuals that had identical ratings before the interaction (i.e., $p = 0.5$) will not alter the ratings. In this way, Elo-rating allows for a more complete power assessment of individuals by including interactions into the rating process that are just as meaningful as clear winner-loser interactions.

Agonistic interactions of different quality

Instead of being fixed throughout the rating process, the constant k could be adjusted according to the quality of the interaction or the experience of the interacting individuals. For example, one could distinguish between low- and high-intensity aggression (e.g., Adamo and Hoy 1995; Lu et al. 2008) and assign interactions involving high-intensity aggression higher values of k. This results in greater changes in ratings after such interactions compared to interactions involving low-intensity aggression.

Choosing *k*

Prior experience of individuals plays an important role in the outcome of agonistic encounters in many animal taxa: the winner of a previous interaction is more likely to win a future interaction, whereas losers are more likely to lose future interactions (Hsu et al. 2006). A meta-analysis on the magnitude of such winner/loser effects demonstrated that the likelihood of winning an interaction is almost doubled for previous winners whereas for previous losers the likelihood of winning is reduced almost five-fold (Rutte et al. 2006). Depending on the size of this effect in the study species, k could therefore be split into a smaller k_w for the winner and a larger k_l for the loser to reflect this phenomenon (de Vries 2009).

Thus, Elo-rating is not limited to decided dominance interactions, but can incorporate undecided interaction and in addition allows for a detailed hierarchy evaluation by weighing interactions according to their properties and the magnitude of winner/loser effects. This surplus of information Elo-rating can utilize allows for a much finer assessment of dominance relationships.

2.5 Testing the Reliability and Robustness of Elo-Rating

So far, we have shown how Elo-rating circumvents the problems associated with matrix based methods. However, we have not yet shown how it compares to other methods in terms of reliability and robustness. We now compare Elo-rating with two widely used ranking methods that are based on interaction matrices (I&SI and David's score), using our own empirical data. Mimicking a variety of social systems, we use data collected on two species of macaques with different aggression patterns, crested (*Macaca nigra*, aggressive interactions frequent, but of low intensity) and rhesus macaques (*M. mulatta*, aggressive interactions less frequent, but of higher intensity) (de Waal and Luttrell 1989; Thierry 2007), and calculate dominance hierarchies for females (more stable hierarchies) and males (more dynamic hierarchies) separately. To facilitate the assessment of these analyses we will first briefly review the two methods we use for our comparisons.

2.5.1 Short Introduction to I&SI and David's Score

The I&SI method (de Vries 1998) is an iterative algorithm that tries to find the rank order that deviates least from a linear rank order. It is based on observed dominance interactions (e.g., winning/losing an agonistic interaction) and tries to minimize the number of inconsistencies (I) produced when building a dominance hierarchy, i.e., minimize dyads for which the relationship is not in agreement with the actual rank order. Subsequently, the strength of inconsistencies (SI), i.e., the rank difference between two individuals that form an inconsistency, is minimized, under the condition that in the iterated rank order the number of inconsistencies does not increase. The result of the I&SI algorithm is an ordinal rank order.

David's score (David 1987) is an individual measure of success, in which for each individual a score is calculated based on the outcome of its agonistic interactions with other members of the social group as $\mathrm{DS} = w + w_2 - l - l_2$, where w is the sum of an individual's winning proportions and l the summed losing proportions. w_2 represents an individual's summed winning proportions (i.e., w) weighed by the w values of its interaction partners and likewise, l_2 equals an individual's summed losing proportions (i.e., l) weighed by the l values of its interaction partners (David 1987; Gammell et al. 2003; see de Vries et al. (2006) for an illustrative example). Thus, David's score takes the relative strength of opponents into account, valuing success against stronger individuals more than success against weaker individuals.

Rank orders generated with I&SI and David's score are generally very similar to each other (e.g., Vervaecke et al. 2007; Neumann et al. unpublished data).

2.5.2 Methods

Study populations

For our tests of Elo-rating, we chose two species of macaques (crested, *Macaca nigra*, and rhesus macaques, *M. mulatta*). Even though our aim was not to test for species differences, we nevertheless aimed at gathering a broad data set including different, but comparable, species. Macaques fit this condition as the different species are characterised by a common social organization but at the same time by pronounced differences in aggression patterns (Thierry 2007).

Data collection

Between 2006 and 2010, we collected data in three groups (R1, R2, PB) of a population of wild crested macaques in the Tangkoko-Batuangus Nature Reserve, North Sulawesi, Indonesia (1°33' N, 125°10' E; e.g., Duboscq et al. 2008; Neumann et al. 2010). Groups comprised between 4 – 18 adult males and 16 – 24 adult females and were completely habituated to human observers and individually recognizable. Between 2007 and 2010, data on rhesus macaques were collected in two groups (V, R) on the free ranging population on Cayo Santiago, Puerto Rico (18°09' N, 65°44' W). The study groups comprised between 20 – 60 females and 16 – 54 males (e.g., Dubuc et al. 2009; Widdig unpublished data).

We collected data on dyadic dominance interactions, i.e., agonistic interactions with unambiguous winner and loser, and displacement (approach / leave) interactions during all occurrence sampling on focal animals and during ad libitum sampling (Altmann 1974). Overall, our data set comprised a total of 12,740 interactions involving 252 individuals. Dominance hierarchies were created separately for the different species, groups and sexes.

Data analysis

Our first aim was to investigate whether dominance rank orders calculated with Elo-rating reflect rankings obtained with more established methods. To answer this, we assessed how similar rank orders generated with Elo-rating are to those obtained with the I&SI method and David's score. From our data on both macaque species, we created time periods based on socio-demographic events, such as changes between mating- and birth season, migration or death of individuals, maturing of subadult individuals and conspicuous status changes (hereafter "full data set", see Table 2.1) and produced corresponding dominance interaction matrices. Two consecutive time periods of a given species/sex combination did not comprise the same set of individuals in the majority of cases (61 out of 66 periods, i.e., 92%).

We tested all 66 matrices for linearity by means of de Vries' (1995) h' index. For the 29 matrices for which the linearity test yielded a significant result, we applied de Vries' (1998) I&SI method. Next, we calculated normalized David's scores from all matrices following de Vries et al. (2006). Finally, we calculated Elo-ratings from all interactions in each of the group/sex combinations as a whole using Elo-ratings on the last day of each time period for the comparison with I&SI ranks and David's scores. Elo-ratings were calculated with 1000 as initial value and k was set to 100.

We computed Spearman's rank correlation coefficients between the rankings and scores for each period. To obtain positive correlation coefficients consistently for all comparisons, we reversed I&SI rank orders (i.e., high-ranking individuals get a high I&SI rank value), since high dominance rank is represented by high David's scores and Elo-ratings. Thus, if two rankings are identical the correlation coefficient will be 1.00.

Table 2.1: General description of the time periods and dominance matrices used in the analysis.

species	group	sex	N periods[a]	duration[b]	N individuals	Unknown relationships[c]		Interactions[d]
						proportion in full	increase in reduced	
mulatta	R	male	8	3.9 (3.1–4.1)	35 (34–42)	0.82 (0.79–0.88)	0.08 (0.06–0.09)	180 (123–234)
	V	female	4	1.8 (1.2–2.5)	22 (19–22)	0.66 (0.44–0.86)	0.13 (0.07–0.20)	116 (34–226)
		male	5	1.4 (1.1–2.9)	16 (16–20)	0.67 (0.58–0.71)	0.13 (0.12–0.14)	90 (41–125)
nigra	PB	female	3	4.0 (3.5–7.6)	18 (18–18)	0.25 (0.16–0.30)	0.19 (0.14–0.22)	299 (228–644)
		male	6	2.4 (2.2–3.5)	8 (7–9)	0.36 (0.25–0.40)	0.14 (0.11–0.16)	91 (50–112)
	R1	female	5	6.3 (5.8–11.2)	21 (21–22)	0.49 (0.47–0.57)	0.14 (0.07–0.16)	254 (158–292)
		male	16	2.6 (2.2–3.1)	10 (10–13)	0.34 (0.09–0.46)	0.16 (0.10–0.18)	159 (114–194)
	R2	female	7	6.7 (4.8–7.5)	18 (16–20)	0.50 (0.45–0.56)	0.13 (0.11–0.15)	194 (136–246)
		male	12	3.1 (2.2–4.0)	8 (6–9)	0.26 (0.13–0.34)	0.10 (0.07–0.12)	64 (33–181)

Values are presented per species, group and sex. Medians are given with interquartile ranges.

[a] Number of time periods created

[b] Duration of time periods in months

[c] Proportion of unknown relationships in the full data matrices and the increase in proportion of unknown relationships in the reduced data set (see text).

[d] Number of agonistic interactions in each matrix.

We present average correlation coefficients with inter-quartile ranges. All calculations and tests were computed in R 2.12.0 and R 2.13.0 (R Development Core Team 2010). A script and manual to calculate and visualize Elo-ratings with R along with an example data set can be found in Appendices D-E.

In a second analysis, we explored whether Elo-rating is a robust method under conditions of sparse data and whether the performance of Elo-rating under such conditions is systematically related to the percentage of unknown relationships in the interaction matrix. Please note that a sparse matrix is not necessarily a matrix with a higher proportion of unknown relationships. For example, a matrix in which each dyad was observed five times and all entries are above the diagonal (i.e., there are no unknown relationships) is more sparse than a matrix with each dyad being observed ten times (likewise, no unknown relationships). Whereas the I&SI ranking will be identical in both cases, David's scores will differ between the two, as will Elo-ratings based on the interactions leading to this matrix.

We created sparse interaction matrices by randomly removing 50% of the observed interactions in each of the 66 time periods ("reduced data set": Table 2.1). These additional matrices were again tested for linearity, resulting in 17 matrices retaining significant linearity and thus justifying the application of the I&SI algorithm. We then calculated for each of the three methods separately correlation coefficients between rankings obtained from full and reduced data sets. For the 49 matrices that did not allow the use of I&SI due to non-significant linearity, we restricted the analysis to Elo-rating and David's score.

To explore the robustness of the method further, we tested whether Elo-rating is affected by increased proportions of unknown relationships and how it compared to the two other methods. In other words, we investigated whether the methods become less reliable as the proportion of unknown relationships increases. An increase in unknown relationships was generated as a consequence of the random deletion of 50% of all observed interactions (increase per period on average: 12.5%, inter-quartile range: 8 – 17%, "reduced data set": Table 2.1). We tested for an association between the increase in unknown relationships and the correlation coefficient between ratings from the full and reduced data set.

2.5.3 Results

Our results show that Elo-ratings correlated highly with both I&SI ranks (median $r_s = 0.97$, quartiles: 0.94–0.99, $N = 29$ periods) and David's scores (median $r_s = 0.97$, quartiles: 0.96–0.99, $N = 29$ periods).

We found that Elo-ratings from the full data set correlated highly with Elo-ratings from the randomly reduced data set (Table 2.2). The performance of Elo-rating is virtually identical to the one of I&SI and slightly higher compared to David's score (Table 2.2). Similarly, Elo-rating produced strong correlations with slightly higher correlation coefficients compared to those obtained with David's score from the remaining 49 time periods for which I&SI could not be applied (Table 2.2).

Table 2.2: Robustness analysis. Correlation coefficients (r_s) between rankings from full and reduced data sets. (Median and inter-quartile range).

Linearity[a]	N	Elo-rating	David's score	I&SI
+	17	0.98 (0.97–0.99)	0.96 (0.95–0.98)	0.98 (0.95–1.00)
–	49	0.94 (0.89–0.98)	0.92 (0.86–0.95)	

[a] Linearity in the reduced data set: + linearity test yielded significant h' index, i.e., $p \leq 0.05$ (de Vries 1995); – linearity test did not yield significant h' index, i.e., $p > 0.05$.

Whereas there was no relationship between the increase in unknown relationships and the correlation coefficient between full and reduced data sets for Elo-rating (r_s = –0.07, N = 17, p = 0.799) and I&SI (r_s = –0.36, N = 17, p = 0.162), we found that as the proportion of unknown relationships increased the correlation coefficients decreased between rankings from full and reduced data sets when using David's score (r_s = –0.52, N = 17, p = 0.031, Figure 2.5). Controlling for the initial proportion of unknown relationships by means of a partial Spearman correlation test leads to similar results (Elo-rating: r_s = –0.02, N = 17, p = 0.927; I&SI: r_s = –0.39, N = 17, p = 0.110; David's score: r_s = –0.59, N = 17, p = 0.006).

Overall, our results indicate that Elo-rating produces rank orders very similar to those obtained with I&SI and David's score. In addition, results of our tests suggest that rankings from Elo-rating and I&SI (given significant linearity test) remain stable in sparse data sets, whereas David's score seems to create less reliable hierarchies in sparse data sets as a result of an increase in unknown relationships.

2.5.4 Discussion

Even though there is abundant literature available that compares the concordance of different methods for the assessment of dominance ranks or scores (e.g., Bayly et al. 2006; Bang et al. 2010), this is the first study to test the reliability of Elo-rating with an extensive data set based on observations of free-ranging animals. Our results on dominance interactions in crested and rhesus macaques show that Elo-rating produces dominance rank orders which closely resemble rankings generated with David's score and the I&SI method. Furthermore, our results indicate that Elo-rating is very robust when data sets are limited in the number of interactions observed. Elo-rating (and I&SI) even seems to produce more reliable dominance hierarchies than David's score when the proportion of unknown relationships is high. One could argue that this effect is due to the initial proportion of unknown relationships, i.e., a relatively high proportion of unknown relationships in a "full" matrix leads to some uncertainty in the ranking which may make the scores from the further reduced matrix even less reliable. However, when controlling for the initial proportion of unknown relationships, our results show that the robustness of Elo-rating (and I&SI) is not attributable to this factor.

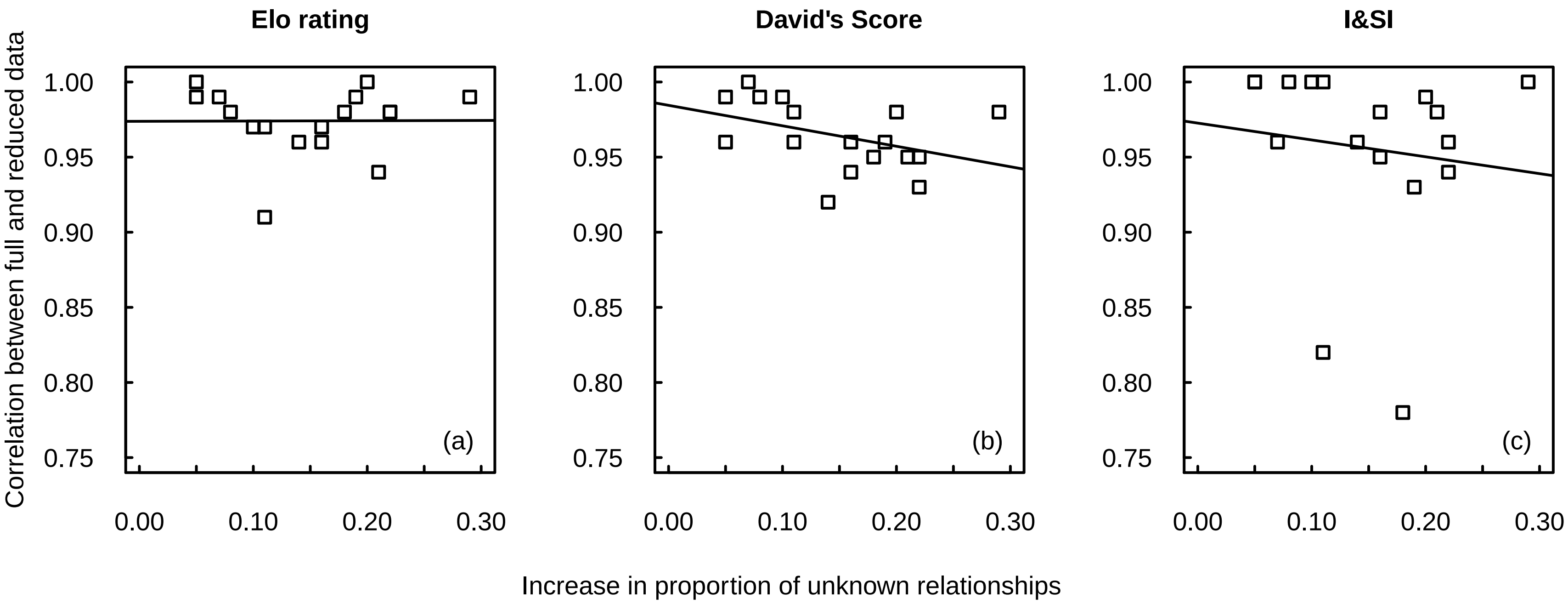

Figure 2.5: Correlation between the increase in unknown relationships and the performance of (a) Elo-rating, (b) David's score and (c) I&SI. The increase in unknown relationships was induced by randomly removing 50% of data points and performance is expressed as the correlation coefficient between rankings from the full and reduced data sets. Elo-ratings and I&SI ranks are not influenced by higher percentages of unknown relationships, whereas the performance of David's score decreases when unknown relationships increase.

2.6 Using Elo-Rating – an Example

We here demonstrate in an empirical example how Elo-rating can improve study results due to its immunity to detrimental effects of assessing dominance status. Data for this example derives from a previous study where we investigated the relationship between dominance status and acoustic features of loud calls in male crested macaques (Neumann et al. 2010). We analyzed seven acoustic parameters and found three of them to be related to dominance status. However, due to frequent migration events and rank changes, and consequently short time periods with high percentages of unknown relationships, we were able to classify dominance only broadly into three rank categories (high, medium, low).

We reanalyzed our original data, using general linear mixed models (R package lme4: Bates et al. 2011, see Neumann et al. (2010) for details on the acoustic analysis and model specifications), and fitted separate models for each acoustic parameter, using Elo-ratings from the day a loud call was recorded as predictor variable instead of rank categories. We additionally fitted models using monthly David's scores as predictor of dominance status.

In addition to the three parameters that we originally found to be affected by dominance rank, using Elo-rating as predictor revealed two more acoustic parameters to be significant at $p < 0.05$ (corrected for multiple testing after Benjamini and Hochberg (1995), p values were assessed with the package languageR (Baayen 2011a)). Using Akaike's information criterion (AIC) to assess how well the models fitted the data (see, e.g., Johnson and Omland 2004), we found that of the five models yielding significant effects of Elo-rating, four had smaller AIC values and thus fitted our data better than the respective models using rank categories as predictor. Surprisingly, when using David' scores as predictor, in none of the models did we find significant effects of dominance status after correction for multiple testing.

2.7 General Discussion

We have shown that Elo-rating has several important advantages over common methods, such as the potential to: 1) monitor the dynamics of hierarchies and extract rank scores flexibly at any given point in time; 2) detect rank changes; 3) objectively identify hierarchy stability; 4) visualise hierarchy dynamics; 5) incorporate demographic changes into the rating procedure; 6) compare periods differing in demographic composition; 7) incorporate undecided interactions; and 8) objectively adjust the rating process based on species-specific information.

We furthermore showed that Elo-rating can increase power of analyses and explain more variation in our data under certain circumstances. Whether a reanalysis using Elo-rating (as described above) will recover unexplained variation in general or not will mostly depend on how severe the potential negative effects of the data were on the ranks derived from matrices. For example, analysing a data set based on a single matrix with few unknown relationships will probably give very robust results, using either David's Score or I&SI. Elo-rating, in such a case will probably replicate the results obtained already, but not necessarily improve model fit. In contrast, a cross-sectional study on several groups, varying in the number of individuals and/or with high proportions of unknown relationships (as in our example above), may warrant a reanalysis using Elo-rating.

We can however see one context in which Elo-rating may not be the first choice to assess rank relationships. Unlike the I&SI method (given its application is feasible), Elo-ratings do not necessarily reflect the rank order corresponding to a linear hierarchy in which an alpha individual is dominant (c.f. Drews 1993) over all other individuals and a beta individual is dominant over all other individuals except the alpha, and so on (de Vries 1998). Such a feature of a ranking algorithm may be desirable when, for example, investigating the relationship between parental and offspring rank (Dewsbury 1990; East et al. 2009; reviewed in Holekamp and Smale 1991). Such a situation is found in the matrilineal rank organization of many Old World monkeys, which is characterized by a linear structure in which a daughter ranks below her mother, and among all daughters of one mother the youngest one ranks highest (Kawamura 1958; Missakian 1972; but see Silk et al. 1981). Elo-rating nevertheless produces rankings close to a linear hierarchy (see above), and may therefore still allow for appropriate rank assessment in such cases, especially when the I&SI method cannot be applied due to data limitations.

In conclusion, all the advantages mentioned in this paper make Elo-rating a useful tool for assessing and monitoring changes of dominance relationships – particularly in highly dynamic animal systems.

Chapter 3

Personality in wild male crested macaques *Macaca nigra*

with

Muhammad Agil, Anja Widdig, Antje Engelhardt

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3.1 Abstract

Animal personalities, i.e. consistent differences in behavior across time and/or context, have received increased attention of behavioral biologists over the last years. Recent research shows that personalities represent traits on which natural and sexual selection work and which can have substantial fitness consequences. The aim of this study is to establish the personality structure of crested macaque (*Macaca nigra*) males as foundation for future studies on its adaptive value. We collected behavioral data through focal animal sampling and additionally conducted two sets of playback experiments. Results of a factor analysis on the behavioral data revealed a four factor structure with components we labeled Anxiety, Sociability, Connectedness and Aggressiveness. Results from the experiments revealed an additional and independent Boldness factor but the absence of Neophilia. Overall, this structure resembles other macaque and animal species with the exception of Connectedness, which might be a consequence of the species' tolerant social style. Our results thus not only form the basis for future studies on the adaptive value of personality in crested macaques but also contribute an important data point for investigating the evolution of personality structure from a comparative perspective by refining, for example, which personality factors characterized the last common ancestor of hominids and macaques.

3.2 Introduction

In recent years, the phenomenon that individuals in many, if not all, animal species differ from each other consistently in their behavior has received increasing attention from biologists and psychologists (Gosling and John 1999; Gosling 2001). If such individual differences are stable over time and/or across contexts they are referred to as animal personality or temperament (Réale et al. 2007). Animal personalities are identified either by humans familiar with the study subjects via rating items in questionnaires (e.g. Stevenson-Hinde and Zunz 1978; Weiss et al. 2011; Konečná et al. 2012) or through observational/experimental data (e.g. Koski 2011b; Dammhahn 2012; Seyfarth et al. 2012). Both approaches usually subject primary data to factor analysis or related statistical methods, which allow identification of underlying dimensions that are then referred to as personality factors. Generally, both approaches lead to similar results when describing the personality structure (the combination of all present personality factors) of a given animal species (e.g., Konečná et al. 2008, but see Uher et al. 2008, reviewed in Koski 2011a). Since personality can have profound effects on reproductive fitness, it is an important feature of animal biology that selective processes can work on (Dingemanse et al. 2004; Smith and Blumstein 2008; Schuett et al. 2010).

Personalities of non-human primates (from here on: primates) are reasonably well studied (reviewed in Freeman and Gosling 2010) due to the phylogenetic proximity of primates to humans and the complexity of the social systems exhibited by most primate species (Mitani et al. 2012). This growing body of data allows us to investigate the biological roots of human personality (Gosling and John 1999; Gosling 2001; Uher 2008) and recently, a first formal attempt was made to describe the evolution of personality within the catarrhine primates (Weiss et al. 2011, see also King and Figueredo 1997). Weiss and colleagues (2011) hypothesize that the personality structure of humans is the evolutionary consequence of a series of changes along our phylogenetic history, with the human personality structure resembling more other hominid personality structures than those of more distantly related species such as rhesus macaques (*Macaca mulatta*). They further suggest that degree of sociality (i.e., differences in social organization and social relationships) has been the major selective pressure leading to the observed interspecific differences in personality. This latter proposition however raises the question as to how personality structures differ in closely related species in which sociality may not be confounded by overall social organization (as is likely to be the case, for example, within the hominids).

In an alternative scenario, it has been suggested that the evolution of different types of sociality in different species is the result of differences in personality (Thierry et al. 2000b; Capitanio 2004). For example, species in which individuals prefer close spatial proximity with conspecifics (an exemplified personality factor) may face increased feeding competition as compared to species in which individuals prefer greater spatial distance to conspecifics. This might then lead to more intense or more frequent aggressive behavior, which in turn may lead to the evolution of specific conflict management strategies not found in species that show lower levels of proximity (Capitanio 2004). This example illustrates how differences in personality could lead to changes in patterns of social behavior and shape social styles as sets of correlated behavioral patterns (Thierry et al. 2000b).

Among primates, the macaques (*Macaca*) represent a particularly well suited genus to look into the evolution of personality structures and its link to social behavior. On the one hand all of the approximately 20 species share some fundamental features of social organization such as living in temporally relatively stable multi-male/multi-female groups and male dispersal around sexual maturity (Thierry 2011). On the other hand, macaques differ markedly in social style (Thierry 2007, see also de Waal and Luttrell 1989; Thierry 1990, 2000), for example in regard to patterns of aggression and the degree of dominance asymmetries, conflict management strategies, and degree of kin bias in social interactions (e.g. Thierry 2000; Thierry et al. 2000b; Berman and Thierry 2010; Duboscq et al. 2013). This particular diversity of social traits has led to the classification of macaque species into four grades of social styles ranging from so called despotic to tolerant species (Thierry 2007) and therefore represents an interesting model to study the link between sociality and personality.

Several macaque species have been studied in the context of personality. Our current knowledge about macaque personalities nevertheless comes foremost from studies on a single species, the despotic rhesus macaque (e.g., Stevenson-Hinde and Zunz 1978; Bolig et al. 1992; Capitanio 1999; Weiss et al. 2011). In this species, at least three personality factors have been determined consistently across different studies: sociability (also labeled affiliation or not being solitary), aggressiveness (also labeled hostility), and fearfulness (also labeled excitability). These three factors seem to have deep phylogenetic roots beyond primates given that they appear not only in macaques (Konečná et al. 2012; Sussman et al. 2013), but also in many other non-primate taxa (reviewed in Gosling and John 1999). Incidentally, they are thought to correspond to three dimensions of the dominating model of human personality – the Five Factor Model, i.e. Extraversion, Agreeableness, and Neuroticism (Digman 1990; Gosling and John 1999; John and Srivastava 1999). Despite these possible similarities, there are also differences in personality structure between different macaque species and deviations from the human model. For instance, a distinct and separate personality factor Dominance (King and Figueredo 1997; Weiss et al. 2006, 2011, 2013), has been described for hominids, but not for humans, and similar variation can be observed in the macaques: whereas in despotic rhesus macaques Dominance has been described as a distinct personality factor (Weiss et al. 2011), it seems to be absent in the more tolerant Barbary macaques (*M. sylvanus*, Konečná et al. 2012). Collectively, the available data suggest that personality structures of macaque species share some similarities but simultaneously show differences that are possibly linked to differences in species-specific social styles.

As illustrated within the macaques, this interplay of personalities and social styles is still poorly understood and certainly more data in all these domains are needed to form the basis for broader inter-species comparisons. An extensive body of data on macaque personality, social behavior and ecology already exists, that allows us to investigate this interaction within this interesting genus. Still, species at the tolerant end of the spectrum of social styles are under-represented in all these respects and to the best of our knowledge, studies assessing personality structure in the most tolerant macaque species are completely missing.

The overall aim of this study is therefore to describe the personality structure of crested macaque males (*M. nigra*) as a foundation for future studies on its adaptive value. Following the macaque-typical pattern, crested macaques live in permanent multi-male/multi-female groups from which males disperse around reaching adulthood. Crested macaques have been classified into the very tolerant end of the macaque social style spectrum (c.f. Thierry 2007), based on the observation that, for example, social networks are diverse and that aggressive conflicts are frequently reconciled, and are of relatively low intensity with frequent occurrence of counter-aggression (Petit et al. 1997; Thierry 2000; Thierry et al. 2000b; Sueur et al. 2011; Duboscq et al. 2013). We therefore expect crested macaque personality to be more similar to personalities of tolerant species as compared to more despotic species. In particular we expect it to reflect the species-typical tolerant social style, which should manifest itself in the absence of a Dominance factor and the emphasis of factors in the social positive domain (Koski 2011b; Konečná et al. 2012). In describing the crested macaque personality structure, we will enhance our knowledge on personality structures in tolerant primates as well as contribute to the clarification of the evolutionary history of personality within the macaques and primates including humans in general.

3.3 Methods

3.3.1 Ethics Statement

All research was conducted non-invasively on a wild population of crested macaques and in accordance with the Animal Behaviour Society's guidelines for the treatment of animals in behavioural research and teaching. In addition, we adhered to all relevant regulations of Indonesia and Germany. Permission to conduct the study in the Tangkoko-Batuangus Nature Reserve in Indonesia was granted by the Indonesian State Ministry of Research and Technology (RISTEK, permit 1189/FRP/SM/VI/2008), the Directorate General of Forest Protection and Nature Conservation (PHKA, permit SI.154/Set-3/2008) in Jakarta and the Department for the Conservation of Natural Resources (BKSDA, permit 58/SIMAKSI/BKSDA-SU/2009) in Manado. Since the study was non-invasive and approved by the local authorities in Indonesia, our institutions did not require approval by an ethics committee. *Macaca nigra* is classified as critically endangered (Supriatna and Andayani 2008) and our study did not affect the animals' welfare.

3.3.2 Study subjects and site

Between March 2009 and May 2011, we studied 37 males of two wild, non-provisioned, groups of crested macaques, groups R1 and PB, living in the Tangkoko Nature Reserve, Sulawesi, Indonesia (Neumann et al. 2010; Duboscq et al. 2013). The two groups comprised up to 85 individuals each, with 7 – 18 adult males present and are subject of research intermittently since the 1990's. All animals were completely habituated to human observers and adults were individually recognizable based on facial features and body markings, e.g., scars or broken limbs.

3.3.3 Data collection

To assess personality, we used a combination of behavioral observations and experiments. First, we used *focal animal* and *scan sampling* (Altmann 1974) of 37 adult males (mean = 66.1h, range = 0.6 – 130.0h per male), and collected data on a range of specific behaviors and identities of other adults in spatial proximity of focal subjects. The selection of behavioral variables to include (Table 3.1) was designed to cover a broad field of social behavior and was based on a published account of the behavioral repertoire of crested macaques (Thierry et al. 2000a) and supplemented with variables suggested by a recent study on chimpanzee personality (Koski 2011b, see also Konečná et al. 2008). Focal protocols lasted 60 minutes during which continuous data on social and aggressive behavior and interaction partner identities were recorded. While following focal animals, these observational data were entered in hand-held computers (Psion Workabout Pro G2) in real-time using spread-sheet software (PTab Spreadsheet v.3.0; Z4Soft). Additionally, we conducted scans at intervals of one, five, and thirty minutes to record general focal animal activity, identity of adult individuals in proximity, and whether the focal animal was outside vs. inside of the group, respectively (see Table 3.1). Data were collected by four observers and inter-observer reliability of the observed behaviors ranged between 0.75 and 1.00 as assessed by Pearson correlation coefficient and Cohen's kappa (Martin and Bateson 1993).

Table 3.1: Definitions of 22 behavioral variables.

Variable	**Description**
prop time spent active	Proportion of scan samples out of all scan samples not spent resting or self-grooming (at one minute interval)
prop time spent outside group	Proportion of scan samples in which animal was not in the center or periphery of the group; scans were taken twice per focal protocol: after 30 minutes and after 60 minutes
rate self-grooming	Hourly rate of self-grooming bouts (bouts were considered distinct if separated by >2 seconds)
rate self-scratching	Hourly rate of self-scratching bouts (bouts were considered distinct if separated by >2 seconds)
rate yawning	Hourly rate of yawns
rate status display	Hourly rate of loud call vocalization, a signal indicating dominance status (Neumann et al. 2010)
prop time spent grooming	Proportion of scan samples out of all scan samples spent grooming other individuals (at one minute interval)
diversity grooming partners	Diversity index of adult females grooming was received from and given to; assessed from scan samples at one minute intervals
diversity grooming given	Diversity index of adult females grooming was given to; assessed from scan samples at one minute interval
number of female neighbors	Absolute number of adult female neighbors within five body lengths; assessed at scans every five minutes
diversity female neighbors (close)	Diversity index of adult females in close proximity (within one body length or in body contact); assessed during scans every five minutes
diversity female neighbors (far)	Diversity index of adult females in proximity (within five body lengths, but further than one body length); assessed during scans every five minutes
diversity male neighbors (close)	Diversity index of adult males in close proximity (within one body length or in body contact); assessed during scans every five minutes
diversity male neighbors (far)	Diversity index of adult males in proximity (within five body lengths, but further than one body length); assessed during scans every five minutes

Table 3.1 – *Continued from previous page*

Variable	Description
rate approaching males	Hourly rate of approaching adult males within a range of five body lengths
rate approaching females	Hourly rate of approaching adult females within a range of five body lengths
rate affiliation towards males	Hourly rate of affiliative behavior (lip smack, mount, genital touch, friendly touch, play) directed at adult males
rate affiliation towards non-males	Hourly rate of affiliative behavior (lip smack, mount, genital touch, friendly touch, play) directed at individuals other than adult males
rate threats towards males	Hourly rate of threats directed at adult males
rate threats towards non-males	Hourly rate of threats directed at individuals other than adult males
rate aggression towards males	Hourly rate of overt aggression (bite, chase, hit) given to adult males
rate aggression towards non-males	Hourly rate of overt aggression (bite, chase, hit) given to individuals other than adult males

For more detailed description of behaviors and calculation of indices see Cheney 1992; Thierry et al. 2000a; Koski 2011b

Second, we used playback experiments on 18 of our focal males, to assess two possible personality factors that are hard to quantify by passive observations alone: boldness and neophilia (Koski 2011b; Carter et al. 2012). Boldness was assayed with the presentation of a dog bark bout. Both crested macaque groups from time to time meet dogs from the nearby village in the forest and give alarm calls upon their sighting (Engelhardt et al., pers. obs.). Neophilia was measured as the reaction to a donkey bray (unknown to test animals). We conducted a total of 57 ($N = 17$ males) and 43 ($N = 16$ males) experimental trials in the dog and donkey condition, respectively. Males were presented with each of the stimuli repeatedly (up to 3 times), two consecutive trials of the same condition being separated by at least three weeks, and each male participating only once per day in an experiment. Stimuli were presented from a concealed DavidActive speaker (Visonik, Germany) connected to a Marantz PMD660 Flash-Disc recorder, placed 10 – 20 meters from the subject. The speaker was operated by an assistant hiding behind natural obstacles, for instance a tree trunk or buttress root, in such a way that neither the assistant nor the speaker was visible to the subject. Playbacks were only carried out when the subject sat calmly on the ground facing the direction in which the group was generally travelling. The speaker was placed in a 90° (±45°) angle relative to the subject's body orientation (see Micheletta et al. 2012 for more details and an illustration of the experimental setup). The response to the playback stimulus was filmed with a digital video camera (Sony DCR-HC 90E) operated by the experimenter standing at a distance of about five meters from the subject. In each experimental condition, we used the same recording as stimulus during all trials. We can therefore not rule out that subjects habituated to the repeated presentations of the same stimulus. Analytical methods, however, allow accounting for this possible bias in results (see methods on adjusted repeatabilities below).

3.3.4 Data analysis

Behavioral data

We divided the overall data collection period into blocks of two months and calculated frequencies of behaviors, number of individuals in proximity and indices describing the diversity of individuals in proximity and grooming partners in each of these time blocks separately for each male (Table 3.1). There are two reasons for creating these time blocks. First, we wanted to assess temporal stability of our behavioral variables by calculating repeatabilities and repeated measurements are needed for each individual to obtain this measure (Lessells and Boag 1987; Nakagawa and Schielzeth 2010). Second, group composition, particularly with respect to adult males, changed frequently (Chapter 2). Such an approach would lead to difficulties in the calculation of diversity indices, because in order to make these indices comparable they need to be standardized by accounting for maximum number of potential interaction partners (Cheney 1992).

An individual data point was included if the cumulative observation time for a given male and time block was at least six hours. If necessary, the raw behavioral variables were transformed (log, square root, arcsine) to achieve symmetric distributions. Variables were then standardized to a mean of zero and a standard deviation of one. Subsequently, all variables were tested for repeatability (Lessells and Boag 1987; Nakagawa and Schielzeth 2010). We considered variables to be significant if the 95% confidence interval around their repeatability estimate did not include zero. Only significantly repeatable variables, i.e. variables that showed temporal stability, were subsequently subjected to factor analysis (see below). Repeatability estimates we present are well in the range of other studies on primates and non-primates (e.g., Schuett and Dall 2009; Koski 2011b; David et al. 2012; Carter et al. 2012; Dammhahn and Almeling 2012). We tested the behavioral variables for group differences by means of Mann-Whitney U tests. One variable (number of female neighbors) differed significantly between the two study groups. Recalculating repeatability controlling for this group difference lowered the repeatability estimate of this variable, but did not change its statistical significance.

Since factor analysis requires independent data, and our data structure consisted of repeated measurements of individuals, we averaged values of the two-month time blocks to obtain single values for each male, thereby avoiding pseudo-replication. This procedure resulted in a data set comprising 30 males, with at least one two-month time block during which a male was observed for at least six hours. The Kaiser-Meyer-Olkin measure of sampling adequacy (KMO = 0.60) indicated that our data were suitable for factor analysis (Field et al. 2012), even though overall sample size and case-variable ratio were small. We performed our analysis using the correlation matrix and a minimum residual solution. We decided to extract four factors based on visual inspection of a scree plot and eigenvalues (Field et al. 2012). We used an oblique (type “oblimin”) instead of an orthogonal rotation to allow for factors to be correlated (Budaev 2010). We chose this approach because there is no a priori reason to assume that personality factors are independent of each other (Field et al. 2012). To gauge the relative importance of the behavioral variables to the extracted factors, we used factor loadings (Field et al. 2012). For interpretation, we considered variables that loaded saliently (absolute value greater than 0.40) to contribute to a given factor (Field et al. 2012). If a variable loaded saliently on more than one factor we interpreted this variable as contributing to the factor on which it loaded with the highest absolute value (e.g., Konečná et al. 2008).

Playbacks

Male responses to the playback stimuli from all experimental trials were coded from videotapes frame-by-frame by two coders, one being blind to study design and experimental condition. We discarded 19 experimental trials that were judged non-valid by both coders, due to technical problems, or subject distraction. Response variable was the time subjects oriented themselves towards the speaker in the first 10 seconds after the start of the stimulus presentation (hereafter: orientation duration) (Micheletta et al. 2012; Maciej et al. 2013). We considered such a response to occur when the subject oriented its head towards or approached the speaker within an angle of about 22.5°. We considered stronger responses, i.e. longer orientation durations, to indicate bolder and more neophilic males. Both raters expressed high agreement in the orientation duration these responses had (Pearson correlation: $r = 0.92$, $N = 81$, $p < 0.001$). Average duration values from both coders were used in subsequent analyses. We calculated adjusted repeatabilities (R_{adj}, c.f. Nakagawa and Schielzeth 2010) controlling for trial number within male subject and experimental condition to account for possible habituation effects. Since this algorithm does not permit confidence interval borders to be smaller than zero, we used p-values to determine statistical significance (Nakagawa and Schielzeth 2010).

Finally, we computed correlations between the factors as well as between the factors and the responses to the two experiments. For this we extracted regression scores from the factor analysis for those males that were also subjects in the playback experiments, i.e. $N = 17$ (dog condition) and $N = 16$ (donkey condition). For the experimental data we used average male orientation durations (within each condition) for this calculation. We calculated Pearson correlation coefficients and since we had no specific hypotheses regarding possible relationships between personality factors, corrected the resulting p-values for multiple testing (Benjamini and Hochberg 1995). All analyses were conducted in R 2.15.0 (R Core R Development Core Team 2012) with the packages psych (Revelle 2012) and rptR (Schielzeth and Nakagawa 2011).

3.4 Results

3.4.1 Behavioral data

The majority of the 22 behavioral variables were moderately repeatable, indicating that their expression was stable over time (Table 3.2). Five of the behavioral variables we considered were not repeatable, from which four reflected behavior towards other adult males: diversity of male neighbors (in close proximity) and the rates with which other males were approached, threatened and aggressed. In addition, rates of affiliation directed at individuals other than adult males, were not repeatable.

Table 3.2: Repeatabilities and confidence intervals of behavioral variables. Variables for which the confidence interval included zero (bold) were excluded from the subsequent factor analysis.

behavior	R	CI_l	CI_u
prop time spent active	0.33	0.16	0.51
prop time spent outside group	0.21	0.05	0.36
rate self-grooming	0.30	0.13	0.47
rate self-scratching	0.33	0.16	0.50
rate yawning	0.48	0.31	0.65
rate status display	0.70	0.57	0.83
prop time spent grooming	0.20	0.04	0.35
diversity grooming partners	0.16	0.02	0.31
diversity grooming given	0.26	0.10	0.42
number of female neighbors[a]	0.55	0.39	0.72
diversity female neighbors (close)	0.20	0.05	0.35
diversity female neighbors (far)	0.26	0.10	0.43
diversity male neighbors (close)	**0.10**	**-0.03**	**0.23**
diversity male neighbors (far)	0.23	0.07	0.39
rate approaching males	**0.09**	**-0.04**	**0.21**
rate approaching females	0.19	0.04	0.34
rate affiliation towards non-males	**0.12**	**-0.01**	**0.26**
rate affiliation towards males	0.16	0.02	0.31
rate threats towards non-males	0.26	0.09	0.42
rate threats towards males	**0.01**	**-0.09**	**0.10**
rate aggression towards non-males	0.14	0.00	0.28
rate aggression towards males	**-0.01**	**-0.10**	**0.08**

[a] after controlling for group differences: $R = 0.14$, $\mathrm{CI}_l = 0.00$, $\mathrm{CI}_u = 0.27$.

The factor analysis based on the remaining 17 repeatable variables explained 62% of the total variance. All variables loaded on at least one of the four factors with an absolute value of > 0.4 with six variables loading on two factors. The solution of loadings of variables onto the extracted factors after oblimin rotation is presented in Table 3.3.

The first factor we extracted explained 21% of the variance with loadings of anxiety related behaviors (self-grooming, self-scratching). Additionally, males scoring higher on this factor were less active, gave less dominance displays (loud calls) and approached females more rarely. We labeled this factor *Anxiety* (Table 3.3).

The second factor explained 17% of variance and included variables that reflect diversity of male and female neighbors (diversity of close female neighbors, diversity of far female neighbors, diversity of far male neighbors) and the diversity of female grooming partners (female groomees). Additionally, this factor was related to smaller frequencies of yawning and spending more time in the core of the group. We labeled this factor *Connectedness* (Table 3.3).

The third factor accounted for 13% of variance with variables reflecting general social behavior, i.e. proportion of time spent grooming, diversity of grooming partners

Table 3.3: Loadings of the four extracted personality factors after oblimin rotation. Only loadings with absolute values ≥ 0.40 and communalities (h^2) are reported. Values in brackets were not interpreted as belonging to this factor as they loaded higher on a different factor.

behavioral variable	anxiety[a]	connectedness	sociability	aggressiveness	h^2
prop time spent active	-0.89				0.88
rate self-grooming	0.45				0.34
rate self-scratching	0.90				0.84
rate status display	-0.41				0.24
rate approaching females	-0.74	(0.41)			0.81
prop time spent outside group	(0.48)	-0.49			0.74
diversity female neighbors (close)		0.84			0.88
diversity female neighbors (far)		0.77			0.61
diversity male neighbors (far)		0.44		(0.42)	0.49
diversity grooming given	(-0.46)	0.47			0.48
rate yawning		-0.64		(0.46)	0.61
prop time spent grooming			0.68		0.50
number of female neighbors	(0.48)		0.55		0.56
rate affiliation towards males			-0.73		0.55
diversity grooming partners			0.68		0.82
rate threats towards non-males				0.89	0.80
rate aggression towards non-males				0.64	0.43
Eigenvalue	3.52	2.90	2.26	1.90	
Proportion Variance explained	0.21	0.17	0.13	0.11	
Cumulative Variance explained	0.21	0.38	0.51	0.62	

Analysis based on correlation matrix ($N = 30$).

[a] loadings were reflected.

Table 3.4: Pearson correlation coefficients between personality factors and the responses to the donkey playback.

	conn	sociab	aggr	bold	donkey
anxiety	–0.19	–0.17	0.09	–0.39	–0.15
connectedness		0.37	–0.07	–0.13	–0.04
sociability			0.01	0.35	0.14
aggressiveness				–0.33	–0.39
boldness					0.32

N = 17 for correlations with boldness, N = 16 for correlations with responses to donkey playback, and $N = 15$ for correlation between boldness and responses to donkey playback.

in general, and number of female neighbors. Interestingly, positive (affiliative) behavior directed at adult males loaded negatively on this factor. We named this factor *Sociability* (Table 3.3).

The fourth factor explained 11% of variance and reflected threat and overt aggression directed at individuals other than adult males. We labeled this factor *Aggressiveness* (Table 3.3).

3.4.2 Playback experiments

Males reacted to the dog stimulus in all of the 39 trials. In the donkey condition, males reacted in 36 trials, while no reaction of males was visible on the video tapes in 6 trials. We found significant repeatability in response to the dog condition (R_{adj} = 0.55, 95% CI: 0.20 – 0.63, p = 0.002). We therefore considered the responses to this playback reflecting Boldness. In contrast, we did not find responses to the donkey condition to be repeatable (R_{adj} = 0.05, 95% CI: 0.00 – 0.27, p = 0.099) and therefore consider Neophilia to be absent.

3.4.3 Relationships between the factors

After controlling for multiple testing, we did not find any significant correlation between any pair of the four observationally assessed factors and the boldness factor (Pearson correlation coefficients, mean = –0.05, range = –0.39 – 0.37, p value range: 0.047 – 0.940, ten pairwise comparisons, Table 3.4). In addition, we found no significant relationship between any of these five factors and orientation duration in response to the donkey playback (Pearson correlation coefficients, mean = –0.02, range = –0.39 – 0.32, p value range: 0.131 – 0.877, five pairwise comparisons, Table 3.4).

3.5 Discussion

Our results on observational and experimental data suggest that crested macaque personality comprises five distinct and unrelated factors: Anxiety, Connectedness, Sociability, Aggressiveness and Boldness (summarized in Table 3.5). This structure is generally similar to the structures observed in other macaque species (e.g., Weiss et al. 2011; Konečná et al. 2012; Sussman et al. 2013). In addition, the structure our data suggest is characterized by the presence of two distinct factors that reflect socio-positive

Table 3.5: Summary of personality factors for crested macaque males. Descriptions refer to animals scoring high on the respective factor.

Personality factor	**Description**
Anxiety	High rates of self-directed behavior, reluctance to approach females
Connectedness	Diverse neighbor and grooming network, spatial position in the core of the group
Sociability	High rate of grooming, high number of female neighbors, diverse grooming network
Aggressiveness	High rates of threats and aggression
Boldness	Reacts strong towards threatening situation

behavior (Connectedness and Sociability). Most notably, we identified a factor, Connectedness, which, to our knowledge, has not been described in studies of primate personalities before, and which covers aspects of social network diversity, a feature that might be of particular importance in tolerant as opposed to despotic primate species.

Our study is focused on adult males because ultimately we are interested in the fitness consequences of personality among males. Given this, we cannot exclude the possibility that our description of the personality structure of crested macaques is incomplete. However, to our knowledge no empirical study so far has shown sex-specific differences in personality structure within a species.

Anxiety, Aggressiveness and Sociability in our study matched factors that have been described in previous studies of macaque personalities (Weiss et al. 2011; Konečná et al. 2012; Sussman et al. 2013) and are widespread among other primate and non-primate species (reviewed in Gosling and John 1999; Freeman and Gosling 2010). Anxiety is commonly used to describe general unease and distress (Weiss et al. 2011). That the factor we name Anxiety reflects the individual degree of unease and distress in our study species is evident through the loading of self-directed behavior onto this factor, which is a behavioral manifestation of physiological stress levels (Maestripieri et al. 1992). In our study, males scoring high on Anxiety approached females less frequently than less anxious males. Anxiety might therefore reflect the reluctance or willingness of males to approach females, possibly mediated through general unease whilst in female proximity (see also Evers et al. 2011). In addition, our measure of general activity also loaded on the Anxiety factor. Similarly, in Barbary macaques, questionnaire items, i.e. adjectives to be rated by human observers, typically describing distress (e.g., *tense*, *irritable*, *excitable*) loaded on one single factor alongside items that describe general activity (*active*, *lazy*). Consequently, this factor has been labeled Activity/Excitability in this study (Konečná et al. 2012). We suggest, however, that Anxiety might in fact be the more fitting label for crested and possibly also Barbary macaques since it captures more of an intrinsic feature as compared to Activity which may well be constrained by external factors, such as the environment. For example, Barbary macaques are more active (i.e. they rest less) when their home-range is covered with snow (Majolo et al. 2013). Given that Barbary macaques are also classified as relatively tolerant, this combination of anxiety and activity represented in only one personality factor might constitute a general feature of the more tolerant macaque species. In contrast, in despotic rhesus macaques both factors are distinct (Weiss et al. 2011, see also Koski 2011b for this pattern in chimpanzees, *Pan troglodytes*).

In crested macaque males, the personality factor Aggressiveness covers threat behavior and overt aggression directed at females, sub-adults, juveniles and infants. Interestingly, aggressive behavior directed at adult male group members was not part of this factor. The reason for this was that rates of aggression towards adult males were not stable over time and hence not included into our factor analysis. As previously mentioned, we observed frequent changes in composition as well as in dominance relationships among adult males in our groups, whereas among adult females, group composition and dominance hierarchy remained much more stable over the course of our study (Chapter 2; Duboscq et al. 2013). It could be argued that temporal stability or instability in behavior is the consequence of a stable or instable social environment, and consequently, stable behavioral patterns may not reflect an intrinsic property (i.e. personality), but rather are the result of external constraints (Dingemanse et al. 2010; Koski 2011b). Therefore, the lack of repeatability in our study of aggression towards other males may have been a consequence of these dynamics. Indeed, having a stereotypic aggression rate towards other males regardless of the dynamics among adult males might be mal-adaptive in the sense that this might lead to costs imposed by overly frequent and possibly injuring aggression depending on how many males co-reside in the group.

Aggressiveness has also been found in other primate (including macaques) and non-primate species, but it is frequently labeled Confidence or Dominance in studies based on observers' ratings such as *aggressive*, *bullying*, *dominant*, *submissive* and *confident* (Capitanio 1999; Weiss et al. 2011; Konečná et al. 2012, but see Sussman et al. 2013). It often correlates with behaviorally assessed (agonistic) dominance ranks (Caine et al. 1983; Mondragón-Ceballos and Santillán-Doherty 1994; Bolig et al. 1992; Konečná et al. 2008, 2012). In studies of animal behavior, dominance is however considered a dynamic individual property that changes over time due to external events (e.g., challenges by other individuals or migration) and which, in the strictest sense, is the property of a single individual within a dyad where the other individual is subordinate at a given time (Drews 1993)). Given the possible confusion with the term dominance as used in behavioral biology (Drews 1993; Gosling and John 1999; see Capitanio (2011) for an illustrative example how such confusion between personality Dominance and behavioral dominance might easily arise) we suggest that the label of the Dominance facet of primate personality should be reevaluated. For rhesus macaques, for example, based on the items that describe it (see above) the label Dominance could, in alignment with our study, be replaced by Aggressiveness. Such more consistent labeling of personality factors would facilitate inter-specific comparisons.

The final personality factor that crested macaques share with other macaques is Sociability. This factor covers behavior that seems essential for building and maintaining social relationships with female group members, particularly the amount of grooming, the diversity of grooming partners and the number of female neighbors. Sociability as defined in our study, matches the Friendliness and Sociability components of other macaque species' personality structures (Capitanio 1999; Weiss et al. 2011; Konečná et al. 2012; Sussman et al. 2013), in which it is associated with rating items like *sociable*, *gentle* and *friendly* (Weiss et al. 2011; Konečná et al. 2012).

In addition to the three above mentioned personality factors that appear to generally occur in macaques, we found a further personality factor in crested macaques, Connectedness. Interestingly, this factor in addition to Sociability also covers behavior in the socio-positive domain. It describes the diversity of females which are groomed by a specific male, the diversity of adult individuals in proximity to him and the time males spend in the core of their social group. Connectedness has no obvious homologue in other macaque species. However, given the overall socio-positive notion of this factor we speculate that in rhesus and Barbary macaques it may be part of the Friendliness factor. Consequently, whereas Friendliness (or Sociability) constitutes a single factor in some species, we find that in crested macaques, socio-positive behavior is reflected in two distinct personality factors, Sociability and Connectedness.

Finding such an additional socio-positive dimension might be a consequence of the complex social network that individuals of tolerant macaque species, such as crested macaques, have as compared to individuals of more despotic species (Thierry 2007; Sussman et al. 2013). This wide network connecting also not related individuals shows that relationships between group members are far less constrained than in despotic species where relationships are maintained predominantly within fixed kin networks (e.g., Berman and Thierry 2010; Micheletta and Waller 2012). Two possible ways in which scoring high on such a personality factor might thus be biologically adaptive (fitness increase) are through a more diverse network of allies that could provide support in agonistic conflicts or through increased attractiveness to the opposite sex (e.g., McDonald 2007; Sih et al. 2009; Kulik et al. 2012; Wilson et al. 2013). Further studies will be necessary to determine whether Connectedness indeed has fitness benefits and whether it is a general feature of socially tolerant primates such as crested macaques.

The final personality factor we identified in crested macaque males is Boldness as evidenced by repeatable reactions towards the auditory presentation of a threating stimulus. Boldness has rarely been studied in primates in general (Freeman and Gosling 2010). Such a factor might however evolve under the selective pressure of predation, particularly in species in which predators are mobbed upon detection as is the case for crested macaques on sight of reticulated pythons (*Python reticulatus*), their presumed primary predator (Micheletta et al. 2012). Scoring high in Boldness could under these circumstances not only help to roust the predator, but may also be used as a potentially costly signal of social status or as a means of attractiveness to potential mating partners. In this sense, we cannot rule out the possibility that the composition of the audience present during the playback trials influenced males' reactions to the stimulus. Intuitively, crested macaque Boldness appears to be similar to the Confidence factor found in other macaques. This notion is however rather speculative and based on rating items used in questionnaire studies, such as *fearful* or *timid* (Weiss et al. 2011; Konečná et al. 2012). At the same time, since we also consider our Aggressiveness factor as equivalent to rhesus and Barbary Confidence, we would have to expect a salient positive correlation between crested macaque Boldness and Aggressiveness, which was absent. For now, we hypothesize that Boldness makes up a unique factor in crested macaques, but cannot rule out that this is due to the different approaches with which we determined Boldness and Aggressiveness. Given the prevalence of Boldness in non-primate animals in general (Gosling 2001; Réale et al. 2007) and its hypothetical absence in primates (Freeman and Gosling 2010, but see Carter et al. 2012), future studies of primate personality should incorporate either items like bold into their questionnaires or try to assess Boldness experimentally (Carter et al. 2012). This should clarify in how far Boldness constitutes an independent factor of primate personality, or is just a facet of some other factor, such as Aggressiveness or Confidence.

In agreement with most studies of macaques, we found no evidence for the existence of a distinct Neophilia dimension (but see Openness with the items curious and inventive in rhesus macaques, Weiss et al. 2011). Neither did we observe any significant correlation between the response to our novelty experiments and any of the other five personality factors. This absence is somewhat surprising, since a Neophilia/Exploration factor (or the human equivalent Openness) is present in many animal species including primates (McGuire et al. 1994; Gosling and John 1999; Réale et al. 2007, see also Drea 1998; Bergman and Kitchen 2009). However, the actual correlation coefficients of the playback response with Aggressiveness and Boldness were modest, but not negligible (-0.39 and 0.32), suggesting that the absence of significant relationships in our study might potentially have been a problem of statistical power or inappropriate stimulus choice (Carter et al. 2012). In line with this possible overlap with other factors, studies in other macaque species found rating items that describe Neophilia such as *curious* or *exploratory* load on diverse factors such as Sociability (Mondragón-Ceballos and Santillán-Doherty 1994; Capitanio 1999), Friendliness (Weiss et al. 2011) or Activity/Excitability (Stevenson-Hinde and Zunz 1978; Konečná et al. 2012). An alternative explanation for the absence of Neophilia may be related to the modality in which we presented the stimulus. Macaques, as many primates, are vision-dominant, suggesting that an auditory stimulus may be less likely to elicit consistent responses in our experimental setup. More studies are certainly needed to confirm or reject the absence of Neophilia in macaques.

Based on our results, some tentative comparisons can also be made between macaque and human personality in order to investigate the evolutionary roots of the current human personality structure as posited in the Five Factor Model (Digman 1990; Weiss et al. 2011). The combination of the two socio-positive factors we found in crested macaques (Connectedness and Sociability) appear to match human Extraversion, whereas Aggressiveness may reflect the human Agreeableness vs. antagonism axis (Gosling and John 1999). Anxiety and, to a lesser degree, Boldness fit the descriptors of human Neuroticism (Gosling and John 1999). In contrast, human Conscientiousness and Openness appear not to be reflected in crested macaque personality as distinct factors. Although crested macaque personality factors do not match perfectly with those of humans, our results shed important light onto the evolution of personality structures within the primate taxon.

Our attempt to directly link crested macaque with human personality structure is however a simplification of the hypothetical evolutionary scenario proposed to explain the evolution of human personality structure from a macaque-like ancestor (Weiss et al. 2011). Here we will use two examples to illustrate how incorporating data from additional species may help to formulate alternative hypotheses to explain the evolutionary history of personality structures. In their personality phylogeny using rhesus macaques as an outgroup to hominids, Weiss and colleagues (2011) suggest that Anxiety and Activity are two distinct ancestral factors. Our data and recent work on Barbary macaques, however, allow an alternative scenario. In both Barbary and crested macaques, a single factor describes a combination of Anxiety and Activity (labeled Anxiety in crested macaques (see above) and Activity/Excitability in Barbary macaques (Konečná et al. 2012)). Given that Barbary macaques represent the sister taxon to all other extant macaque species (Morales and Melnick 1998; Li et al. 2009), it may thus be that such a broader, singular Anxiety/Activity factor is the actual ancestral state. In addition, the presence of a single Sociability factor in Barbary and rhesus macaques may also represent the ancestral macaque state, whereas the occurrence of the two distinct factors we identified in crested macaques (Sociability and Connectedness) most likely is a derived feature. We therefore speculate that a hypothetical ancestor to macaques (and hominids) was characterized by a single Anxiety/Activity factor and a single Sociability factor, similar to present-day Barbary macaques (Konečná et al. 2012).

Based on this suggested proto-macaque, we can formulate alternative hypotheses of how personality factors evolved in higher lineages. For example, according to a recently proposed scenario, the hominid Extraversion factor evolved from a combination of a “pure” Activity factor and a Sociability factor (Weiss et al. 2011). Our results, however, indicate the possibility that such a single Activity factor was not the ancestral state of catarrhine primates. Hence, in order to evolve Extraversion in the hominid lineage (c.f. Weiss et al. 2011), a separation of our suggested ancestral Anxiety/Activity factor into two distinct factors needs to occur, after the phylogenetic split of hominids and macaques. With the currently available data, both scenarios are equally parsimonious and only future studies that contribute more data will help to fully understand the evolution of primate personality structures.

Whereas a thorough treatment of the possible evolution of primate personalities is well beyond the scope of this paper, we find overall support for the hypothesis of Weiss and colleagues (2011) in that crested macaque personality structure resembles more other macaque personality structures than hominid personalities. The comparative approach is thus surely a promising one and the more data points we acquire the clearer the overall picture of personality evolution will become. In addition, more and more data are being generated concerning neurobiological and endocrinological mechanisms underlying personality variation (e.g., Young and Wang 2004; Anestis 2011; Higley et al. 2011; Yokoyama and Onoe 2011). By integrating these approaches with ethological data and with the recent progress in behavior genetics (e.g., Higley et al. 2011; Adams 2011), new avenues will open to study the evolutionary paths and selective pressures leading to the striking variation in personality structures we observe across the animal kingdom.

Chapter 4

Personality factors predict future male dominance rank in a social mammal

with

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Manuscript to be submitted.

4.1 Abstract

Personalities are stable differences in behavioral tendencies over time. They are a common feature of many animal taxa and are known to affect fitness. One possible pathway through which personality shapes fitness is through dominance status. Here we explore the relationship between personality and dominance status and specifically look at the temporal relationships between the two variables. We collected personality and dominance status data on wild crested macaque (*Macaca nigra*) males over two years. We found that four out of five personality factors co-varied with current status. Independent of this co-variation, past status did not predict current personality factors while two out of these four factors predicted future dominance status. These results emphasize the importance of personality with regard to competitive abilities among primate males and suggest that factors other than mere physical traits also contribute to males' dominance careers.

4.2 Introduction

Personalities are stable between-individual differences in behavior over time and/or context (Réale et al. 2007). They have long been neglected in evolutionary studies but are nowadays known to have fitness consequences in many species across the animal kingdom including humans (Eaves et al. 1990; Smith and Blumstein 2008; Alvergne et al. 2010; Dingemanse and Wolf 2010; Seyfarth et al. 2012). In which way personality translates into fitness remains, however, mainly unclear. One potential way is through influencing male careers since dominance is known to significantly impact individual fitness, particularly in males living in permanent social groups (e.g., Clutton-Brock 1988; Cowlishaw and Dunbar 1991; Rodriguez-Llanes et al. 2009).

Studies investigating the link between personality and rank to this point focused mainly on traits affecting dominance acquisition during group formation (Fairbanks et al. 2004; Colléter and Brown 2011). For example bold rainbowfish males, *Melanotaenia duboulayi*, achieve higher dominance rank during experimental group formation as compared to shy males (Colléter and Brown 2011). Similarly, more impulsive vervet monkey (*Chlorocebus pygerythrus*) males are more likely to become alpha males than less impulsive individuals when newly housed together (Fairbanks et al. 2004). The value of such studies to behavior in natural environments is limited, however, because in contrast to these experiments in captivity, in nature, permanent groups such as those of many primate species are usually not formed by aggregation of individuals unknown to each other. Rather, individuals join existing groups. In which ways personality and male social careers interact under natural conditions has so far not been studied.

The overall goal of our study therefore was to investigate dynamics in the relationship between personality and dominance status in a wild social mammal. Particularly, we aimed at clarifying as to whether personality influences future dominance status or whether personality is a consequence of rank. Ultimately, we are interested in whether personality can affect fitness mediated through dominance status. Crested macaques (*Macaca nigra*) are a particularly well suited taxon to study the relationship between dominance status and personality because dominance relationships between males are quite dynamic, both at the level of male group composition (emigration/immigration) and frequent changes in the hierarchy while group composition is stable (Chapter 2).

Given these dynamics, we expect factors other than age or mere fighting ability to contribute to individual rank trajectories, and personality constitutes a promising aspect of individual characteristics to be involved (Sapolsky 1990; Gosling and John 1999). Finally, a link between personality and dominance status would also contribute to our understanding of the mechanisms by which males achieve higher fitness, given that high status reflects increased mating and reproductive success for male crested macaques (Engelhardt et al. in prep; Reed et al. 1997; Higham et al. 2012; Engelhardt et al, unpublished data). To address these questions, we studied free-ranging crested macaque males at Tangkoko Nature Reserve on Sulawesi, Indonesia, living in two permanent groups each comprising around 10 adult males and 20 adult females and totaling up to 85 individuals (Neumann et al. 2010; Higham et al. 2012).

In a previous study (Chapter 3), we determined the personality structure of crested macaques by means of behavioral observations and playback experiments. Based on the observational data we identified four distinct and independent factors: Anxiety, Connectedness, Sociability and Aggressiveness. Results from playbacks indicated an additional Boldness factor. In the current study, we modeled the relationship between these factors and dominance status. For the four observationally assessed factors we created two-month time blocks for which we extracted regression scores from the factor solution for each male (Appendix F). In this way, we obtained 190 data points for each personality factor from 30 males (median = 6.5, range 1 – 11 data points, i.e. time blocks, per male). To model the response of Boldness we used individual responses during playback trials (Chapter 3), resulting in 39 data points from 17 males (median = 2, range 1 – 3 responses per male). To assess dominance status we used Elo-rating (Chapter 2; Albers and de Vries 2001). Elo-rating allows assigning each male a continuous rating at any given point in time and independent of changes in group composition (Chapter 2). For our analyses, we determined current male Elo-ratings on the date in the center of the two month time block or on the date an experimental trial was conducted. With regard to our study question, we extracted Elo-ratings on two additional dates: future and past rating refers to the Elo-rating 90 days after and before the current rating, respectively. Since using repeated ratings of the same individuals may lead to collinearity in our models, we did not use true Elo-ratings but calculated differences between current ratings and future and past ratings, respectively.

Overall, we ran two sets of five linear mixed models each (Appendix F). The first set modeled the five personality factors as a function of current Elo-rating and the rating difference between current and past ratings. The second set modeled the difference between future and current rating as a function of the personality factors and current rating. Significance testing was done in a two-step approach. First, we used likelihood ratio tests (Quinn and Keough 2002) to determine whether the full model (including all fixed and random effects) differed from a reduced model (only including age, the random effects, an autocorrelation term if applicable (Appendix F) and trial number in the Boldness models). Only if this step revealed that a full model differed from the corresponding reduced model did we continue to assess significance of individual effects.

4.3 Results

The first set of linear mixed models revealed that none of the five tested personality factors was predicted by the difference between current and past rating. However, four out of the five tested personality factors co-varied with current Elo-rating: higher rated males were less anxious, more connected, more aggressive and bolder (Table 4.1).

The second set of models revealed that scores of two personality factors predicted subsequent rating changes. More connected and less anxious males achieved higher future Elo-ratings (after three months) than others (Table 4.2). This effect was independent of the co-variation between current factor scores and current rating as we controlled for this relationship in the models (i.e. higher-rated males did not increase or decrease stronger in ratings than lower-rated males).

4.4 Discussion

Our results demonstrate a relationship between dominance status and personality factors in males of a wild primate on two levels. Four personality factors, anxiety, connectedness, aggressiveness and boldness co-vary with current dominance status. More importantly, independent of the co-variation between current rank and personality, anxiety and connectedness predict whether males will rise or decline in status in the future. We however did not find any evidence that personality is a consequence of dominance status.

Most importantly, our models showed that specific personality factors predict future dominance rank in male crested macaques. It has already previously been suggested that social competence might enable individuals to achieve higher future dominance status (McGuire et al. 1994). That is exactly what we find for crested macaque males, in which more connected males achieve higher future dominance status. The mechanism by which such a factor could work might be that adult male Old World monkeys, in contrast to females, usually cannot rely on relatives for support in their groups and therefore need to establish a network of social partners in the groups they migrate into (Kulik et al. 2012). Of course, whether males that score high in connectedness also effectively have more numerous or more diverse partners, for example in the context of agonistic support, than individuals with lower scores remains to be examined. Interestingly, these results point to the possibility that the evolutionary roots of a similar phenomenon observed in humans can be found already in Old World monkeys. Evidence from humans shows that more connected males benefit from their networks, as more extraverted (the human personality factor that best reflects connectedness) men not only are more likely to be of high social status but also are more likely to be polygynous and have more children (Alvergne et al. 2010).

The observation that also less anxious males increase their status might be related to physiology (Maestripieri et al. 1992; Capitanio 2004; Anestis 2011). In our case, low anxiety might reflect a physiological profile that allows individuals that cope better with challenging and stressful situations in their social environment, such as increased competition following male immigrations or the loss of an ally due to his emigration or death. Such social instability has been shown to be stressful in terms of increased fecal glucocorticoid excretion (Gesquiere et al. 2011). Less anxious individuals may be better adapted to cope with such unpredictability (Sapolsky and Ray 1989) and the associated costs of long-term elevated glucocorticoid levels (Sapolsky 2005). Again, these results hint to the evolutionary roots of similar behavior found in humans, where

Table 4.1: Effect of current Elo-rating and past rating differences on five personality traits. Response variables are the single personality traits.

Trait (**response**)	Intercept		Current Elo		Past EloDiff (**predictor**)	
	Estimate±se	p_{MCMC}	Estimate±SE	p_{MCMC}	Estimate±SE	p_{MCMC}
Connectedness	-0.413±0.208	0.4566	0.321±0.084	0.0006	-0.057±0.065	0.4514
Sociability[a,b]	-0.221±0.139		0.184±0.069		-0.038±0.067	
Aggressiveness[b]	0.034±0.355	0.9530	0.222±0.078	0.0030	0.014±0.064	0.8694
Anxiety[b]	0.108±0.127	0.7084	-0.221±0.059	0.0002	0.001±0.057	0.9310
Boldness	-0.266±0.332	0.3808	0.638±0.221	0.0072	0.084±0.173	0.6972

[a] Full model was not significantly different from null model (LRT: $p > 0.1$). For this model, only parameter estimates but not p-values are shown. Null models contained age as predictor. For Boldness, trial number was included as additional predictor variable. p-values were derived running 10,000 cycles.

[b] Full model contained significant auto-correlation term.

Table 4.2: Effect of five personality traits on differences between current and future Elo-ratings.

Trait (**predictor**)	Intercept		Current Elo		Future EloDiff (**response**)	
	Estimate±se	p_{MCMC}	Estimate±SE	p_{MCMC}	Estimate±SE	p_{MCMC}
Connectedness	0.250±0.117	0.2610	-0.095±0.065	0.1194	0.174±0.069	0.0142
Sociability[a]	0.237±0.119		-0.052±0.063		0.070±0.063	
Aggressiveness[a]	0.216±0.118		-0.049±0.065		0.042±0.066	
Anxiety	0.222±0.116	0.4474	-0.065±0.062	0.2096	-0.143±0.061	0.0146
Boldness[a]	0.250±0.459		-0.460±0.328		0.269±0.181	

[a] Full model was not significantly different from null model (LRT: $p > 0.1$). For these models, only parameter estimates but not p-values are shown. Null models contained age as predictor. For Boldness, trial number was included as additional predictor variable. p-values were derived running 10,000 cycles.

more neurotic men are more likely to be of higher social status compared to less neurotic men (Alvergne et al. 2010).

The above mentioned hypotheses on how personality might influence future success both relate to male-male competition, and might therefore be under intra-sexual selection: higher status, whether current or future, translates into higher mating and reproductive success (Higham et al. 2012; Engelhardt et al. in prep; Engelhardt et al., unpublished data). An additional, not necessarily mutually exclusive, mechanism by which personality might be beneficial for fitness is in the context of female mate choice. Numerous studies have shown female preferences of certain personalities (Schuett et al. 2010). For example, female guppies (*Poecilia reticulata*) prefer brightly colored males as mates (Godin and Dugatkin 1996). Incidentally, coloration correlates with boldness in these fish, and when the two traits were experimentally decoupled, females exhibited a preference for bolder males regardless of their coloration (Godin and Dugatkin 1996). Females therefore can use personality as proxy for male quality including male abilities/genes to achieve higher (future) status. This might particularly be the case for traits for which the expression bears costs. Obviously, being bold in the context of predator deterrence bears potentials costs related to survival whereas highly connected males might be prone to increased risk of diseases transmission. Showing preferences for such males ensures females' offspring being equipped with good genes. In species, like crested macaques, in which female mate choice is likely to be limited given high-ranking males monopolize access to fertile females to a high degree (Engelhardt et al. in prep; Engelhardt et al., unpublished data), female preferences for certain personalities might still manifest themselves by females being more cooperative during male mate-guarding, i.e. females may try less escaping monopolization from males with preferred personality than from males with non-preferred personality. Finally, females could use the assessment of male personalities to ensure reproducing with partners of opposing personality, in order to achieve assortative matings. This strategy has been found in great tits, *Parus major*, in which pairs of opposing expression of a particular personality factor had higher reproductive success than pairs with similar expression of a factor (Both et al. 2005). These arguments point to possible links between personality and fitness independent of dominance status as mediator.

Our results are also important for the discussion on whether dominance itself constitutes a personality factor. Our data show that personality is not a consequence of dominance status, though we found co-variation between personality factors and concurrent status. This questions the validity of dominance as part of personality. Dominance as a personality factor has been described for great apes and rhesus macaques (*Macaca mulatta*), but not for humans (King and Figueredo 1997; Weiss et al. 2011, 2013). From this arises the hypothesis that dominance is a personality factor that developed early on in primate evolution, but merged with extraversion in humans after chimpanzees and humans split (Weiss et al. 2011). The notion that such a separate dominance personality factor exists in non-human primates however seems unlikely. In many situations, dominance status follows fairly predictable trajectories over an individual's life (Sprague et al. 1998). For example, in rhesus macaques, males usually attain higher rank by passively queuing, i.e. they rise in rank as a consequence of individuals above them in the hierarchy leaving or dying (Missakian 1972; Drickamer and Vessey 1973). Further, dominance status often is not even predictable in such general terms and is the outcome of dynamics in social relationships between individuals (Chase et al. 2002).

Yet, personality is, by definition, a temporally stable attribute, even though it may change over life (Roberts et al. 2006). It seems far more likely that dominance status is, at least partly, the consequence of personality and that in this sense personality features may predict strategies individuals follow to maximize their fitness (van Noordwijk and van Schaik 2004; Wolf et al. 2007).

We are at the beginning of understanding the mechanisms by which consistent differences in behavior (i.e. personalities) contribute to differential fitness in animals, departing from the notion that behavioral tendencies merely vary around an adaptive average. Our results demonstrate that male social careers can be shaped by more than intrinsic/individual factors such as physical condition, age or aggression. In line with these thoughts, we speculate that in general, certain personality factors equip males with abilities to maintain their status whereas other factors give males advantages in achieving higher future status. As such, personality can also contribute and is likely to interact with other behavioral, physical and physiological traits to the rank trajectories that males follow and ultimately result in differential fitness outcomes.

Chapter 5

Coalitions and dominance rank in wild male crested macaques (*Macaca nigra*)

with

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Manuscript to be submitted.

5.1 Abstract

Coalition formation is one of the most striking forms of cooperation found in the animal kingdom. Yet, there is substantial variation between taxa with regards to the mechanisms by which fitness consequences result from coalitions. In this study, we investigate the influence of coalitions on dominance rank trajectories in males of a wild crested macaque (*Macaca nigra*) population. We observed 212 coalitions and used linear mixed models to test how a variety of coalition properties and factors related to the social environment influenced future male rank. In general, the males in our study followed the expected bell-shaped, age-related pattern of rank development of many male primates. Furthermore, our results show that coalitions have additive effects on age-determined rank development, i.e. participating males achieve higher-than-expected future ranks, while targets of coalitions had lower-than-expected future ranks. Additionally, all-up coalitions have stronger effects than all-down and bridging coalitions, and we found differential effects of coalitions based on feasibility and whether coalitions were composed of only males or whether males formed coalitions with females. Finally, our results show that time that passes until the maximal magnitude of change occurs differs between targets and participants. These results provide important new insights regarding the mechanisms underlying coalition formation in male primates and support the idea that one of the major paths by which coalitions affect reproductive success and ultimately fitness is through influencing male rank trajectories.

5.2 Introduction

The evolution of cooperation is one of the hallmarks in biology, with coalitions being one of its most impressive manifestations (Harcourt and de Waal 1992; Dugatkin 1997; Kappeler and van Schaik 2006). Coalitions are joint aggressive events by at least two individuals directed towards at least one other individual (Bercovitch 1988; Harcourt and de Waal 1992). Coalitions appear to be limited in their taxonomic distribution, occurring mostly in mammal species, particularly primates and also in some bird species (Olson and Blumstein 2009; Smith et al. 2010). Classic models on primate coalitions focus mainly on aspects of resource defense among females. In most gregarious primate species females remain in their natal group and form bonds and support networks, preferentially with kin (Chapais 1992, 1995), in order to defend access to food resources (Wrangham 1980; van Schaik 1989).

Most male primates, on the other hand, usually migrate from their natal group around reaching adulthood (Pusey and Packer 1987). This may limit the possibilities of adult males to interact and form coalitions with relatives, though work on managed (i.e. not wild) populations suggests that relatedness between males can determine who a male forms coalitions with (e.g., Silk 1992; Widdig et al. 2000; see also Kulik et al. 2012). In contrast, in wild populations, preferential cooperation between related male adults is either absent (Schülke et al. 2010) or limited to maternally related kin in male-philopatric chimpanzees (Langergraber et al. 2007). Therefore, the consequences of coalitions among males and the conditions under which they occur are far more puzzling and need to be considered in a different framework because kin selection as explanation cannot be readily invoked.

A decade ago, a formal model which aims at explaining under which conditions coalitions among primate males should occur and what fitness consequences of coalitions are to be expected was introduced by van Schaik and colleagues (Pandit and van Schaik 2003; van Schaik et al. 2004, 2006; from here on: PvS model). Two mechanisms by which coalition partners increase their fitness are distinguished in the PvS model. First, at least one of the partners increases in rank, therefore benefitting in the long-term assuming that higher rank translates into higher reproductive success. Furthermore, though not explicitly considered in the PvS model, a rank increase could also be achieved by forming mixed-sex coalitions, in which males form coalitions with females (Chapais 1983; Datta 1983). Second, coalitions among males may serve a leveling function in the sense that by targeting and displacing a male from monopolizing a fertile female at least one of the partners gains direct mating access to a fertile female. Whether these mechanisms are mutually exclusive is unknown, but it is possible that leveling coalitions could increase the ranks of participants in the long-term in addition to being beneficial immediately.

There is some evidence that in both ways coalitions can have fitness consequences for male primates. For example, in baboons (*Papio cynocephalus*) and Barbary macaques (*Macaca sylvanus*), leveling of mating distributions occurs and appears to be a frequently used strategy to increase mating success (Young et al. 2013; Bercovitch 1988; Noë and Sluijter 1990; Bissonnette et al. 2009b). In contrast, beyond several case studies (e.g., Nishida 1983; Higham and Maestripieri 2010), we know surprisingly little about whether male coalitions influence the dominance ranks of males involved in coalitions. While Silk (1993) found no evidence that coalition rates influenced future dominance rank in bonnet macaque males (*Macaca radiata*), two more recent studies on Assamese macaque and chimpanzee males indicate such a link. Gilby and colleagues (2013) suggest that chimpanzee (*Pan troglodytes*) coalition rates over the course of two-year periods increase the likelihood of rising in rank in the subsequent two-year period. In their study on Assamese macaque males, Schülke and colleagues (2010) found similar results, suggesting that males with higher coalition rates in a given time period (where time periods were defined “based on changes in male dominance hierarchy”, p. 2207) achieved high dominance rank in subsequent time periods. In both these studies, dominance rank also translated into higher reproductive success, suggesting that males utilize coalitions to ultimately increase their fitness.

An important characteristic determining whether coalitions can have rank-changing (or leveling) effects is coalition configuration, i.e. the relative ranks of target and participants. In all-up coalitions (“revolutionary”, c.f. Chapais 1995), all coalition participants rank below the target, whereas in the bridging configuration at least one partner ranks above the target while at least one partner ranks below. Both configurations are profitable (c.f. van Schaik et al. 2006) in the sense that at least one participant benefits in ways that would not be available to him if he were on his own. In contrast, in all-down coalitions (the third possible configuration, “conservative”, c.f. Chapais 1995), neither of the coalition partners can profit per se from the coalition (c.f. van Schaik et al. 2006; but see below). All partners are already higher ranking than the target and can therefore displace males from access to females on their own without the cooperation of a coalition partner (see also Young et al. in press).

In order to predict which combination of the two beneficial configurations (all-up and bridging) and whether coalitions work in a leveling or rank-changing fashion, the PvS model utilizes a single predictive parameter, *beta*. *Beta* is the degree of despotism among males (Pandit and van Schaik 2003) and reflects the level of competition between males for access to fertile females. At its highest value, 1, the highest ranking male is able to monopolize all fertilizations, whereas towards its lowest value, 0, contest competition transforms into pure scramble competition where all males are equally likely to achieve fertilizations. For instance, in situations with moderate to high *beta* the PvS model predicts that coalitions should be generally rank-changing and not lead to leveling. At moderate *beta*, coalitions should be of the all-up configuration where very high-ranking (generally the highest-ranking) males are targeted by other high-ranking males ranking just below the target. At high *beta*, bridging coalitions are expected in which the highest ranking male (e.g., 1st) together with other high-ranking males (e.g. 3rd rank) targets another high-ranking male (e.g. 2nd). The PvS model additionally predicts that under moderate to high *beta* values coalitions are expected to be small and to consist of two or three participants. How to actually measure *beta* and whether *beta* is a static species property or a dynamic attribute that changes alongside fluctuations in, for example, number of group males or level of reproductive synchrony among females is still debated (Young et al. in press; van Schaik et al. 2006).

One crucial assumption the PvS model makes is that coalitions need to be feasible, i.e. the combined competitive abilities of the participants need to exceed those of the target (van Schaik et al. 2006). The straight-forward approach as suggested by van Schaik and colleagues (2006, see also Noë and Sluijter 1995) is simply to sum individual competitive abilities, though synergetic effects might be possible (Noë 1994). A recent study by Bissonnette and colleagues (2009a) suggests that cardinal rank scores, in contrast to ordinal ranks, might have the desired properties to measure feasibility of coalitions (see also Chapter 2; Balasubramaniam et al. 2013). With such an approach it becomes possible to distinguish between configurations that are differentially feasible on a continuous scale. For instance an all-up coalition could be highly feasible if the 2nd and 3rd ranking males team up against the 1st rank as compared to 5th and 6th rank teaming up against the 1st rank (less, if at all, feasible).

Partly because they are always feasible by definition, all-down coalitions are considered as not directly beneficial by the PvS model and are therefore not included as meaningful coalition type. They have been hypothesized to constitute a counter-strategy employed to prevent all-up and bridging coalitions from occurring (Chapais 1995; van Schaik et al. 2006; see Kutsukake and Hasegawa (2005) for an illustrative case study). However, all-down coalitions can also be directly beneficial if they function to maintain the ranks of the participants. Empirical evidence for coalitions functioning in such a way to maintain the existing rank order comes from a study on male Tibetan macaques (Berman et al. 2007, see also Widdig et al. 2000).

As became clear, coalitions are usually studied from the perspective of the cooperating individuals, i.e. participants. Following this, there appears to be a predominant disposition to investigate positive or neutral consequences, i.e. do participants of coalitions rise or maintain their rank. Though implicit in this approach are the consequences for targets (whenever somebody rises in rank someone else needs to drop), such effects have, to our knowledge, never been explicitly studied from the perspective of coalition targets.

We also know little about the temporal aspects of coalition consequences. The effects of leveling coalitions are predominantly immediate, i.e. they lead to immediate mating access for at least one of the coalition partners. In contrast, the question of which time-frame rank-changing coalitions work in has, to our knowledge, never been directly asked. Researchers usually select time units whose relevance in terms of dominance rank dynamics for the species studied are mostly unclear. In the empirical studies mentioned so far, the rank-changing consequences of coalitions were measured over time periods ranging in duration from one month to two years. Though case studies suggest that these rank-changing effects can also occur within a very short time (e.g., Nishida 1983; Higham and Maestripieri 2010), systematic data on this important aspect of coalitions are lacking.

Here, we study coalitions in crested macaques (*Macaca nigra*), a species in which the majority of matings during fertile periods of females is monopolized by alpha males (63.5%, Engelhardt et al. in prep). Based on this, we consider crested macaques to have a moderate to high *beta* value (c.f. Pandit and van Schaik 2003; van Schaik et al. 2006), and therefore expect coalitions to be rank-changing, but refrain from predicting the predominant configuration. An additional property of this species which makes it interesting to study coalitions and its effects on rank is that the adult male cohort is highly dynamic, both at the level of rank relationships and composition (Chapter 2).

The overall goal of this study was therefore to investigate the effects of coalitions on male dominance trajectories in a species with highly dynamic rank relationships. The first specific objective was to describe general patterns of coalition formation. Our second objective was to test the effects of coalition characteristics on subsequent changes in dominance status of both, participants and targets of coalitions. Here, we specifically investigated sex-composition, configuration, feasibility and time frame.

5.3 Methods

5.3.1 Study Site

We studied two groups, R1 and PB, of wild crested macaques in the Tangkoko Nature Reserve, Sulawesi, Indonesia between March 2009 and May 2011 (Neumann et al. 2010; Duboscq et al. 2013). Each group comprised up to 85 individuals, with the number of adult males being present at any given time ranging between 7 and 18. All animals of both groups were completely habituated to human observers and adult males and females were individually recognizable based on facial features and natural body markings, e.g., scars or broken limbs.

5.3.2 Behavioral Data

We collected behavioral data using focal animal sampling (Altmann 1974) of 37 adult males (mean = 66.1h, range = 0.6 – 130.0h per male, total = 2447.2h). Focal protocols lasted up to 60 minutes during which continuous data on aggressive behavior and interaction partner identities were recorded. We defined a coalition as simultaneously occurring aggression by at least two individuals (participants) directed towards at least one male (target) upon which the target left or fled the participants. This definition includes the possibility that males and females form mixed-sex coalitions. Note that targets were always male as was at least one of the participants. Coalitions could also target more than one individual, however, since we never observed such coalitions (see results), our operationalization of coalitions is restricted to single targets.

Since rates with which we observed coalitions during focal animal sampling were small compared to other studies on male macaques we supplemented our data set with ad libitum observations of coalitionary events. Note however, that this does not imply that we saw all coalitionary events taking place within the group. The habitat was generally dense and groups often were spread over more than 100 m (pers. obs.). Therefore, rates of participation in and being targeted by coalitions are based on focal animal data, whereas our main analyses are based on single coalitionary events as unit of analysis (see below).

5.3.3 Variables

Current rank, future rank and time distance

We measured rank by calculating Elo-ratings that were based on decided dyadic conflicts and displacements (Chapter 2; Albers and de Vries 2001). In brief, after each dyadic dominance interaction, the Elo-rating procedure updates the ratings of the two individuals involved in way that the winner receives points whereas the loser's points decrease. The amount of points that are won and lost depends on the expected interaction outcome. This expected outcome is based on the rating difference before the interaction took place. The basic idea being that if a strong individual wins against a weak one (as expected based on their rating difference), the winner will gain only few points while the loser loses little. If, against such an expectation, a weaker individual wins against a stronger one the points received and lost will be relatively more. In this way, ratings of individuals are updated after each single interaction, allowing for fine-tuned monitoring of rank over time (for more details see Chapter 2). For the purpose of this study, we used ratings at the end of a given observation day, i.e. if an individual was observed in more than one dyadic interaction on a given day, that day's rating is the one after the last observed interaction. Note also, none of the interactions considered as coalitions contributed to Elo-rating estimation. Elo-ratings have several advantages over commonly used dominance indices (Chapter 2). With respect to our study the most important of these advantages are that (1) ratings are continuously updated, which allows estimation of dominance status on small time scales (in our case on a daily basis), (2) ratings are on an interval scale, i.e. differences between ratings are meaningful, and (3) ratings are not affected by changes in the group composition. The parameter k was set to 100 for all Elo-rating calculations (Chapter 2).

Current rank of a male was defined as his Elo-rating on the date of the observed coalition. Future rank was calculated at time steps of 10 days following the coalition up until 120 days (see data organization, below). This time distance variable was introduced in order to investigate in which time frame coalitions have an effect (see below for how data were organized). We decided to set the upper limit of the time frame to be considered at about four months (i.e. 120 days) because first, previous studies on male macaques indicated that such effects are expected to occur in the magnitude of months (e.g., Silk 1993; Schülke et al. 2010), and second, since we consider single events and not rates of coalitions over observation time we expect changes to occur on relatively small time scales.

We only used ratings that were updated within a maximum of five days from the date in question (including the date of the interaction itself). This ensures that if a rating from a male is identical to the one at the time step before, this is not due to this male not having been observed during a recent dyadic dominance interaction. In this way, also cases were excluded if a male emigrated from the group or died and therefore no current rating was available.

Finally, in order to present results that can be compared to the predictions of the PvS model with regards to what ranks targets and participants held, we transformed Elo-ratings into ordinal ranks. For this, we simply ordered the Elo-ratings of all males present in the group on the day a coalition occurred and assigned the male with the highest Elo-rating rank 1, the male with the second-highest rating was assigned rank 2, and so on.

Role

Individuals were either targets (victims) of coalitions or participated in aggression directed at a target (participants).

Composition

All coalitions considered here were directed at single male targets. Based on the sex composition of the participants, we distinguished between mixed (at least one female participant) and pure (no female participant) types of coalitions.

Configuration

We classified pure (all-male) coalitions into one out of three configurations. Coalitions were considered all-down (all participants had higher Elo-ratings than the target), all-up (all participants had lower Elo-ratings than the target), or bridging (at least one participant had a higher Elo-rating than the target and at least one participant had a lower Elo-rating than the target). Even though it is theoretically possible to apply the pattern of three configurations also to mixed coalitions we refrained from this. Despite having data to create separate hierarchies for the sexes our data are likely biased (particularly with regards to ad-libitum sampling) to intra-sexual interactions which might lead to less reliable estimation of a mixed-sex hierarchy. Additionally, we refrained from working under the assumption that all adult females rank below all adult males.

Feasibility

For pure male coalitions we calculated feasibility as the difference between the sum of Elo-ratings of all participants and the Elo-rating of the target, as measured on the day of the coalition (for a comparable continuous assessment of “asymmetry in strength” see Bissonnette et al. 2009a). Prior to this calculation we standardized ratings in such a way that the highest rating of all males present that day was set to 1 and the lowest to 0 while keeping differences between these standardized ratings proportional to the differences between males as measured on the original Elo-rating scale. A positive feasibility value therefore indicates that the combined "power" of the participants was greater than the "power" of the target, whereas negative values indicate that combined power of participants was smaller than the one of the target.

Control variables

We added several control predictor variables to account for their possible confounding effects on future Elo-rating. Foremost, we added the Elo-rating on the date of the coalition itself. Next, we added age as control factor to account for age related rank trajectories (Sprague 1998; Alberts et al. 2003; Bissonnette et al. 2009b). Since birth years of adult males in the study population were unknown, we classified each male into one of three age categories (young (N = 15 males), middle (N = 11 males) and old (N = 11 males)), based on size, appearance and tooth wear. In addition, we added individual aggression rates (aggressive acts received from adult males per hour of focal observation time) into the model (e.g. Gilby et al. 2013). The final two control variables measured two characteristics on the group level. We incorporated a quantitative measure of hierarchy stability assessed +/- five days around the date of the coalition (c.f. Chapter 2), reasoning that coalitions might affect future rank differentially depending on whether the competitive situation among group males is stable or instable. Finally, as a measure of degree of competition between males for access to fertile females we calculated a competition index akin to the operational sex ratio. For the day of the coalition and for each of the five days before and after, we counted the number of fertile females present in the group. The decision on whether a female was fertile or not was based on hormonal and morphological markers of a four day fertile phase during which ovulation is most likely to occur (see Higham et al. (2012) for details). For each day, this number was then divided by the number of adult males present. A single fertile female present on a given day represents the highest possible degree of competition possible, which then linearly decreases as more females become fertile, leading to the lowest possible degree of competition if there are (at least) as many fertile females as there are males. To account for the possibility that no fertile female is present and therefore the index would be zero and faultily indicate highest possible competition, we replaced index values of 0 with 1. This assured that the index captures the similarity (i.e. no competition) between situations regardless of whether there are no fertile females available or as many as there are males. In this way, an index value close to zero represents high competition whereas values approaching 1 indicate less competition. Having calculated this index for each day, we then calculated the mean of these values over the 11-day time window, which we incorporated into the model.

5.3.4 Data organization

Since we were interested in the effects of coalition characteristics on future male rank, we organized our data set in such a way that for a given coalitionary event, each individual involved (target and participants) was represented as a single case, i.e. line, in our data set. We then discarded all lines representing females, since our response variable was future male rank. For example, a pure male coalition with two participants and one target was represented as three lines in our data set, whereas a mixed coalition with one male target and one female and male participant was represented as two lines (one for the male participant and one for the male target). We repeated this step 12 times, for each of the time steps we considered. In this way, the example coalitions from above resulted in 3 * 12 = 36 and 2 * 12 = 24 lines in the data set, respectively. The different lines in our data set differed with regard to future rank and the time distance variable. The data set then comprised 7764 lines, representing 197 coalition events. As stated above, 2862 lines (36.9%) were excluded because either future rating was not available due to emigration/death or if a rating was not recently updated due to lack of observation of dyadic dominance interactions.

5.3.5 Statistical analysis

Our general approach was to model future male rank as function of several predictor variables that related to single coalitionary events and the time distance from the original event. For our first question, i.e. whether coalitions that differ in sex composition (pure versus mixed) have different effects on a male's future rank, we used only a subset of predictor variables. In particular, we excluded two parameters that could not be measured (feasibility) or classified (configuration) for a given event if the coalition was of mixed composition. For our second question, i.e. how coalition characteristics, including feasibility and configuration, influence future male ratings, we restricted the data set to coalitions composed of only males (pure composition).

We built linear mixed effects models (LMMs) in R 2.15.0 (R Development Core Team 2012) using the `lmer` function in the lme4 package (version 0.999999-0, Bates et al. 2012). Prior to analysis all numeric variables were checked for symmetric distributions and transformed if necessary. Following this step, we standardized all variables to mean = 0 and standard deviation = 1 (Schielzeth 2010).

In addition to the main effects described above, we added several additional terms to the models. First, considering the time distance variable, we hypothesized that the effect might be non-linear, i.e. the effect of time distance on future rank might not be strictly linear and might show a local optimum at some intermediate time distance value. We therefore added the quadratic term of time distance as additional fixed effect to allow for such a potential local optimum. Next, we added an interaction term between time distance (and its quadratic term) and role, expecting that any effect that time distance might have on future rank, will be different for targets as opposed to participants of coalitions. For the second model, we also added the interaction between role and configuration, expecting that future rank of targets and participants differs depending on what configuration the coalition had. In order to account for repeated observations, we added male and group ID as random effects. Additionally, we incorporated random slope parameters for current rank and role in the random term for male ID. Finally, we controlled for temporal autocorrelation which is likely to be present in our data in the following way: first, we built the two full models with all main, random and interaction terms as described above. From these models, we derived the residuals. For each data point separately, we calculated the weighted average of the residuals of all other data points of the same male, with the weights being equal to the time lag to that particular data point. The weight followed a normal distribution with its standard deviation determined by minimizing the AIC of the model including this autocorrelation term as additional fixed effect (R. Mundry, pers. comm., see also Barelli et al. 2011; Fürtbauer et al. 2011).

The initial models were then checked for whether the assumptions of linear models were met (Quinn and Keough 2002). Several diagnostic tools indicated violations of these assumptions. Particularly, Cook's measure of influence (assessed with the R package influence.ME, Nieuwenhuis et al. 2012) indicated a range of influential cases. Inspection of these cases revealed that most of them could be attributed to data of two specific males (IM, WJ). Both males underwent severe rank drops in January 2010, likely due to severe injuries they suffered, the origins of which are not known to us. In one case (IM), we suspect that the injuries were the consequence of a dyadic fight between IM and OM, both of which were seen with fresh and in the case of IM severe wounds within a few minutes. We did, however, not observe the actual event that led to these injuries. IM, in contrast to OM, dropped to the bottom of the hierarchy and was repeatedly harassed by the group, including being targeted by adult coalitions in the days following his injury. With WJ, the circumstances are less clear. He also suffered severe injuries, though no other male showed obvious signs of having been involved in a fight with WJ on the day the injuries were detected by us. Unlike IM, WJ left the group for seven days before rejoining the group at the bottom of the hierarchy. We decided to exclude these influential cases because we suspect that these rank drops were not the immediate consequence of coalitions, but more likely were the consequence of dyadic fights between males and the associated injuries. In addition, in this study, we are interested in the gradual changes in dominance relationships, which in these two cases were interrupted by abrupt changes.

After exclusion of the influential cases, we ran model diagnostics again. Residuals were homogenously and normally distributed. Variance inflation factors were calculated with the function `vif` from the car package (Fox and Weisberg 2011) from linear models excluding the random effects and were all below 10 (max: 2.6), indicating collinearity between predictor variables not to be of concern (Quinn and Keough 2002).

To assess the statistical significance of our results, we used the following approach. First, we calculated likelihood ratio tests (LRT, Quinn and Keough 2002) to assess whether a full model (with all main effects and interactions) was different from its respective null model (only comprising the control variables, see above). Next, we assessed the significance of the interaction terms by using likelihood ratio tests to compare the model including the interaction to the model without the interaction. If an interaction was not significant at $p < 0.05$ as inferred from the likelihood ratio test, we removed the interaction to be able to interpret the respective main effects. Finally, statistical significance of single main effects was assessed using the `pvals.fnc` function from the languageR package (Baayen 2011b). Note that during the results presentation, parameter estimates need to be interpreted as being the estimate while all other numeric variables are at their means, i.e. zero (see above). Similarly, since we used dummy coding for our categorical predictors (role, composition, configuration, and age), parameter estimates refer to the situation when the categorical predictors are at their reference level.

5.4 Results

5.4.1 General characteristics of coalitions

We observed a total of 212 coalitionary events between adult individuals, all of which were targeted at single adult males. Out of these, 137 (64.6%) were composed of only males, while the remaining 75 (35.4%) comprised at least one female participant. The average number of participants was 2.22 (median = 2, range: 2 – 6) in pure coalitions and 2.28 (median: 2, range: 2 – 5) in mixed coalitions. For 129 pure male coalitions we were able to identify the target and all participants, and therefore able to determine the configuration. The majority of pure male coalitions was all-down ($N = 90$, 69.8%), while bridging ($N = 23$, 17.8%) and all-up ($N = 16$, 12.4%) coalitions were rarer. Targets of all-up coalitions had an average ordinal rank derived from Elo-rating of 3.8 (range: 1 – 8), while the rank of the highest rated participant was on average 6.5 (range: 4 – 14). The average size of these pure all-up coalitions was 2.25 (range: 2 – 3). Targets of bridging coalitions had an average ordinal rank of 7.8 (range: 2 – 14), while the highest ranking participant of bridging coalitions had an average ordinal rank of 3.6 (range: 1 – 6). On average, 2.6 males (range: 2 – 6) participated in bridging coalitions.

During the cumulative focal animal sampling time of 2447.2h, we observed 81 coalitions (mixed and pure), i.e. 0.33 events per 10 hours , or one event about every 30h. Individual males were targets of coalitions on average 0.16 times per 10 hours (median: 0.00, range: 0.00 – 2.63) and participated 0.15 times per 10 hours (median: 0.00, range: 0.00 – 0.86). Only considering pure male coalitions, rates per 10 hours observation time were 0.09 (median: 0.00, range: 0.00 – 1.97) and 0.11 (median: 0.00, range: 0.00 – 0.86) for targets and participants, respectively. All individual rates are based on data from 37 males.

None of the coalitions were observed in the context of displacing a target male from monopolizing a fertile female to gain mating access to such a female.

5.4.2 Consequences of coalition composition

The full model based on the data set including pure and mixed coalitions was significantly different from its respective null model (excluding composition and the composition-role interaction, LRT: $\chi^2 = 21.1$, df = 2, $p < 0.0001$). The interaction between role and composition by itself did not improve model fit (LRT: $\chi^2 = 1.7$, df = 1, $p = 0.1869$) and was therefore removed at this point. Males had higher future Elo-ratings after pure male coalitions as compared to mixed coalitions including female participants (b = 0.043, se = 0.010, $p_{\mathrm{MCMC}} = 0.0001$, Figure 5.1). Results of the final model are presented in Table 5.1.

5.4.3 Consequences of pure coalitions

The full model based on the data set comprising only pure coalitions differed from the null model (LRT: $\chi^2 = 1115.3$, df = 12, $p < 0.0001$), meaning that the combination of predictor variables and their interactions which were not present in the null model (role, configuration, time distance, feasibility) significantly improved model fit. Results of this model are given in Table 5.2.

Table 5.1: Results of the LMM testing for the effects of coalition composition on future Elo-ratings. For categorical predictor variables, the factor levels *not* included in the intercept are given in parentheses. Two predictors (configuration and feasibility) included in model 2 (see Table 5.2) are omitted here because they could not be measured for mixed coalitions.

	estimate	se	t
Intercept	0.286	0.258	1.11
Composition (pure)	0.043	0.010	4.40
Role (target)	-0.194	0.118	-1.65
Time distance	0.001	0.005	0.19
Time distance^2	0.006	0.005	1.14
Current Elo-rating	0.443	0.041	10.72
Aggression rate	-0.047	0.067	-0.71
Hierarchy stability	-0.042	0.004	-9.96
Age (old)	-0.586	0.234	-2.50
Age (young)	-0.293	0.246	-1.19
Competition index	-0.030	0.004	-7.14
Autocorrelation	0.342	0.004	90.53
Role (target) : Time distance	0.022	0.008	2.72
Role (target) : Time distance^2	0.015	0.009	1.62

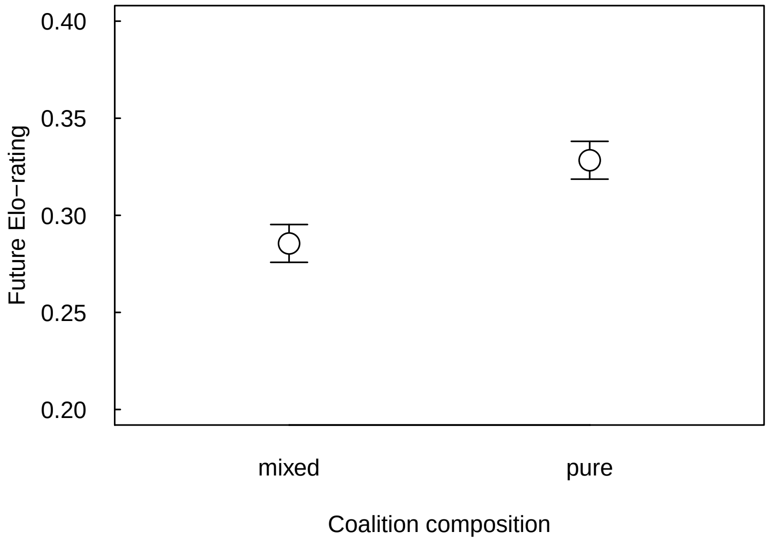


Figure 5.1: Pure coalitions lead to higher future Elo-ratings than mixed coalitions. Open circles depict parameter estimates with associated standard errors. Note that these parameter estimates reflect the difference between mixed and pure coalitions at the reference levels of the remaining categorical factors in the model (role = participant, age = middle) and at the numerical predictor variables being at their means, i.e. 0.

Table 5.2: Results of the LMM testing for the effects of configuration, feasibility, role in a coalition and the time distance that passed from the original event on future Elo-ratings. For categorical predictor variables, the factor levels *not* included in the intercept are given in parentheses.

	estimate	se	t
Intercept	0.149	0.156	0.96
Role (target)	-0.164	0.156	-1.06
Configuration (all down)	-0.019	0.014	-1.32
Configuration (all up)	0.082	0.022	3.72
Feasibility	0.000	0.006	0.02
Time distance	0.009	0.005	1.74
Time distance^2	0.007	0.006	1.18
Current Elo-rating	0.550	0.051	10.85
Aggression rate	0.025	0.062	0.41
Hierarchy stability	-0.046	0.005	-9.26
Age (old)	-0.341	0.196	-1.73
Age (young)	0.039	0.221	0.18
Competition index	-0.053	0.005	-10.20
Autocorrelation	0.388	0.004	88.03
Role (target) : Time distance	0.039	0.010	3.92
Role (target) : Time distance^2	0.021	0.011	1.88
Role (target) : Configuration (all down)	-0.077	0.031	-2.49
Role (target) : Configuration (all up)	-0.502	0.043	-11.78
Role (target) : Feasibility	-0.035	0.013	-2.74

Configuration

The effects of coalitions differed between participants and targets depending on the configuration of the coalition, i.e. the interaction between configuration and role improved model fit (LRT: $\chi^2 = 137.6$, df = 2, $p < 0.0001$). Participating males had higher future Elo-ratings than targets regardless of configuration, though this effect was most pronounced for all-up coalitions (Figure 5.2a). Figure 5.2 also illustrates that though participants had higher future Elo-ratings when compared to targets, this does not necessarily imply that Elo-ratings of participants generally rose (estimates > 0) while they dropped for targets (estimates < 0) after the occurrence of a coalition. As a consequence of dummy coding, these results apply only to middle aged males (our reference level for age). In contrast to middle aged males, old males' Elo-ratings decreased regardless of configuration, i.e. the estimates for all combinations of role and configuration were negative (Figure 5.2c). Yet, Elo-ratings of old males decreased less if they participated in coalitions as compared to when they were targets. In contrast, the Elo-ratings of young and middle-aged males generally rose when they were participants and dropped when they were targets (Figures 5.2a, b). The sole exception to this general pattern were the Elo-ratings of young males who though being targets, rose marginally after bridging coalitions (Figure 5.2b).

Feasibility

The interaction between role and feasibility improved model fit (LRT: $\chi^2 = 7.5$, df = 1, $p = 0.0062$). For participants, feasibility had no obvious effect on future Elo-ratings

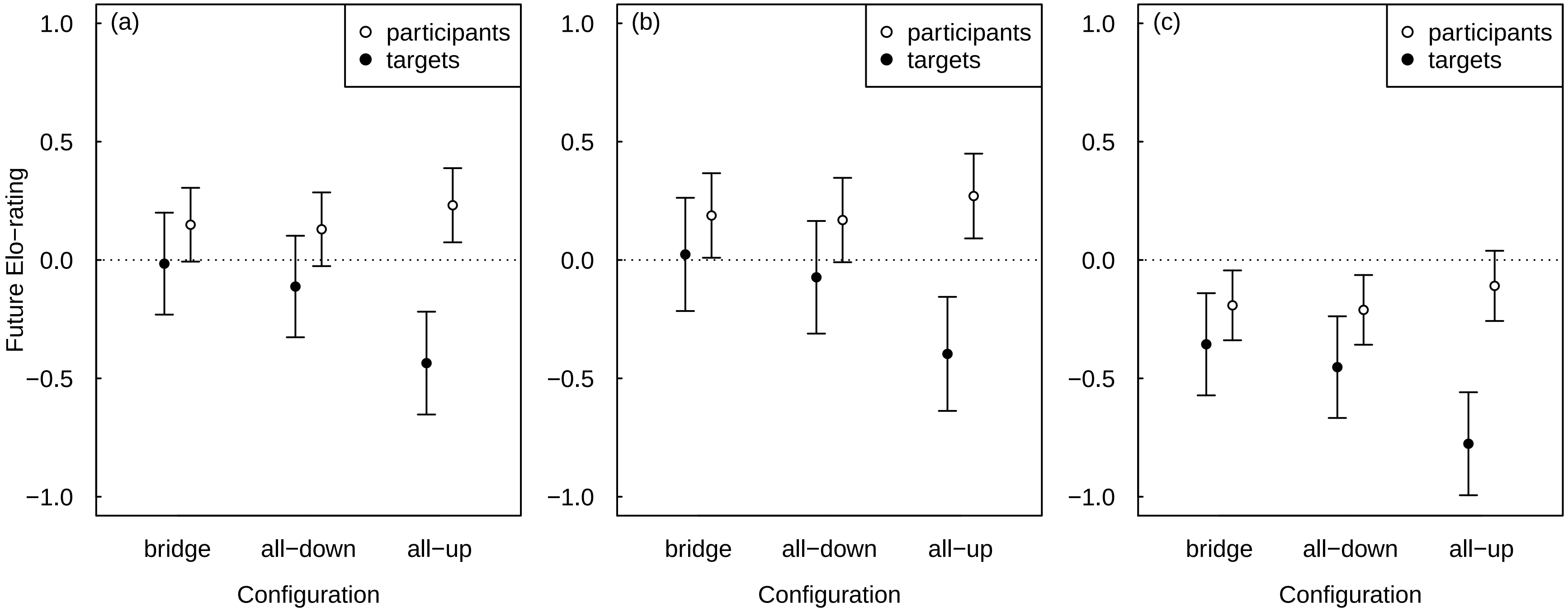


Figure 5.2: Effects of the interaction between role and coalition configuration on future Elo-rating. (a) middle-aged males, (b) young males, and (c) old males. Circles depict parameter estimates with associated standard errors. Parameter estimates above the horizontal line indicate a rise in Elo-ratings while those below indicate a drop. Note that the panels are separated by age because age is the only remaining categorical predictor in the model. All other numerical predictor variables are at their means (i.e. zero).

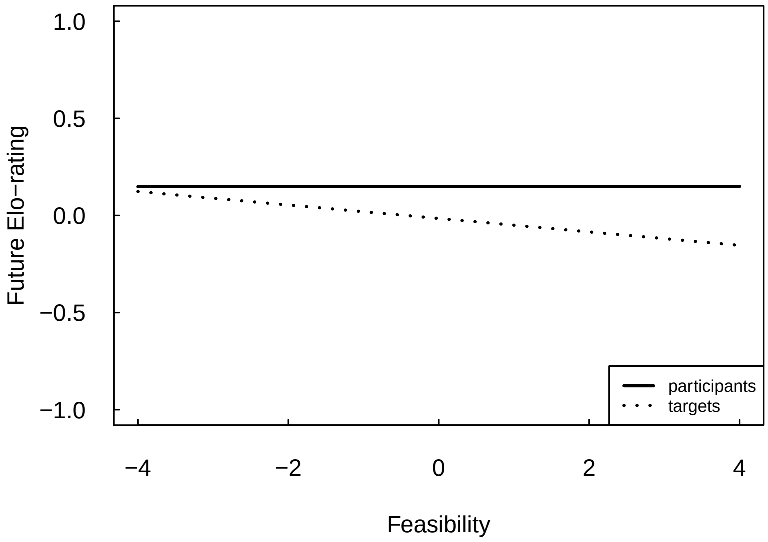


Figure 5.3: Effects of feasibility on future Elo-ratings for participants and targets of coalitions. Note that the plot reflects again the effects of the test variable (here: interaction between feasibility and role) at the reference levels of the remaining categorical factors and the means of the numerical variables (see text).

(Figure 5.3). In contrast, targets had smaller future Elo-ratings when coalitions were highly feasible as compared to when coalitions were little feasible (Figure 5.3). Overall, targets had smaller future Elo-ratings than participants.

Time course

Finally, we looked at the time course over which coalitions had consequences. A reduced model in which the squared time distance variable and its interaction with role were removed differed significantly from the full model (LRT: $\chi^2 = 10.3$, df $= 2$, $p = 0.0059$), indicating that the effects of coalitions differ between participants and targets with respect to when coalitions show their greatest effect. Figure 5.4 illustrates the pattern for bridging coalitions of middle-aged males (age and configuration being the remaining dummy coded categorical predictor variables in the model, and bridging and middle their respective reference levels). For targets, the effect was more pronounced as compared to participants with a local minimum at about 65 – 70 days, i.e. a little more than two months after the coalition event. In contrast, the model shows a much less obvious pattern for participants, with a local minimum at around 40 days after the coalition. In other words, targets had smaller future Elo-ratings than participants, but the biggest rating change for participants occurred a month before the biggest rating change measured for targets.

5.5 Discussion

Our results demonstrate a clear relationship between coalitions and dominance rank trajectories in wild male crested macaques. Coalitions, though relatively rare, appear therefore to function as rank-changing and not as mechanism to level mating distributions. The rank-changing consequences are further corroborated by our finding of differential effects coalitions had on participants and targets. Given that dominance

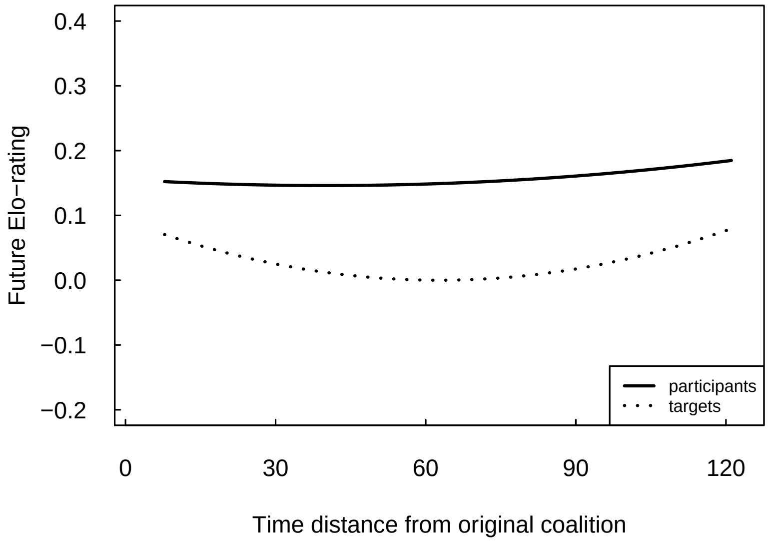


Figure 5.4: The time course over which coalitions influence future Elo-ratings of males. Note that the plot reflects again the effects of the test variable (here: interaction between feasibility and role) at the reference levels of the remaining categorical factors and the means of the numerical variables (see text).

rank translates into reproductive success in male crested macaques (Engelhardt et al. in prep), this suggests that coalition formation is a male strategy to increase fitness. These findings furthermore present the first description of coalition formation in crested macaque males, a species for which male coalitions so far have been presumed absent (Plavcan et al. 1995; Olson and Blumstein 2009).

As one would expect, males in our study attained higher ranks after they participated in coalitions as compared to when males were targeted by coalitions (see Figure 5.2). However, only young and middle aged participants did indeed rise in rank, i.e. they had higher rank after a coalition as compared to before. Old participants, on the other hand, dropped in rank, but they dropped less as compared to when being targets. Similarly, males generally dropped in rank after being targeted by coalitions. This illustrates the interplay between age and the effects of coalitions. Male primates (including crested macaques) often follow fairly predictable rank trajectories over their life-time, increasing in rank during young adulthood, reaching their highest status at an intermediate age, and as they age usually rank declines again (e.g., Sprague 1998; Bissonnette et al. 2009a). Given that there remains some variance in rank unexplained by age alone – for example, not all middle aged males present at one time in a group can have the highest rank – factors other than age must contribute to the ability of males to achieve the highest rank possible. Our results indicate that coalitions can act as such a means to give males an advantage during competition with other males.

In this respect, our results also support the PvS model, in as much as coalitions in crested macaque males have rank-changing consequences and do not level mating distributions. However, the PvS model also predicts that among males in species with strong reproductive skew towards high-ranking males, coalitions should predominantly occur in all-up or bridging configuration. Given the ambiguity in how to estimate skew and consequently *beta* (Young et al. in press; van Schaik et al. 2006), we were not confident in making a more specific prediction other than coalitions in crested macaques should be rank-changing in either of the two configurations. In contrast to the second part of this prediction, we found that the majority of coalitions among males were of the all-down configuration, while the two expected configurations accounted for only about 30% of coalition events. van Schaik and colleagues (2006) argue that all-down coalitions are not profitable in the sense that they do not provide benefits to coalition partners that either of the partners could not obtain alone. They rather see all-down coalitions as a consequence of rank-changing bridging and all-up coalitions to maintain any changes brought about by previous rank-changing coalitions and also as a means to ascertain the reliability of the partners' commitment to each other. In contrast, our results do show rank-changing consequences of all-down coalitions, though changes in rank after all-down coalitions were smaller than after all-up coalitions. This suggests that all-down coalitions can indeed be profitable beyond pure maintenance of the status quo (e.g., Kutsukake and Hasegawa 2005; Berman et al. 2007). The winner/loser effect is well established in a range of animal taxa (Hsu et al. 2006), therefore predictably losing an interaction to an all-down coalition may reduce the victim's chance of winning subsequent dyadic encounters. Regular all-down coalitions could also be utilized to induce stress and anxiety in victims and thereby functioning to prevent challenges from low-ranking individuals towards high-rankers (Young et al. in press; van Schaik et al. 2006; see also Silk 2002; Berghänel et al. 2011). It therefore seems that all-down coalitions can be beneficial, though in a different way from rank-changing all-up and bridging coalitions, and that the non-profitability of all-down coalitions assumed in the PvS model needs to be reevaluated.

In addition to the configuration of coalitions, our results indicate that feasibility of coalitions can influence the magnitude of rank changes. While the magnitude of change is independent of feasibility for participants, changes in rank become smaller with higher feasibility for targets. In other words, the more pronounced the difference in competitive abilities is between participants and targets, the smaller are the consequences for the target. This suggests a pattern for coalition targets that resembles the underlying principle of Elo-rating, i.e. if an interaction ends with the expected outcome (i.e. high feasibility) the consequences are smaller as when an interaction outcome violated the expectations (i.e. small, possibly negative, feasibility) (Chapter 2; Elo 1978). It further adds to our suggestion that we need to distinguish between participants and targets in coalitions. Differences between individuals in coalition consequences may be influenced by other factors that are less obvious than whether an individual was a target or participated. For example, in a study on male Barbary macaques, coalition targets were more likely to direct counter aggression at their aggressors if feasibility ('asymmetry') was low as when it was high (Bissonnette et al. 2009b). Given that feasibility appears to be perceived (likely with some error, Bissonnette et al. 2009b) on a continuous scale, this suggests that the assumption found in current models of coalition formation of coalitions being either feasible or not needs to be reevaluated. The study of dyadic conflicts has profited from incorporating such continuous measures of symmetry (Flack and de Waal 2004; de Vries et al. 2006; Balasubramaniam et al. 2012) and future studies will have to show, for example, whether the degrees of dyadic and polyadic power asymmetries are correlated across species and whether these properties interact with each other to influence patterns of coalition formation.

We also found differences between participants and targets with regard to the time course over which coalitions had effects. Our model suggests that there is a point in time at which the effects of coalitions are most pronounced. This seems to be logical given that rank trajectories are unlikely to be linear over a male's entire life (see above). Our results also highlight the possibility that the time course which consequences of behavior (here coalitions) take, may differ within the same species based on some confounding factor not considered. Imagine we had looked at differences in rank-consequences of coalitions between participants and targets with a fixed interval, say two months. The difference we had found would have been almost double in magnitude as compared to looking at the effects as observed after two weeks (Figure 5.4). It suggests that we need to consider the time frame carefully, when studying behavior and attempting to predict future behavior.

The final result of our study concerns the possible influence which females may have on male-male relationships. Males had higher future rank after pure coalitions than after mixed coalitions (including females). Surprisingly though, the interaction between coalition composition and role was not significant and therefore this pattern holds for both, participants and targets of coalitions. This means that while participants had higher ranks after pure coalitions, suggesting that it is more effective for males to participate in pure coalitions, targets also had higher ranks after being victim of a (possibly more effective) pure coalition as compared to being victim of a mixed coalition. At present, we have no explanation as to why the pattern did not reverse depending on the role. The reason for this counterintuitive result may relate to the omission from the model of factors that contributed to rank consequences in pure coalitions alone (feasibility and configuration) and indirectly highlights the likely importance of these two factors. Feasibility and configuration were not included since we were not confident enough due to our data collection regime to include females into hierarchies, which is the prerequisite to measure feasibility and assign configuration.

Besides the difficulties in interpretation, our results on differences between pure and mixed coalitions nevertheless support the notion that coalition consequences for participants depend on partner choice. Work on a range of species suggests that coalition formation occurs more often between individuals of the same sex who form strong social bonds (Seyfarth and Cheney 1984; Hemelrijk 1994; Silk 1994; Schülke et al. 2010; see also Hemelrijk and Puga-Gonzalez 2012). On the other hand, there is no reason to assume that such a mechanism could not work between the sexes. Kulik and colleagues (2012) recently demonstrated that male rhesus macaques are more likely to support females with which they share strong bonds. We do not know whether such male-female bonds exist in crested macaques and more generally what the factors are which influence the choice of coalition partners. Previous research suggests that crested macaque males maybe use a strategy of having available a diverse network of potential partners, as opposed to species in which coalition partners are predominantly drawn from a pool of closely bonded partners (e.g., Schülke et al. 2010). We found male crested macaques possess a personality factor, Connectedness (Chapter 3), which reflects the diversity of a male's social network, including males and females. Incidentally, this factor positively influences male rank trajectories, i.e. males with more diverse networks achieve higher future rank as compared to males with less diverse networks (Chapter 4). In addition, the composition of the male group in our study population is very dynamic with frequent migration events (Chapter 2), making us speculate that the benefits of building up strong bonds for males may be small as compared to the investment in such relationships. Therefore, we hypothesize that coalitions among crested macaque males are opportunistic in as much as partner choice is not driven by social bonds. Clearly, more research is needed to investigate whether the opportunity to form bonds (duration of co-residency) and male personalities influence coalition formation among crested macaques specifically and other in species more generally.

Dominance trajectories of male primates are resulting from the interplay of a variety of individual properties and under the influence of environmental pressures (Alberts 2012). Our study describes the consequences of coalitions for male crested macaques as one important facet of such a dynamic system. Participating in coalitions provides males with benefits through higher rank than expected without utilization of coalitions. In the future we will investigate whether higher rank translates into higher reproductive success. In this respect, our study contributes to our understanding of the strategies used by males to maximize fitness given the different career paths available to them (van Noordwijk and van Schaik 2004).

Chapter 6

General Discussion

Dominance is a complex phenomenon. The results of this thesis corroborate this view: not only does dominance status vary within individuals (Chapter 2), but two variables were found to determine future rank of individual crested macaque males. The first, personality (or more precisely, two specific personality factors, connectedness and anxiety, Chapters 3 and 4) represents an individual feature. The second, coalitions (Chapter 5), goes beyond individual features and represents an influence of the social environment. As dominance rank is associated with benefits in crested macaque males (Engelhardt et al. in prep; Engelhardt et al., unpublished data), being connected and little anxious as well as participating in coalitions provides male crested macaques with advantages in reproduction.

Further, the results of this thesis provide evidence for the complex interplay between factors in the way they collectively contribute to dominance rank trajectories. Both, personality and coalitions added to the effects of age (see Figure 5.2), as a likely measure of general physical prowess. Further interactions must be expected, for example through the hypothesized link between personality and coalition formation. Yet, more connections are possible and future studies should take an integrative perspective when looking at the determinants of dominance. In sum, there is no single factor that by itself explains dominance, but likely it is a suite of traits which interact with each other to determine collectively an individual's ability to achieve the optimal dominance status.

6.1 Competitive abilities

A very common assumption about dominance is (regardless of whether it is explicitly stated or not), that dominance relationships are transitive, i.e. if an individual A is dominant over B, and B is dominant over C, then it follows that A is dominant over C. This is the pattern implicit in the pecking order concept. The commonly used I&SI method adheres to this principle, i.e. it attempts to find an ordering that provides the best fit of the given data to transitivity (de Vries 1998).

Elo-rating, as a measure originally developed to quantify the performance of chess players, lacks this property, and in fact purposefully avoids the issue of transitivity by considering competitive ability not as fixed entity, but as an average around which it varies, for example due to fluctuations in motivation. Therefore, among contestants of roughly equal abilities, "the poorest player on a good day will play about as well as the best player on an off day" (Elo 1978, p. 17). The further apart these average abilities are, the less likely they are to overlap, and hence the less likely is the competitor with the smaller average ability to win an encounter.

How are these remarks relevant for the study of animal behaviour? And what, then, are competitive abilities in animals? Originally, Parker (1974, p. 225) defined resource holding power as a "measure of the absolute fighting ability of a given individual". Later, de Waal (1989, p. 246) extended this view by defining competitive ability as the "ability to claim a resource by means of force or the threat of force". Although competitive abilities are believed to reflect (at least partly) an individual's rank (e.g., Noë 1994), it is noteworthy to repeat that dominance and dominance rank are only meaningful within a dyad and a group, respectively, as they represent relationship properties. Yet, often dominance rank is treated as if it were an individual attribute even though it clearly is not (Bernstein 1981; Drews 1993). In contrast, competitive ability is an individual attribute, which theoretically could be used to predict the outcome of encounters between individuals unknown to each other (an impossible feature for dominance or dominance rank). Empirically, dominance orders and rank-orders derived from competitive abilities often correlate strongly, thereby lessening the problem somewhat (Chapter 2; Balasubramaniam et al. 2013; de Vries 1998; Bayly et al. 2006). Yet, this becomes more problematic in practice, where competitive abilities and dominance rank orders are commonly inferred from the outcomes of observed interactions, rather than measuring actual competitive abilities or dominance rank (see Chapter 1; Bernstein 1981; Bissonnette et al. 2009a).

As such, Elo-rating, as a measure of competitive ability, is similarly meaningful only within the set of individuals that were measured, although not every possible pair has had to be observed (Chapter 2). If one wanted to compare measures of competitive ability *across* groups, this were only possible if individuals migrate between groups, and therefore serve to calibrate ratings to an absolute reference. For example, if the strongest (here: highest rated) individual in one group migrates to another group and upon arrival is defeated by every individual in the new group, it can be assumed that all members of the second group have higher competitive abilities. Whether such calibration is necessary depends on the research question at hand, and possibly several migrations are necessary in order to achieve a reliable calibration. However, a further way of dealing with this issue is possible. At the level of statistical analysis, one can account for such group differences, for example by incorporating random effects into regression models, which is the approach taken in this thesis (Chapters 4 and 5). A final note on the interpretation of Elo-ratings refers to the fact that changes in competitive abilities do not necessarily correspond to rank changes in the common sense (in transitive orders, whenever an individual rises in rank, another one has to drop, see for example Chapter 5), but should rather be seen as a more precise estimate of an individual's competitive abilities.

In this respect, Elo-rating is a measure of competitive ability, from which a rank order can be inferred, yet without meeting assumptions about transitivity in relationships. As such, it provides us with information beyond those reflected in ordinal ranks. Not only does Elo-rating predict whether an individual is able to claim a resource, even more so – it predicts how likely it is that an individual can claim a resource. That being said, it might be time for a paradigm shift away from ordinal and transitive ordering systems towards using a measure of competitive ability that is probabilistic in the sense that it conveys information about the *likelihood* that an individual can monopolize a resource. Although, this might be considered a controversial proposition, yet a similar (and rewarding) change has occurred, for example, in the case of interpreting exaggerated sexual swellings of female primates. Until recently, one of the most widely accepted functions of these swelling has been that they "pinpoint the timing of ovulation" (Nunn 1999, p. 237). Nowadays however, sexual swelling are generally believed to *probabilistically* signal that ovulation has occurred (Nunn 1999; Zinner et al. 2002, 2004).

6.2 The complexity of dominance determinants

In this thesis, I used personality as an example for how individual attributes can impact male dominance careers (Chapters 3 and 4). First having suggested a personality structure, I further demonstrated that personality factors can influence future rank trajectories of male crested macaques. In contrast, I found no evidence that personality is the consequence of dominance trajectories.

Several studies have shown that personality factors can be correlated with dominance rank in primates (e.g., Mondragón-Ceballos and Santillán-Doherty 1994; Konečná et al. 2008, 2012). However, as described in Chapter 1, such correlations tell us little about the predictive value of personality for individual rank trajectories. Ergo, this thesis aimed at taking a more predictive approach by relating personality factor scores with the development of rank in the future, i.e. rank trajectories, while testing the reverse relationship as "control" condition.

The two factors with predictive value regarding future rank trajectories were connectedness and anxiety. Furthermore, these factors demonstrate to some extent the interactions between individual properties and social environment in their contribution to dominance careers, which are likely present in social primates. Both, connectedness and anxiety can be seen as describing the propensity of individual males to engage in social interactions, and with whom – even though this applies somewhat less to the anxiety factor, which mainly represents self-directed behaviour, but also the frequency with which females are approached. As such, connectedness (and to a lesser degree, anxiety), provides a link between individual characteristics and social interactions.

One way by which connectedness, through social interactions, could contribute to male dominance careers is the potential for recruiting coalition partners. In Chapter 5, I showed that coalitions impact rank trajectories of crested macaque males. However, an important parameter that remains yet to be investigated for crested macaque males is partner choice for coalitions, i.e. which males and females team up in coalitions. Combining the results of the personality and coalition studies can give us some ideas about what to expect. For instance, coalition partners are often recruited from among closely bonded individuals (e.g., Silk 1994; Schülke et al. 2010). Given that highly connected males, i.e. those males that rise in rank, have more diverse networks than little connected males, it seems that for rising males such bonds might be either absent or of little importance. Rather, it seems more likely that the strategy of males for recruiting coalition partners in order to improve their rank might be opportunistic, without the need for close bonds to facilitate cooperation in the context of coalitions. At the same time, males that do not rise as a consequence of their connectedness score (i.e. little connected males) might form close bonds as indicated by more focussed, as opposed to diverse, networks. Since these males drop in rank it can be expected that bonds, if formed, do not benefit such males in recruiting coalition partners. However, that is not to say that bonds cannot be beneficial outside the context of partner recruitment. Recent results on rhesus macaques (*Macaca mulatta*) demonstrate the potential of such bonds with regards to fitness. Kulik and colleagues (2012) showed that the strength of social bonds determined coalition formation between males and females, while at the same time males did not benefit from coalition formation in terms of future dominance rank. Crucially, the strength of bonds between males and females determined males' reproductive success (Kulik et al. 2012).

The ability to form bonds as foundation for preferential partnerships in coalitions may be further constrained by the time individuals co-reside in a group (e.g., Kulik et al. 2012). Regardless of the factors underlying migration events (reviewed in van Noordwijk and van Schaik 2004), co-residence for pairs of crested macaque males varies dramatically from just a few days to more than five years (personal observation), thus limiting the possibility to form bonds from which to recruit future coalition partners. An interesting follow-up here is the further investigation of whether newly immigrated males are able to judge the potential value of the resident males in the group, with respect to the expected co-residency. Likewise, it would be of great interest to see whether less connected males have longer residence times, because, as argued above, males with such focussed networks presumably might form bonds and could utilize coalitions to secure benefits other than positive rank trajectories. In this respect, females make better partners for social bonds given that males can rely on their continued presence in the group. However, these arguments need to be considered with caution because as of now, our data for close social bonds in crested macaques are limited to female-female bonds (Micheletta and Waller 2012; Micheletta et al. 2012).

In sum, the arguments presented so far show a possible path by which personality factors that relate to network diversity and coalition formation can interact with regard to dominance careers. Moreover, they highlight the likely importance of integrating the study of male-male relationships alongside male-female relationships. Although the influence of females on patterns of male rank acquisition is generally little studied (Raleigh and McGuire 1989; van Hooff 2000), the results of this thesis suggest that this influence indeed exists. Firstly, connectedness comprised the diversity of male and female individuals in proximity of a given male. Second, males formed coalitions with both, males and females. However, coalition consequences differed depending on whether coalitions were composed of only males (pure) or included females (mixed), and this clearly warrants further research because important confounding factors (feasibility, configuration) could not be addressed in the model investigating the effects of sex composition. Finally, a further question that arises relates to the benefits for females when participating in disputes between males. Here, it needs to be noted that the coalition study (Chapter 5) did not distinguish individual roles beyond participant and target. It remains to be seen whether females did indeed join conflicts that initially started between males, or whether conflicts originally started taking place between a female and a male, during which an additional male provided support for the female (e.g., Kulik et al. 2012). More detailed studies on social bonds, partner choice, differences between mixed and pure coalitions and patterns of support are certainly needed in order to clarify the exact extent of the complex interplay between personality and coalition formation and the prospective social consequences of how crested macaque males benefit from expressing these traits.

For the personality factor anxiety, an additional mechanism appears possible to account for differences between males in how anxiety contributes to differential rank trajectories. Anxiety, in male crested macaques, represents rates of self-directed behaviours (i.e. self-scratching and self-grooming), which is usually considered the behavioural manifestation of stress with higher rates of self-directed behaviour displayed in individuals experiencing more stress (Maestripieri et al. 1992; see also Aureli et al. 1999; for a counter example: Higham et al. 2009). Essentially, the results of this thesis show that low-anxiety males were those that rose in dominance rank, while high-anxiety males dropped. Pioneering studies by Robert Sapolsky on olive baboons (*Papio anubis*) indicated highly dynamic interactions between personality, dominance dynamics and stress hormone profiles (e.g., Sapolsky and Ray 1989; Sapolsky 1990; see also Abbott et al. 2003; Gesquiere et al. 2011). Despite high-ranking baboons generally having lower levels of cortisol than low-ranking males, Sapolsky and Ray (1989) observed substantial variation in hormone levels within high-ranking males. Those high-ranking males that showed "high degrees of social skilfulness, control, and predictability" (Sapolsky and Ray 1989, p. 12) had low cortisol levels, while males lacking these features had cortisol levels similar to those of low-ranking individuals (see also Virgin and Sapolsky 1997). While differences in methodology make it impossible to assess which olive baboon personality traits match those described here for crested macaques, it is nevertheless possible that in crested macaque males, similarly to olive baboon males, differences in personality reflect differences in the ability to cope with stress. However, it remains to be seen whether anxiety can be related to physiological markers of stress, such as faecal glucocorticoid metabolites, in crested macaque males, or whether other personality factors better reflect physiological stress in this species.

The relationship between endocrine measure of stress, personality and dominance rank is further complicated by the fact that hierarchy dynamics can reverse the relationship between rank and physiological stress. Generally, when hierarchies are stable, i.e. all relationships are settled and no challenges or changes are occurring, high-ranking individuals usually have lower glucocorticoid levels than lower-ranking individuals (Sapolsky 1983; Abbott et al. 2003; Gesquiere et al. 2011). As hierarchies become unstable (i.e. challenges and changes occur), this relationship reverses (Sapolsky 1983, 1993; but see Gesquiere et al. 2011). In this regard, the above described personalities of olive baboons are thought to provide males with additional coping mechanisms to respond to such social stressors (Sapolsky and Ray 1989). Future studies will show whether similar patterns occur in crested macaques. Given the significant effect that hierarchy stability had on future ranks following coalitions (see Tables 5.1 and 5.2), it can be tentatively assumed that the degree of stability in the hierarchy has at least some influence on the interplay between personalities, dominance rank and stress.

6.3 Other benefits of personality and coalitions

Besides the here discussed consequences in terms of rank trajectories, both personality and coalitions can affect individual fitness in other, sometimes more direct ways. As illustrated by the example of olive baboons above, one focus of animal personality research is on the (neuro-) endocrinological basis of personality dimensions (Gosling 2001; Anestis 2011). For instance, in rhesus macaques low levels of the neurotransmitter serotonin are linked with certain personality factors, such as impulsive and unrestrained aggression and risk taking (Mehlman et al. 1995; Higley et al. 1996b). Males that possess these traits show increased mortality rates during adolescence and are less likely to sire offspring (Higley et al. 1996a; Gerald et al. 2002), indicating a link between personality and fitness in this species. More recent results on female chacma baboons (*Papio h. ursinus*) further support the presence of such an endocrinological underpinning of personalities and subsequent fitness consequences in primates (see also above). For example, females scoring low on the "loner" factor (i.e. spending much time alone, being "unfriendly") excreted lower glucocorticoid metabolites and had stronger social bonds than females scoring high on this factor (Seyfarth et al. 2012). Although no direct evidence for fitness consequences is presented in this study, the authors argue for the presence of such benefits of personality given the costs of elevated glucocorticoids and the benefits of social bonds found in separate studies (Crockford et al. 2008; Silk et al. 2009, 2010; see also Goymann and Wingfield 2004).

Likewise, coalitions can provide fitness benefits via pathways other than contributing to rank. Often, the proximate strategy to monopolize access to fertile females employed by males comes in the form of mate-guarding, in which a male persistently follows a female and thereby excludes other males from access to this female (Alberts et al. 1996). In some species, males utilize coalitions to break up such mate-guarding episodes, i.e. several males cooperate to displace the mate-guarding male, thereby gaining mating and possibly reproductive benefits as a direct consequence of coalition formation (e.g., olive baboons: Bercovitch 1988; Barbary macaques, *Macaca sylvanus*: Kuester and Paul 1992; Bissonnette et al. 2011). Such levelling coalitions can be extremely effective as they can dramatically alter mating distributions as expected by male dominance rank alone (Bercovitch 1988; Alberts et al. 2003; Alberts 2012). Lastly, one additional aspect about coalitions as a means to increase mating success is the fact that age appears to be an important predictor of which males form such levelling coalitions: mostly old, post-prime males gain access to females through this strategy (Bercovitch 1988; Bissonnette et al. 2011). In sum, coalitions can be beneficial in ways other than solely increasing future rank. Likewise, the mechanisms underlying levelling coalitions further underline the importance of considering possible confounding factors (here exemplified by age) when studying reproductive strategies.

6.4 Conclusions and Outlook

The results of this thesis provide evidence for the impact of personality factors and coalition formation on dominance rank trajectories in male crested macaques. As such, these two characteristics serve as examples of both, individual traits (personality) and influences of the social domain (coalitions). Both characteristics were shown to co-vary with age, thereby illustrating the interplay between several factors, both, individual and social, in their collective impact on male careers. The complexity of traits and their interactions is highlighted by several additional traits that can be expected to contribute to male careers (social bonds, endocrine status).

With regards to the overall picture about what determines the ability to become high-ranking in crested macaque males, the most pressing issues surely relate to investigations of what determines coalition formation, i.e. whether males form bonds, and if yes, with whom? Additionally, obtaining hormone profiles of males could help to clarify the relationship between personality traits and a possible physiological basis of personality and rank trajectories. Finally, data on physical attributes, for example canine size, could help untangling general age effects from more direct measures of physical condition and fighting abilities.

In general, the results of this thesis suggest that the ability to dominate other individuals is likely not determined by one single trait only. Future studies on rank determinants should therefore keep in mind that dominance is a complex phenomenon. That being said, if we want to understand what determines rank-related reproductive skew, we need to go further than merely considering the complexity of mechanisms within a single species. Given that the benefits of high rank vary not only within but also between species, taking a comparative perspective will help us to ultimately disentangle the causes and consequences of variation in reproductive performance among individual animals.

Appendix A

Example of Elo-rating principles

To illustrate the principles of Elo-rating, it is useful to consider the basic unit of any dominance hierarchy, the dyad. In the example presented here, two individuals A and B interact through a sequence of four interactions. At the start of this sequence their competitive abilities are unknown and thus there is no knowledge of their ratings, and both A and B are assigned an initial rating of 1000. At this stage of the rating process, both individuals are expected to be equally likely to win an interaction between each other since there is not yet a higher rated individual, i.e., $p = 0.5$.

If A wins the first interaction against B, the ratings will be updated to $\mathrm{Elo}_{\mathrm{A}} = 1000 + (1 - 0.5) \times 100 = 1050$ (Equation 2.1) and $\mathrm{Elo}_{\mathrm{B}} = 1000 - (1 - 0.5) \times 100 = 950$ (Equation 2.2, Figure 2.1: Interaction 1). Individual A thus gained 50 points whereas B lost 50 points.

Given that A has won the first interaction, A is expected to win the next interaction against B with $p = 0.64$ due to the rating difference between A and B of 100 (Figure 2.1: Interaction 2, upper panel). If A wins the second interaction, ratings will be updated as follows: $\mathrm{Elo}_{\mathrm{A}} = 1050 + (1 - 0.64) \times 100 = 1086$ (Equation 2.1) and $\mathrm{Elo}_{\mathrm{B}} = 950 - (1 - 0.64) \times 100 = 914$ (Equation 2.2).

In a third interaction between A and B, the expectation of individual A winning rises to $p = 0.73$ (Figure 2.1: Interaction 3, upper panel). If A wins again, this leads to $\mathrm{Elo}_{\mathrm{A}} = 1086 + (1 - 0.73) \times 100 = 1113$ and $\mathrm{Elo}_{\mathrm{B}} = 914 - (1 - 0.73) \times 100 = 887$ (Equation 2.1 and Equation 2.2). Note that the expected probability of A winning against B increases alongside the increasing difference between A's and B's ratings, while at the same time, the amount of points won and lost by each individual decreases (50, 36, 27, respectively).

If, however, in a fourth interaction, B wins against A against the expectation (A is expected to win with $p = 0.79$), the amount of points gained and lost rises to 79, and the new ratings are $\mathrm{Elo}_{\mathrm{A}} = 1113 - 0.79 \times 100 = 1034$ (Equation 2.4) and $\mathrm{Elo}_{\mathrm{B}} = 887 + 0.79 \times 100 = 966$ (Equation 2.3, Figure 2.1: Interaction 4).

Appendix B

Details on the stability index S

The calculation of S is based on the assumption that it is justified to linearly extrapolate Elo-ratings for days during which individuals were present but not observed. Therefore, S is clearly an approximate index.

We introduced a weighing factor to account for the notion that the higher in the hierarchy a rank change occurs, the more effect such a rank change has on stability. In other words, a rank reversal among the two highest individuals will have a stronger impact on the stability index than a rank reversal between the two lowest ranking individuals.

The weighing factor w_i, by which the sum of rank changes C_i is multiplied, is the standardized Elo-rating of the highest rated individual involved in a rank change. Standardized Elo-ratings are set between 0 and 1, for the lowest and highest rated individual present on a given day, respectively. Ratings of the remaining individuals are scaled in between. Thereby the differences between standardized and original ratings are proportional to each other. A rank reversal among the two highest individuals will therefore be weighed by $w_i = 1$, whereas a rank reversal among the two lowest individuals will be weighed by a value near 0. Please note that in the latter case the value of w_i depends on the standardized Elo-rating of the second lowest rated individual and therefore does not equal 0.

Additionally, in case one individual leaves, we raised the ranks of all individuals below by one, thus defining $C_i = 0$ in such a case, given that rank changes other than those induced by one individual leaving the hierarchy did not occur.

Appendix C

R functions to calculate Elo-ratings

This section contains functions written to calculate Elo-ratings based on a supplied sequence of interactions (“`elo.single`”, “`elo.sequence`”). Additionally, functions are provided to extract Elo-ratings from specific individuals and/or dates (“`elo.extract`”). Finally, a function is provided to create figures akin to those presented in (“`elo.plot`”), and to calculate the stability index *S* (“`stability.index`”). Lines starting with a hashmark (#) denote comments with respect to the presented R code.

```
elo.single <-
function(ELO1old, ELO2old, outcome, constant_k=100) {

  # outcome must be one of the following:
  # "1" = first individual wins and second looses
  # "2" = second individual wins and first looses
  # "0" = interaction ends in a draw/tie (no winner and no looser)

  # make sure ELO ratings are given as numerics
  ELO_1 <- as.numeric(as.character(ELO1old))
  ELO_2 <- as.numeric(as.character(ELO2old))

  # calculates the difference between the two ratings
  ELO_diff <- (ELO_1 - ELO_2)

  # z score based on fixed SD=200 (see Elo 1978)
  z_score <- ELO_diff/(200*sqrt(2))

  # calculates the winning probabilty
  p_win <- pnorm(z_score)

  # product of winning probabilty and k-factor
  kp <- constant_k * p_win

  # the actual updating calculations
  if(outcome==1) { ELO1new <- ELO_1 - kp + constant_k
                   ELO2new <- ELO_2 + kp - constant_k }
  if(outcome==2) { ELO1new <- ELO_1 - kp
                   ELO2new <- ELO_2 + kp }
```

```
  if(outcome==0) { ELO1new <- ELO_1 - kp + 0.5 * constant_k
                   ELO2new <- ELO_2 + kp - 0.5 * constant_k }

  # returning the updated ratings
  return(round(c(ELO1new, ELO2new), 0))
}

#---------------------------------------------------------------

elo.sequence <-
function(datafile = "d:\\ESM example data.xls", XLSsheet = "Albers_
   deVries2001", startingvalue = 1000, constant_k = 200){

  # 'datafile' : the path and file name of the excel data file with
     the interaction data
  # 'XLSsheet' : the worksheet name of the excel data file given
     above
  # 'startingvalue' : the amount of points each individual has at
     the beginning of the rating process (default is 1000, see
     example in Albers and de Vries, 2001)
  # 'constant_k' : specify the amount your constant 'k' should take
     (default is 200, see example in Albers and de Vries, 2001)

  # loads the package that is necessary to open excel files in R
  library(xlsReadWrite)

  # reads the data file into the R workspace
  IA_data <- read.xls(datafile, sheet = XLSsheet , colClasses=c("
     isodate", "isotime", "character", "character"))
  IA_data[, 1] <- as.Date(IA_data[, 1])

  # assembles all individuals that are present in the data sheet
  all_ids <- unique(c(as.character(IA_data$Winner), as.character(IA_
     data$Loser)))

  # create a temporary table with the most recent Elo rating of each
      individual throughout the following loop
  currentELO <- rep(startingvalue, length(all_ids))
  names(currentELO) <- all_ids

  # creating the table, in which the new ratings after each
     encounter are saved (the first values equal the initial values
     that were defined in the step above)
  log_table <- as.data.frame(matrix(ncol=4, nrow=(length(IA_data[,
     1]) * 2 + length(all_ids))))
  colnames(log_table) <- c("IA_no", "ID", "Date", "elo")
  log_table[, 2] <- as.character(log_table[, 2])

  # the first (starting) values are now filled into first rows of
     the table (depending on the number of individuals)
  # interaction no. '0'
  log_table[1:length(all_ids), 1] <- 0
  log_table[1:length(all_ids), 2] <- as.character(all_ids)
  # formatting the Date column
  class(log_table$Date) <- "Date"
  # the starting value of the Elo rating process (e.g. 1000)
```

```
  log_table[1:length(all_ids), 4] <- currentELO

  # this is the actual loop that calculates the new Elo-ratings
     after each interaction and adds them into the 'log_table', and
     also keeps the 'currentELO' table updated
  for(i in 1:length(IA_data[,1])) {
    # makes sure the IDs are formatted as character strings
    cont1 <- as.character(IA_data$Winner[i])
    cont2 <- as.character(IA_data$Loser[i])

    # calculates the new ratings for the two interacting individuals
    log_table[(length(all_ids) + (2 * i - 1)):(length(all_ids) + (2
       * i)), 4] <- as.numeric(elo.single(currentELO[which(names(
       currentELO)==cont1)],
    currentELO[which(names(currentELO)==cont2)], outcome=1, constant
       _k=constant_k))

    # fills the respective date of the interaction
    log_table[(length(all_ids) + (2 * i - 1)):(length(all_ids) + (2
       * i)), 3] <- as.Date(IA_data$Date[i])

    # fills the IDs of the two interacting individuals
    log_table[(length(all_ids) + (2 * i- 1)):(length(all_ids) + (2 *
        i)), 2] <- c(cont1, cont2)

    # count of the interaction
    log_table[(length(all_ids) + (2 * i- 1)):(length(all_ids) + (2 *
        i)), 1] <- i

    # updates the 'currentELO' table with the above calculated
       ratings of the two interacting individuals
    currentELO[which(names(currentELO)==cont1)] <- log_table[(length
       (all_ids) + (2 * i - 1)), 4]
    currentELO[which(names(currentELO)==cont2)] <- log_table[(length
       (all_ids) + (2 * i)), 4]

    # end of the loop
  }

  # returns a table with all ratings
  return(log_table)
}

#-----------------------------------------------------------------

elo.extract <-
function(Elotable, extractDate, individuals = "all"){

  # returns the ratings that each individual had on the specified
     date
  # if ratings were not updated on the specified date, the most
     recently updated values are given
  # along comes the information on how long ago (in days) the rating
      was last updated
  # if individuals were not yet rated on the specified date, their
     ratings (i.e. their starting values) will be omitted from the
```

```
     output
  # 'Elotable' : an object resulting from the function 'Elo_rating'
  # 'extractDate' : the date on which you want to obtain the ratings

  # if not 'all' is selected as the individuals from which the
     ratings are to be obtained, here the specified individuals are
     incorporated
  ifelse( individuals=="all",
    IDs <- sort(unique(as.character(Elotable[, 2]))), # obtains all
       individual IDs that appear in the data
    IDs <- individuals) # otherwise, the IDs are used that were
       specified in the function call under 'individuals = ...'

  # makes sure the date is correctly formatted
  extractDate <- as.Date(extractDate)

  # creates the table in which the results will be presented
  resultstable <- as.data.frame(matrix(ncol=3, nrow=length(IDs)))
  resultstable[, 1] <- IDs

  # checks for every ID the Elo points on the date specified
  for (i in 1:length(IDs)) {
    temp <- Elotable[Elotable[, 2]==IDs[i], ]
    temp <- temp[temp[, 3] <= extractDate, ]
    resultstable[i, 2] <- temp[length(temp[, 1]), 4]
    resultstable[i, 3] <- temp[length(temp[, 1]), 3] - extractDate #
        calculating the offset, i.e. how "old" is the rating
  }

  # adds names to the results table
  names(resultstable) <- c("ID", "Elo", "offset")

  # sorts the results table by ratings (highest on the top)
  resultstable <- resultstable[order(resultstable$Elo, decreasing=T)
     , ]

  # clears the rownumbers
  rownames(resultstable) <- NULL

  # returns the results table
  return(resultstable)
}

#---------------------------------------------------------------

elo.plot <-
function(Elotable, daterange = c("2010-01-01", "2010-02-02"),
   individuals = "present"){

  # creates a graph of the specified individuals across the selected
      date range
  # 'Elotable' : an object resulting from the function 'Elo_rating'
  # 'daterange' : the time range the graph covers
  # 'individuals' : specify the individuals that should appear in
     the graph, one of two options can be used here:
```

```
# 1) individuals = "present" : selects those individuals that were
     present (i.e. for which data is available) in the specified
    date range (is the default setting)
# 2) individuals = "..."

# if an individual had more than one interaction on a given day,
    the ratings of that day are averaged
Elotable <- aggregate(Elotable[, 4], by=list(Elotable[, 2],
    Elotable[, 3]), median)

# opens a graphic device for plotting, possibly Windows specific
    and might need adjustment for Mac and/or Linux
windows(12, 6)

# creates a layout with two 'fields' for the plot: the bigger one
    is for the actual plot, the smaller one is for the legend
layout(matrix(1:2,1), widths=c(8, 1))

# makes sure that the dates are correctly formatted as dates
daterange <- as.Date(daterange)

# if not 'present' is selected as the individuals to be plotted,
    here the specified individuals are incorporated
ifelse( individuals=="present",
  # obtains all individual IDs that appear in the data within the
      selected date range
  IDs <- sort(unique(as.character(Elotable[which(Elotable[,2] >=
      daterange[1] & Elotable[,2] <= daterange[2]), 1]))),
  # otherwise, the IDs are used that were specified in the
      function call under 'individuals = ...'
  IDs <- individuals)

# sets the symbols that will be used for plotting (a total of five
     different symbols; if more than five individuals, different
    colours will be used [see next step])
chars <- rep(21:25, ceiling(length(IDs)/5))[1:length(IDs)]

# sets the colors of the symbols that will be used for plotting
cols <- sort(rep(heat.colors(ceiling(length(IDs)/5)), 5))[1:length
    (IDs)]

# sets the range for the y-axis of the plot to be created
yrange <- range(Elotable[, 3])

# plotting the axes of the graph
plot(daterange, yrange, type="n", xlab="Date", ylab="Elo Rating",
    las=1)

# prints the lines for each individual of its Elo ratings on a
    given date as a function of the date
for(i in 1:length(IDs)) {
  lines(Elotable[which(Elotable[, 1]==IDs[i]), 2], Elotable[which(
      Elotable[, 1]==IDs[i]), 3], lty=3)
}
```

```
  # prints a point for each interaction an individual had on top of
     the line
  for(i in 1:length(IDs)) {
    points(Elotable[which(Elotable[, 1]==IDs[i]), 2], Elotable[which
        (Elotable[, 1]==IDs[i]), 3], pch=chars[i], bg=cols[i])
  }

  # creates a legend to right of the plot
  par(mar=c(0,0,0,0))
  plot(1:10, 1:10, type="n", axes=FALSE, xlab="")
  legend(1, 9, legend=IDs, pch=chars, pt.bg=cols, bty="n")

}

#---------------------------------------------------------------

stability.index <-
function(Elotable, startdate="2010-01-02", duration=30) {

  elo.fill <-
  function(ratings) {
    # for each individual Elo ratings for days without observation
       are interpolated
    # bases are the ratings last known and nearest in the future
    # intermittent ratings are calculated with linear regression
       from these ratings on the number of days without ratings
    # e.g., day1 = 1000, day2 = NA, day3 = NA, day4 = 1030, then the
        new ratings for day2 and 3 are 1010 and 1020, respectively

    # remove leading and trailing 'NA'
    # how many NAs leading and trailing?
    firstENTRY <- min(which(ratings != "NA")); lastENTRY <- max(
       which(ratings != "NA"))
    TOTAL <- length(ratings)
    ratings <- ratings[firstENTRY : lastENTRY]

    while(length(which(is.na(ratings))) > 0) {

      firstNA <- which(is.na(ratings))[1]
      NAS <- firstNA
      m <- 1
      while(is.na(ratings[firstNA + m])) { NAS <- c(NAS, firstNA + m
         ); m <- m + 1 }

      X <- c(firstNA - 1, firstNA + m)
      Y <- c(ratings[(firstNA - 1)], ratings[firstNA + m])
      NEW <- data.frame(X = NAS)

      ratings[NAS] <- round(as.numeric(predict(lm(Y ~ X), NEW, se.
         fit = TRUE)$fit),0)
    }

    # adding the original leading and trailing NAs
    if(firstENTRY != 1) ratings <- c(rep(NA, firstENTRY -1), ratings
       )
```

```
  if(lastENTRY != TOTAL) ratings <- c(ratings, rep(NA, TOTAL -
     lastENTRY))

  return(ratings)
}

elo.stdz <-
function(ratings) {

  # subfunction to calculate standardized ratings, used for
     weighing the stability index
  # standardized ratings range between 0 (for the individual with
     the lowest rating) and 1 (for the individual with the highest
      rating on the given day)
  ratings <- ratings - min(ratings, na.rm=TRUE)
  return(round(ratings/max(ratings, na.rm=TRUE), 3))
}

elo.daily <-
function(Elotable) {

  # creates a table with estimated ratings on days on which an
     individual was not observed

  MyElo <- Elotable

  AllIDs <- unique(c(MyElo$ID))
  MyElo <- MyElo[(length(AllIDs) + 1) : length(MyElo[, 1]), ]
  AllIDs <- unique(c(MyElo$ID))

  # reduction to one value per day and individual (median)
  MyElo <- aggregate(MyElo[, 4], by=list(MyElo[, 2], MyElo[, 3]),
     median)
  colnames(MyElo) <- c("ID", "Date", "Elo")

  # creating a table with the dates of first and last observed
     interaction for each ID
  First <- AllIDs ; Last <- AllIDs

  for(ID in AllIDs){
    temp <- which(MyElo$ID == ID)
    First[First==ID] <- as.character(MyElo[min(temp), 2])
    Last[Last==ID] <- as.character(MyElo[max(temp), 2])
  }

  MinMaxDates <- data.frame(AllIDs, as.Date(First), as.Date(Last))
     ; colnames(MinMaxDates) <- c("ID", "First", "Last"); rm(temp,
      First, Last, ID)

  # if there are individuals with only one observation (i.e. min =
      max date), this ID(s) are removed here (and from further
     evaluation)
  ZEROS <- which(MinMaxDates$First==MinMaxDates$Last)
  if (length(ZEROS) > 0) MinMaxDates <- MinMaxDates[-c(ZEROS),]
  rm(ZEROS)
```

```
  AllIDs <- as.character(MinMaxDates[,1])

  ALLDATES <- seq(min(MinMaxDates$First), max(MinMaxDates$Last), "
     day")

  MAT <- as.data.frame(matrix(ncol=length(AllIDs)+1, nrow=length(
     ALLDATES)))
  class(MAT[,1]) <- "Date"
  MAT[,1] <- as.Date(ALLDATES)
  colnames(MAT) <- c("Date", AllIDs)

  for(i in 1:length(MyElo[,1])) {

    MAT[which(MAT[,1] == MyElo[i,2]), MyElo[i,1]] <- MyElo[i,3] };
        rm(i)

    # generating intermediate values (estimating Elo ratings on
       days without observed interaction)
    for(ID in AllIDs) {

      tempRatings <- MAT[,ID]
      MAT[,ID] <- round(elo.fill(tempRatings),0)
    }

  return(MAT)
}

# create a matrix with the linearly interpolated ratings so that
   each individual gets a rating each day
dailymat <- elo.daily(Elotable)

stability.indexA <-
function(dailyratingmatrix) {
  # a function to calculate rankings for each day, and based on
     those rankings obtain the number of rank changes between two
     consecutive days
  drm <- dailyratingmatrix

  # get the IDs of all individuals present in the data
  AllIDs <- colnames(drm)[2:length(colnames(drm))]

  # create empty vectors for the three variables of interest
  rankdiffs <- c(); Idspresent <- c(); eloweights <- c()

  # this loop calculates Ci for each day (except for the first one
     )
  for(u in 2:(length(drm[, 1]))) {

    # calculates the ranks the day before the actual day
    r1 <- rank(drm[u-1, 2:(length(AllIDs)+1)] * (-1), na.last = NA
       , ties.method = c("average"))

    # calculates the ranks on the test day
    r2 <- rank(drm[u, 2:(length(AllIDs)+1)] * (-1), na.last = NA,
       ties.method = c("average"))
```

```
    # which IDs were present on both days
    present <- c(names(r1), names(r2))[duplicated(c(names(r1),
       names(r2)))]

    # if one animal leaves, the index increases the ranks of all
       individuals below, i.e. if no other rank change occurs, the
        rank difference will be zero in such a case
    if(length(r1) > length(r2)) {
      leavers <- names(which(table(c(names(r1), names(r2))) == 1))
      for(n in 1:length(leavers)) {
        r1[which(r1 > r1[leavers[n]])] <- r1[which(r1 > r1[leavers
           [n]])] - 1
      }
      r1 <- r1[-c(which(names(r1) %in% leavers))]
    }

    # calculate the weights of change (if there is none, the
       weight is '0')
    standardratings <- elo.stdz(drm[u - 1, present])
    changers <- r1[r1[present] != r2[present]]
    stabweight <- 0
    if(length(changers) > 0) {
      stabweight <- as.numeric(standardratings[names(changers)[
         changers==min(changers)][1]])
      rm(changers)
    }

    # calculate the sum of the absolute differences in the two
       rankings
    rankdiffs <- c(rankdiffs, sum(abs(r2[present] - r1[present])))

    # how many individuals were present on both days
    Idspresent <- c(Idspresent, length(present))

    # the standardized elo rating of the highest rated individual
       involved in a rank change
    eloweights <- c(eloweights, stabweight)
    rm(stabweight, present, r2, r1)

  } # end of loop through dailyratingmatrix

  # the first day of the entire (!) date range is excluded because
      no stability can be assessed (no data for the day before...)
  results <- data.frame(drm[2 : (length(drm[,1])), 1], rankdiffs,
     Idspresent, eloweights)
  colnames(results) <- c("Date", "Rank.Differences", "IDs.present"
     , "weight")

  return(results)
}

step1 <- stability.indexA(dailymat)
ST <- startdate; DUR <- duration

stability.indexB <-
function(dailystab, startdate=NULL, duration=NULL) {
```

```
    # sums the rank differences over the specified duration, then
       sums the IDs present over the same period, and gives the
       ratio of the sum of rank differences (after they have been
       multiplied by the day’s weighing factor) and IDs present, i.e
       . the stability index S
    startline <- which(dailystab[, 1] == as.Date(startdate))
    LINES <- startline : (startline + duration - 1)

    results1 <- data.frame(sum(dailystab[LINES, 2]), sum(dailystab[
       LINES, 3]), round(sum(dailystab[LINES, 2] * dailystab[LINES,
       4]) / sum(dailystab[LINES, 3]), 3))

    names(results1) <- c("rank.differences", "IDs.present", "
       stability.index")

    return(results1)

  }

  step2 <- stability.indexB(step1, ST, DUR)

  return(step2)
}
```

Appendix D

Manual to calculate Elo-ratings

In this manual, we will describe how to calculate Elo ratings and to create simple graphics with the provided scripts. First, there are some general notes, followed by a worked example (data in Appendix E) and last we include some information to apply the scripts to your own data.

D.1 Before starting

The scripts supplied are working in R, which is a free software environment for statistical computing. It can be downloaded from `http://cran.r-project.org/`.

D.1.1 Requirements for R

Once you have a working R environment, there is one additional R package that needs to be installed if you would like to use data prepared in MS Excel. You can download "xlsReadWrite" from `http://stat.ethz.ch/CRAN/web/packages/xlsReadWrite/index.html` (or use the command

```
install.packages("xlsReadWrite")
```

in R directly. This package allows reading Excel files directly into R.

D.1.2 Getting the functions

The functions are supplied in the accompanying text file. To make the functions available in R just paste the entire content of the text file into R, or use the command

```
source("d:\\Elo_rating_ESM 01 R functions.txt")
```

where the text file is saved in the root directory of drive D. Alternatively, copy the functions (supplied in Appendix C) into the clipboard, and paste them into the active R workspace. The command `ls()` should then include the following five entries:

```
> ls()
[1] "elo.extract" "elo.plot" "elo.sequence" "elo.single"
    "stability.index"
```

D.1.3 Testing the functions

If you wish to proceed directly to the example you can skip this section.

We use the calculation example provided by Albers and de Vries (2001). That is, if two individuals A and B with Elo ratings of Elo_A=1200 and Elo_B = 1000 interact and A wins this interaction, the new ratings should be Elo_A = 1224 and Elo_B = 976. Type in R:

```
elo.single(ELO1old = 1200, ELO2old = 1000, outcome = 1, constant_k
   = 100)
```

[the first two numbers represent the Elo ratings of the two individuals, the third number indicates the outcome of the interaction (1 = first individual won, 2 = second individual won, 0 = interaction ended in a draw/tie), and the fourth number represents the constant *k* (see Albers and de Vries, 2001, by default set to 100)]
should result in:

```
[1] 1224 976
```

where the first number is the updated rating of the individual specified first in the function call above, and the second number is the updated rating of the individual specified second.

Likewise, typing the same interaction in a different way:

```
elo.single(ELO1old = 1000, ELO2old = 1200, outcome = 2, constant_k
   = 100)
```

should give the same result in reversed order (even though the actual interaction was the same):

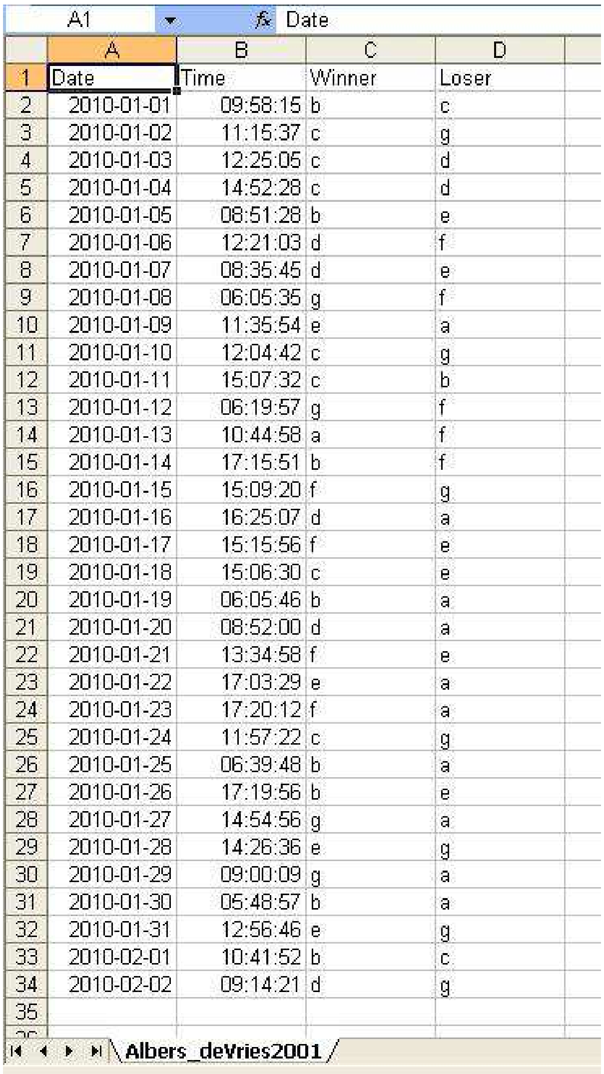
```
[1] 976 1224
```

If you get these results, everything seems to be working so far.

D.2 A worked example

D.2.1 Calculating ratings from an interaction sequence

We will now present a guide through the script as applied to an exemplary data set that is published in Albers and de Vries (2001). For the script to work, you need to create an xls-file (for example in Excel) that resembles Figure D.1. The data are supplied in Appendix E. The data sheet contains 33 interactions between seven individuals, labelled “a” – “g”. The sequence of the interactions is identical to the sequence as presented in Albers and de Vries (2001). Winners and losers are noted in the respective columns. We arbitrarily added dates and times (corresponding to the original sequence), as this addition makes the data set somewhat more realistic (see Figure D.1).



	A	B	C	D
1	Date	Time	Winner	Loser
2	2010-01-01	09:58:15	b	c
3	2010-01-02	11:15:37	c	g
4	2010-01-03	12:25:05	c	d
5	2010-01-04	14:52:28	c	d
6	2010-01-05	08:51:28	b	e
7	2010-01-06	12:21:03	d	f
8	2010-01-07	08:35:45	d	e
9	2010-01-08	06:05:35	g	f
10	2010-01-09	11:35:54	e	a
11	2010-01-10	12:04:42	c	g
12	2010-01-11	15:07:32	c	b
13	2010-01-12	06:19:57	g	f
14	2010-01-13	10:44:58	a	f
15	2010-01-14	17:15:51	b	f
16	2010-01-15	15:09:20	f	g
17	2010-01-16	16:25:07	d	a
18	2010-01-17	15:15:56	f	e
19	2010-01-18	15:06:30	c	e
20	2010-01-19	06:05:46	b	a
21	2010-01-20	08:52:00	d	a
22	2010-01-21	13:34:58	f	e
23	2010-01-22	17:03:29	e	a
24	2010-01-23	17:20:12	f	a
25	2010-01-24	11:57:22	c	g
26	2010-01-25	06:39:48	b	a
27	2010-01-26	17:19:56	b	e
28	2010-01-27	14:54:56	g	a
29	2010-01-28	14:26:36	e	g
30	2010-01-29	09:00:09	g	a
31	2010-01-30	05:48:57	b	a
32	2010-01-31	12:56:46	e	g
33	2010-02-01	10:41:52	b	c
34	2010-02-02	09:14:21	d	g
35				

Figure D.1: Data layout necessary for the R functions to work.

We assume you saved the example file as “example data.xls” in the root directory of drive D and that the worksheet containing the data set is named “AlbersdeVries2001”. Using the call

```
elo.sequence(datafile = "d:\\example data.xls", XLSsheet =
    "AlbersdeVries2001", startingvalue = 1000, constant_k = 200)
```

will return a table that contains all interactions and the new Elo ratings AFTER the respective interaction. The first seven lines (according to seven individuals in the data set in this example) represent the starting Elo values (set to 1000 in the example). Each single interaction is then represented by two lines: one for each involved individual. Here, for example, individual “b” won against “c” in the first interaction. The resulting new values (1100 and 900) can be found in lines 8 and 9 of the log table.

```
   IA_no ID       Date  elo
1      0  b       <NA> 1000
2      0  c       <NA> 1000
3      0  d       <NA> 1000
4      0  g       <NA> 1000
5      0  e       <NA> 1000
6      0  a       <NA> 1000
7      0  f       <NA> 1000
8      1  b 2010-01-01 1100
9      1  c 2010-01-01  900
10     2  c 2010-01-02 1028
11     2  g 2010-01-02  872
...
24     9  e 2010-01-09  988
25     9  a 2010-01-09  860
26    10  c 2010-01-10 1216
27    10  g 2010-01-10  920
28    11  c 2010-01-11 1304
29    11  b 2010-01-11 1084
30    12  g 2010-01-12  978
31    12  f 2010-01-12  706
...
```

For purposes of easier managing in the following examples we save this table in a new object named `MyEloTable` by calling:

```
MyEloTable <- elo.sequence(datafile = "d:\\example data.xls",
    XLSsheet = "AlbersdeVries2001", startingvalue = 1000, constant_k
    = 200)
```

D.2.2 Getting ratings on a specific date

If you are now interested in the Elo ratings at a specific date, the function `elo.extract` can be used. In the example we used here, all interactions took place between 1 January 2010 and 2 February 2010. If one is interested in the ratings and the hierarchy at the end of the observation period, i.e. on February 2nd, type in R:

```
elo.extract(Elotable = MyEloTable, extractDate = "2010-02-02",
    individuals = "all")
```

[where \`MyEloTable`" is the above described table with the Elo ratings after each interaction; and `"2010-02-02"` is the date from which we wish to obtain the Elo ratings. If not otherwise specified, all individuals present in your data will appear in the resulting table]

will result in the following table:

```
  ID  Elo offset
1  b 1320     -1
2  c 1184     -1
3  d 1178      0
4  f 1048    -10
5  e 1008     -2
6  g  732      0
7  a  530     -3
```

In this table you can see for all individuals the ratings on the specified date. The last column gives the information on "how old" the data point is. In the example here, individuals "d" and "g" interacted on the same day the ratings were obtained (the offset is "0"), whereas "b" and "c" interacted the day before (the offset is "–1"). The last observed interaction of "f" was ten days prior the specified date (the offset is "–10") and thus "f"'s Elo rating is "ten days old"

The individuals presented in the results can be limited by specifying particular IDs in the call to the function `elo.extract`. If we are interested in the ratings of 'a', 'b', 'd' and 'e' on 5 January, typing:

```
elo.extract(Elotable = MyEloTable, extractDate = "2010-01-05",
    individuals = c("a", "b", "d", "e"))

  ID  Elo offset
1  b 1172      0
2  e  928      0
3  d  863     -1
4  a   NA     NA
```

Please note that during the first five interactions (i.e. between 1 and 5 January) individual "a" was not involved in any observed interaction and hence the rating of "a" is not known and thus omitted (represented as \`NA`" ["not available".])

D.2.3 Visualizing Elo-ratings

`elo.plot` is a basic function to visualize the ratings over time. Typing:

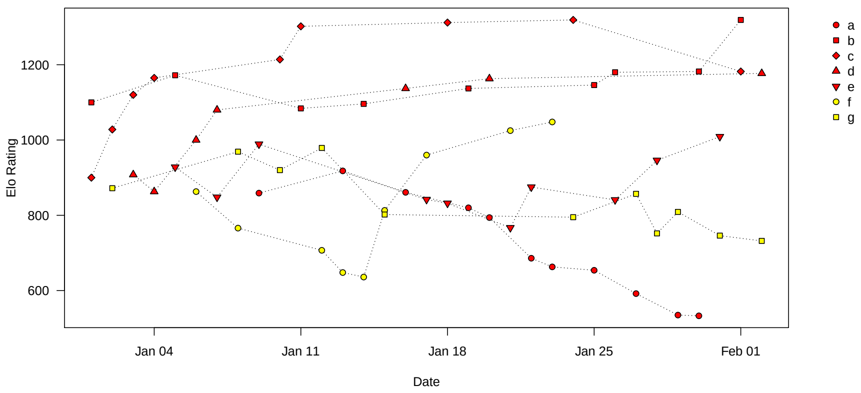


Figure D.2: Elo-ratings over time from seven individuals.

```
elo.plot(Elotable = MyEloTable, daterange = c("2010-01-01",
    "2010-02-02"), individuals = "present")
```

[where ‘MyEloTable’ is the above-described table with the Elo-ratings after each interaction; and c(”2010-01-01”, ”2010-02-02”)is the date range to be plotted. If not otherwise specified, all individuals present in the specified date range will appear in the resulting plot]

will result in a figure similar to Figure D.2.

In Figure D.2, each symbol represents one interaction in which a given individual was involved. Since we prepared the data in a way that exactly one interaction occurs each day, there are exactly two data points in the plot each day representing the updated ratings of the two interacting individuals. In a data set based on real observations, there may be more than one interaction of a specific individual on a given day. In such a case, the ratings will be averaged over that day. As such, per day there will be one (averaged) data point per interacting individual.

The figure resembles Figure 1 from Albers and de Vries (2001) with some changes:

- the X axis is a timescale whereas in Albers and de Vries’s paper the actual interactions are depicted;
- ratings do not originate graphically at the starting point 1000 at the beginning of the interaction sequence and do not extend to the end of the sequence for all individuals.

Analogously to the `elo.extract` function, if one is interested only in the ratings of a subset of individuals and/or a different time window, you can adjust the call to `elo.plot`, for example, Figure D.3 can be generated with:

```
elo.plot(Elotable = MyEloTable, daterange = c("2010-01-10",
    "2010-01-20"), individuals = c("c", "f", "g"))
```

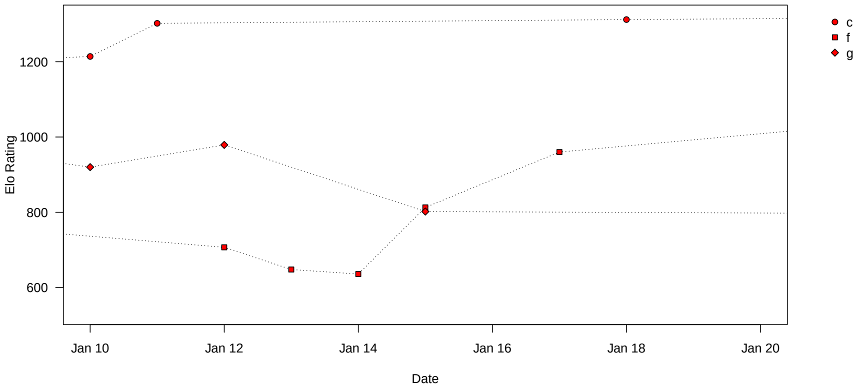


Figure D.3: Elo-ratings over time from three individuals during a subset of the observation time.

D.2.4 Calculating the stability index *S*

Last, we show how to obtain an index to describe the stability of a hierarchy. This function is made up of several subfunctions, which for ease of use we wrapped into one.

```
stability.index(Elotable = MyEloTable, startdate="2010-01-02",
    duration=30)
```

where `"MyEloTable"` is once more the above-described table with the Elo-ratings after each interaction; and `"2010-01-01"` is the date from which S is to be calculated for a duration of 30 days. The output of this call is:

```
  rank.differences IDs.present stability.index
1               41         181           0.088
```

Again, the function allows specification of the desired date range:

```
stability.index(MyEloTable, startdate="2010-01-10", duration=7)
```

```
  rank.differences IDs.present stability.index
1               16          49           0.124
```

D.3 Your own data

D.3.1 Preparation of the data sheet

We assume data were prepared in a Microsoft Excel 2003 spreadsheet. An example file is provided with the data from Albers and de Vries (2001). You may want to use this file as a template for your data by entering your data directly into this sheet. Of course you can create your data sheet yourself. However, ensure that data files are set up analogously to the figure above, i.e. the NAMES and ORDER of the columns must be identical to those seen in the example file.

Also, at this stage it is crucial that you put your interactions in the correct sequence in your data sheet. The oldest interactions must be at the top of the file, whereas the most recent interaction must appear at the bottom of the file.

The columns of the file are in detail:

1. Date: use the following format YYYY-MM-DD [**obligatory**];
2. Time: the 'time' column is merely to help put the interactions in the correct order if there was more than one interaction on a given date; preferred format is HH:MM:SS;
3. Winner: the ID of the winning individual in the given interaction [**obligatory**];
4. Loser: the ID of the losing individual in the given interaction [**obligatory**].

To summarize, these are the assumptions that need to be fulfilled by your data (sheet).

- The sequence of interactions in your data file needs to be correct.
- There is a winner and a loser in each interaction.
- Column names are 'Date', 'Time', 'Winner' and 'Loser' (first letter capitalized!)

Remove spaces and special characters [!, $, %, &, (,), ?, …] from the IDs you use for your individuals, e.g. use '_' [under dash] as spacing character instead of blank space.

There may be future extensions to the functions provided here. For updates and questions please email cneumann@dpz.eu.

Appendix E

Example data to calculate Elo-ratings

The data in Table E.1 are fictional dominance interactions adapted from Albers and de Vries (2001) and serve as an example with which Elo-ratings can be calculated (see Appendix D).

Table E.1: Example data to calculate Elo-ratings

Date	Time	Winner	Loser
2010-01-01	12:10:00	b	c
2010-01-02	13:10:00	c	g
2010-01-03	14:10:00	c	d
2010-01-04	15:10:00	c	d
2010-01-05	16:10:00	b	e
2010-01-06	17:10:00	d	f
2010-01-07	18:10:00	d	e
2010-01-08	19:10:00	g	f
2010-01-09	20:10:00	e	a
2010-01-10	21:10:00	c	g
2010-01-11	22:10:00	c	b
2010-01-12	23:10:00	g	f
2010-01-13	00:10:00	a	f
2010-01-14	01:10:00	b	f
2010-01-15	02:10:00	f	g
2010-01-16	03:10:00	d	a
2010-01-17	04:10:00	f	e
2010-01-18	05:10:00	c	e
2010-01-19	06:10:00	b	a
2010-01-20	07:10:00	d	a
2010-01-21	08:10:00	f	e
2010-01-22	09:10:00	e	a
2010-01-23	10:10:00	f	a
2010-01-24	11:10:00	c	g
2010-01-25	12:10:00	b	a
2010-01-26	13:10:00	b	e
2010-01-27	14:10:00	g	a
2010-01-28	15:10:00	e	g
2010-01-29	16:10:00	g	a
2010-01-30	17:10:00	b	a
2010-01-31	18:10:00	e	g
2010-02-01	19:10:00	b	c
2010-02-02	20:10:00	d	g

Appendix F

Details on methods and results for Chapter 4

F.1 Study subjects and site

We studied 37 males of two wild groups of crested macaques (*Macaca nigra*), groups R1 and PB, living in the Tangkoko Nature Reserve, Sulawesi, Indonesia (Neumann et al. 2010; Duboscq et al. 2013). Data collection took place between March 2009 and May 2011. The two groups comprised up to 85 individuals each, with 7 – 18 adult males present (see Chapter 2 for details). All animals were completely habituated to human observers and adults were individually recognizable based on facial features and body markings, e.g., scars or broken limbs.

F.2 Personality assessment

Here, we briefly summarize how we determined the personality structure of male crested macaques. A detailed description of this assessment can be found in Chapter 3.

Behavioral data to quantify personality were collected using focal animal and scan sampling (Altmann 1974) of 37 adult males (mean = 66.1h, range = 0.6 – 130.0h per male). During 60 minute focal protocols, we collected data on a range of specific behaviors (socio-positive, agonistic and positional) and noted identities of other adults in spatial proximity of focal subjects. Data were collected by four observers and inter-observer reliability of the observed behaviors ranged between 0.75 and 1.00 as assessed by Pearson correlation coefficient and Cohen's kappa (Martin and Bateson 1993). Factor analysis revealed four distinct and unrelated factors, anxiety, connectedness, sociability, and aggressiveness.

We additionally conducted two playback experiments on 18 of our focal males, to assess boldness and neophilia. Boldness was assayed by presenting subjects with a dog bark bout (threat to test animals) and neophilia was measured as the reaction to a donkey bray (unknown to test animals). We analyzed a total of 39 ($N = 17$ males) and 42 ($N = 16$ males) experimental trials in the dog and donkey condition, respectively. Reactions of subjects to playback presentations were recorded on video. All videos were coded by two raters (Pearson correlation: $r = 0.92$). We quantified "orientation to the speaker", which is a composite measure of looking and approaching the speaker

(Micheletta and Waller 2012). Reactions to the dog, but not the donkey, treatment were repeatable (c.f. Nakagawa and Schielzeth 2010). We therefore considered only boldness to represent a personality factor in crested macaques.

F.3 Data analysis

In this study, we model the relationship between five previously described personality factors (anxiety, connectedness, sociability, aggressiveness and boldness) and dominance status. For the four observationally assessed factors we created two-month time blocks for which we extracted regression scores from the factor solution for each male. We discarded time blocks for which the cumulative observation time was less than six hours. In this way we obtained 190 data points for each personality trait comprising 30 males (median = 6.5, range 1 – 11 data points, i.e. time blocks, per male). To be able to obtain repeated personality factor scores for each male, we used a factor solution that was based on this data set ($N = 190$), contrasting with our original analysis where we used a single data point per male (i.e. $N = 30$) as basis for the factor analysis. Overall, the factors extracted with both approaches were judged similar based on the congruence coefficient $\phi = 0.82$ ($p < 0.001$, c.f. Abdi 2010) and Pearson correlation coefficients between factor loadings of the two solutions (anxiety: $r = 0.94$, $p < 0.001$; connectedness: $r = 0.87$, $p < 0.001$; sociability: $r = 0.57$, $p = 0.018$; aggressiveness: $r = 0.81$, $p < 0.001$; all $N = 17$). To model the Boldness factor we used individual responses to the playback treatments (Chapter 3), resulting in 39 data points from 17 males (median = 2, range 1 – 3 playback responses per male).

We ran two sets of linear mixed models to investigate (1) whether personality factors can be predicted from past dominance status and (2) whether personality factors predict future dominance status. In (1) the response variable is the personality factor score and including our predictor of interest (past status) alongside the control variable current rank might lead to collinearity in these models. We therefore decided to use status differences, i.e. current status – past status, instead of raw status scores as predictor in (1). To facilitate comparison between the model sets we used an analogue approach for (2), i.e. we modeled the response future status – current status. In all ten models (2 * 5 personality factors) we controlled for current dominance status and male age (three-level age factor: young, middle, old). For the two Boldness models, we also incorporated trial number as predictor variable to account for possible habituation effects (Chapter 3).

To assess dominance status we used Elo-rating (Chapter 2; Elo 1978; Albers and de Vries 2001). Elo-rating sequentially updates dominance ratings after each single dominance interaction between two males. The change in ratings after each interaction is determined by the rating difference between the two contestants prior to that interaction. Elo-rating therefore allows assigning each male a continuous rating at any given point in time and independent of changes in group composition (Chapter 2). For our analyses we used as current rating male Elo-ratings on the date in the center of the two month time block or on the date an experimental trial was conducted. With regard to our study question, we extracted Elo-ratings on two additional dates: future and past rating refers to the Elo-rating 90 days after and before the current rating, respectively. k was set to 100 (Chapter 2). Even though they change over time, current ratings are likely to be correlated with future ratings, as are past and current ratings. This might lead to collinearity in our models. Instead of true Elo-ratings, we therefore calculated differences between current and past ratings, and between future and current ratings, respectively. Because males migrated between groups or died over the course of the study, we were not able to determine past or future status in some instances. For the four observationally assessed personality factors sample sizes are $N = 165$ cases (i.e. time blocks) representing 25 males (model set (1)), and $N = 164$ cases representing 27 males (model set (2)). For boldness the sample size is 36 cases (i.e. playback trials) representing 14 males in both model sets.

Prior to analysis we checked distributions of our numerical variables and if necessary transformed them to achieve symmetric distributions. We then standardized all numerical variables to mean = 0 and standard deviation = 1. Variance inflation factors (VIF, Field et al. 2012) were derived using the function `vif` of the R-package car (Fox and Weisberg 2011) applied to a standard linear model excluding the random effects (largest VIF: 1.55). We checked whether the assumptions of normally distributed and homogeneous residuals were fulfilled by visually inspecting a qqplot and the residuals plotted against fitted values. We checked for model stability by excluding data points one by one from the data and comparing the parameter estimates derived with those obtained for the full model. In models of set 2 (future rank as response) these assumptions were violated, caused by three particular cases in which two males underwent drastic status changes, i.e. rapid declines in Elo-ratings. These drops in ranks coincided with both males being severely injured. Though we did not observe physical fights directly, we assume these injuries were caused by aggressive interactions within or possibly between the social groups. We decided to exclude these three cases because they appear not directly relevant for male rank trajectories given our study question, i.e. to relate intrinsic (personality) factors with rank. Excluding these cases from the data set and running the models again did not change our conclusions with regard to our study aims. Nevertheless, since our models were more stable without these cases, we present model results based on data sets excluding them.

We ran linear mixed models with the function `lmer` from the lme4 package in R 2.15.0 (Bates et al. 2012; R Development Core Team 2012), to be able to additionally control for repeated measurements and random intercepts of individuals and social groups. We additionally controlled for temporal autocorrelation by calculating an autocorrelation term (c.f. Fürtbauer et al. 2011; R. Mundry, personal communication) which was incorporated into the models and retained only if it was significant (Fürtbauer et al. 2011) as indicated by a likelihood ratio test (see below).

Significance testing was done in a two-step approach. First, we used likelihood ratio tests (Quinn and Keough 2002) to determine whether the full model (including all fixed and random effects) differed from a reduced model (only including age, the random effects, the autocorrelation term if applicable and trial number in the Boldness models). Only if this step revealed that a full model differed from the corresponding reduced model did we interprete significance of individual effects. We used the `pvals.fnc` function of the languageR package to calculate individual p values based on 10,000 Markov chain Monte Carlo samples (Baayen 2008, 2011b).

F.4 Model results and figures

Table F.1: **Connectedness** as a function of current status and past status difference. Likelihood ratio test: autocorrelation, $\chi^2 = 2.06$, df = 1, $p = 0.1511$. Likelihood ratio test: full model vs null model, $\chi^2 = 13.24$, df = 2, $p = 0.0013$.

	estimate	se	t	p_{MCMC}
intercept	-0.413	0.208	-1.980	0.4566
current status	0.321	0.084	3.839	0.0006
past status difference	-0.057	0.065	-0.877	0.4514
age*				
old	0.630	0.259	2.429	0.0218
young	0.154	0.302	0.509	0.8204

* reference level for age-factor is “middle”

Table F.2: **Sociability** as a function of current status and past status difference. Likelihood ratio test: autocorrelation, $\chi^2 = 10.37$, df = 1, $p = 0.0013$. Likelihood ratio test: full model vs null model, $\chi^2 = 0.60$, df = 2, $p = 0.7424$.

	estimate	se	t	p_{MCMC}
intercept	-0.221	0.139	-1.591	0.5596
current status	0.184	0.069	2.670	0.0380
past status difference	-0.038	0.067	-1.000	0.6094
age*				
old	0.415	0.157	2.649	0.0268
young	0.190	0.202	0.943	0.3316
autocorrelation	0.278	0.0617	4.501	0.0004

* reference level for age-factor is “middle”

Table F.3: **Aggressiveness** as a function of current status and past status difference. Likelihood ratio test: autocorrelation, $\chi^2 = 3.09$, df $= 1$, $p = 0.0787$. Likelihood ratio test: full model vs null model, $\chi^2 = 9.05$, df $= 2$, $p = 0.0109$.

	estimate	se	t	p_{MCMC}
intercept	0.034	0.355	0.095	0.9530
current status	0.222	0.078	2.847	0.0030
past status difference	0.014	0.064	0.213	0.8694
age*				
old	-0.161	0.211	-0.760	0.4452
young	-0.329	0.251	-1.310	0.1800
autocorrelation	-0.117	0.059	-1.986	0.1750

* reference level for age-factor is “middle”

Table F.4: **Anxiety** as a function of current status and past status difference. Likelihood ratio test: autocorrelation, $\chi^2 = 57.09$, df $= 1$, $p < 0.0001$. Likelihood ratio test: full model vs null model, $\chi^2 = 13.58$, df $= 2$, $p = 0.0011$.

	estimate	se	t	p_{MCMC}
intercept	0.108	0.127	0.849	0.7084
current status	-0.221	0.059	-3.767	0.0002
past status difference	0.001	0.057	0.011	0.9310
age*				
old	-0.306	0.133	-2.293	0.0270
young	-0.117	0.172	-0.680	0.4716
autocorrelation	0.461	0.052	8.807	0.0001

* reference level for age-factor is “middle”

Table F.5: **Boldness** as a function of current status and past status difference. Likelihood ratio test: autocorrelation, $\chi^2 = 2.42$, df = 1, $p = 0.1200$. Likelihood ratio test: full model vs null model, $\chi^2 = 6.65$, df = 2, $p = 0.0360$.

	estimate	se	t	p_{MCMC}
intercept	-0.266	0.332	-0.803	0.3808
current status	0.638	0.221	2.889	0.0072
past status difference	0.084	0.173	0.488	0.6972
age*				
old	0.557	0.475	1.173	0.2126
young	-0.308	0.528	-0.584	0.5150
trial number	-0.307	0.124	-2.469	0.0392

* reference level for age-factor is "middle"

Table F.6: **Connectedness** as predictor of future rating increase. Likelihood ratio test: autocorrelation, $\chi^2 = 0.39$, df = 1, $p = 0.5333$. Likelihood ratio test: full model vs null model, $\chi^2 = 6.59$, df = 2, $p = 0.0371$.

	estimate	se	t	p_{MCMC}
intercept	0.250	0.117	2.143	0.2610
current status	-0.095	0.065	-1.464	0.1194
connectedness	0.174	0.069	2.518	0.0142
age*				
old	-0.306	0.145	-2.109	0.0402
young	0.049	0.179	0.272	0.8466

* reference level for age-factor is "middle"

Table F.7: **Sociability** as predictor of future rating increase. Likelihood ratio test: autocorrelation, $\chi^2 = 1.02$, df $= 1$, $p = 0.3122$. Likelihood ratio test: full model vs null model, $\chi^2 = 1.61$, df $= 2$, $p = 0.4472$.

	estimate	se	t	p_{MCMC}
intercept	0.237	0.119	1.989	0.3554
current status	-0.052	0.063	-0.822	0.3078
sociability	0.070	0.063	1.117	0.2316
age*				
old	-0.256	0.146	-1.748	0.0650
young	0.039	0.182	0.216	0.9552

* reference level for age-factor is “middle”

Table F.8: **Aggressiveness** as predictor of future rating increase. Likelihood ratio test: autocorrelation, $\chi^2 = 1.14$, df $= 1$, $p = 0.2846$. Likelihood ratio test: full model vs null model, $\chi^2 = 0.77$, df $= 2$, $p = 0.6811$.

	estimate	se	t	p_{MCMC}
intercept	0.216	0.118	1.834	0.3150
current status	-0.049	0.065	-0.762	0.3924
aggressiveness	0.042	0.066	0.633	0.6726
age*				
old	-0.226	0.144	-1.575	0.1058
young	0.055	0.183	0.301	0.8616

* reference level for age-factor is “middle”

Table F.9: **Anxiety** as predictor of future rating increase. Likelihood ratio test: autocorrelation, $\chi^2 = 1.14$, df = 1, $p = 0.2861$. Likelihood ratio test: full model vs null model, $\chi^2 = 5.70$, df = 2, $p = 0.0578$.

	estimate	se	t	p_{MCMC}
intercept	0.222	0.116	1.913	0.4474
current status	-0.065	0.062	-1.054	0.2096
anxiety	-0.143	0.061	-2.329	0.0146
age*				
old	-0.238	0.142	-1.680	0.0698
young	0.063	0.180	0.353	0.8934

* reference level for age-factor is “middle”

Table F.10: **Boldness** as predictor of future rating increase. Likelihood ratio test: full model vs null model, $\chi^2 = 2.80$, df = 2, $p = 0.2468$. The algorithm to assess autocorrelation did not result in a local optimum. Therefore, an autocorrelation term was not incorporated and tested in this model.

	estimate	se	t	p_{MCMC}
intercept	0.250	0.459	0.545	0.6650
current status	-0.460	0.328	-1.402	0.3558
boldness	0.269	0.181	1.485	0.3972
age*				
old	-0.599	0.635	-0.943	0.4392
young	0.442	0.737	0.600	0.5270
trial number	-0.128	0.131	-0.972	0.4296

* reference level for age-factor is “middle”

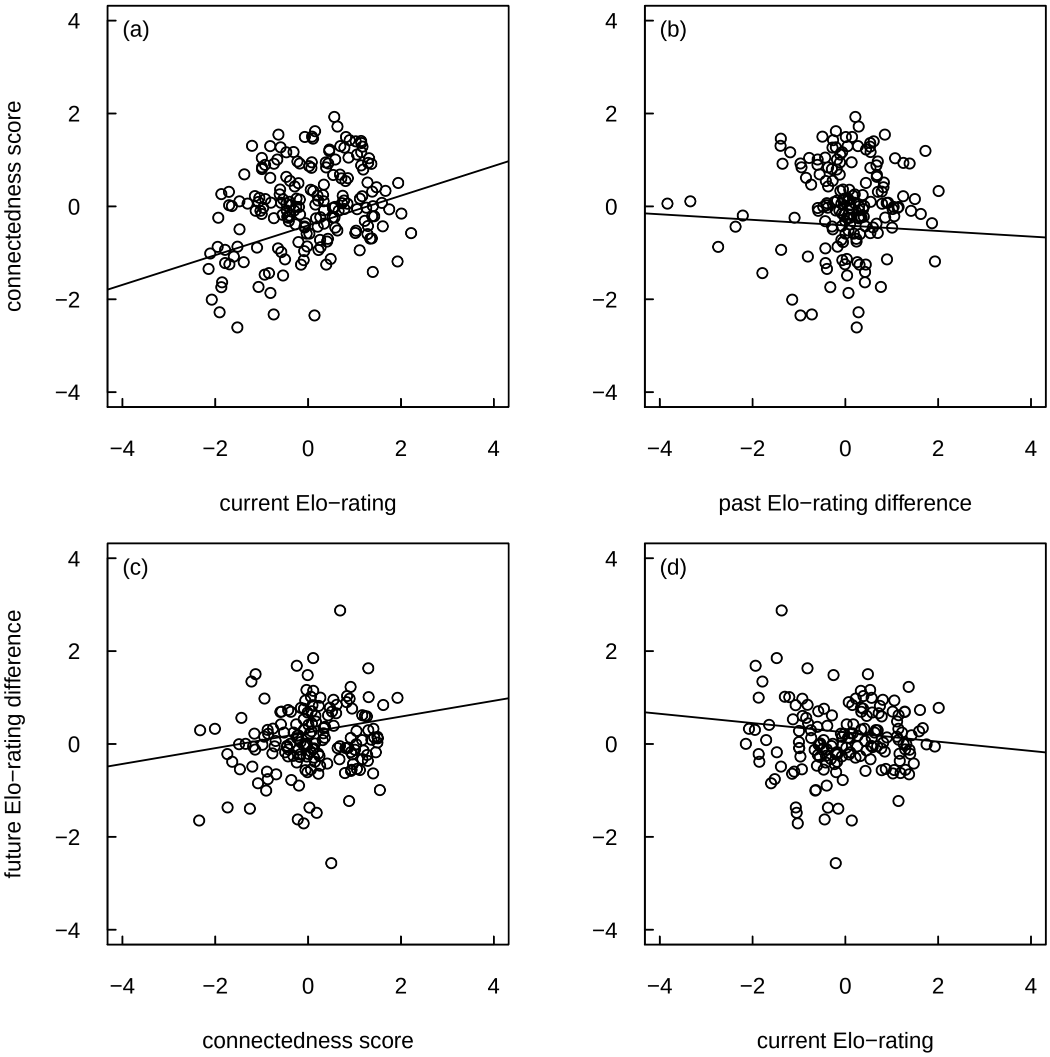


Figure F.1: (a) and (b) depict the relationships between current and past Elo-rating difference and **Connectedness** score. (c) and (d) show the relationships between Connectedness score and current Elo-rating and future Elo-rating difference.

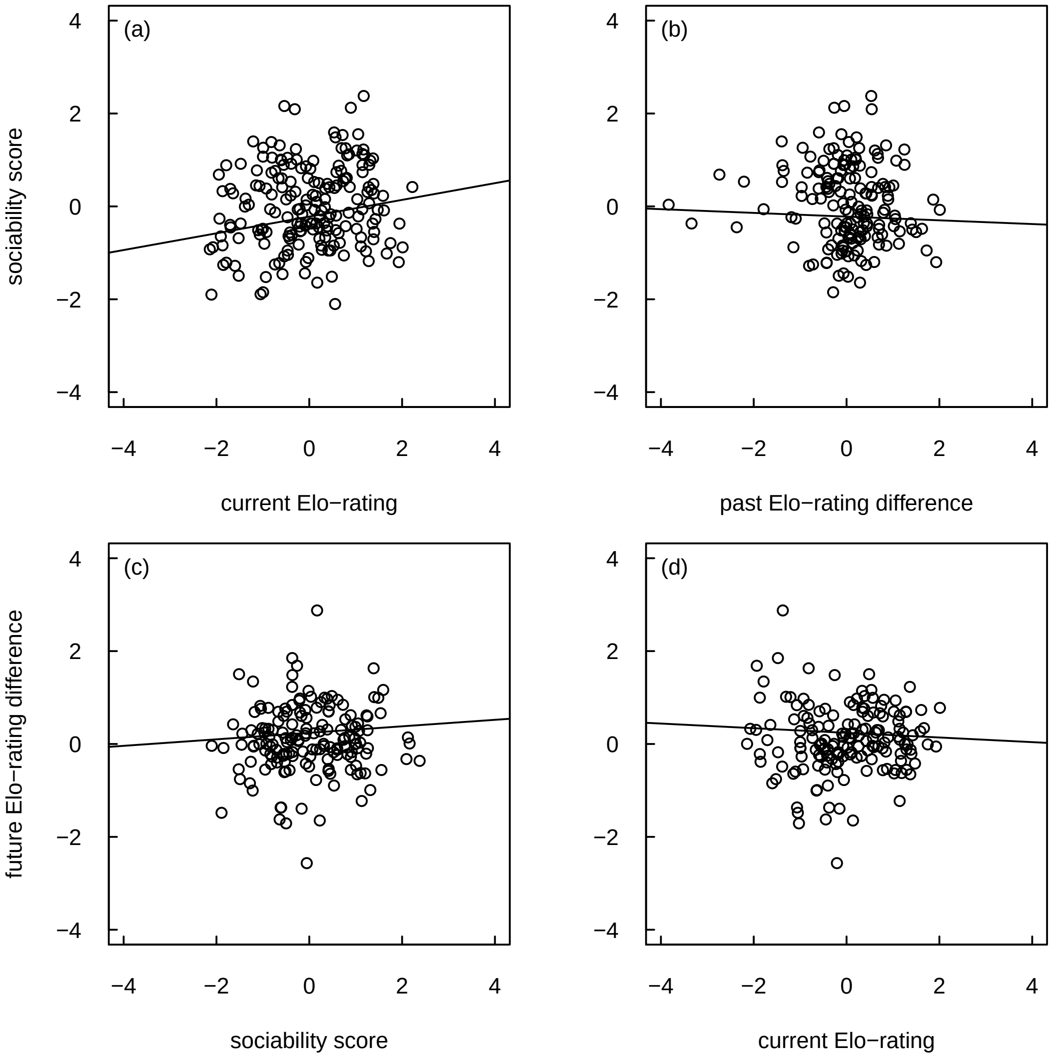


Figure F.2: (a) and (b) depict the relationships between current and past Elo-rating difference and **Sociability** score. (c) and (d) show the relationships between Sociability score and current Elo-rating and future Elo-rating difference.

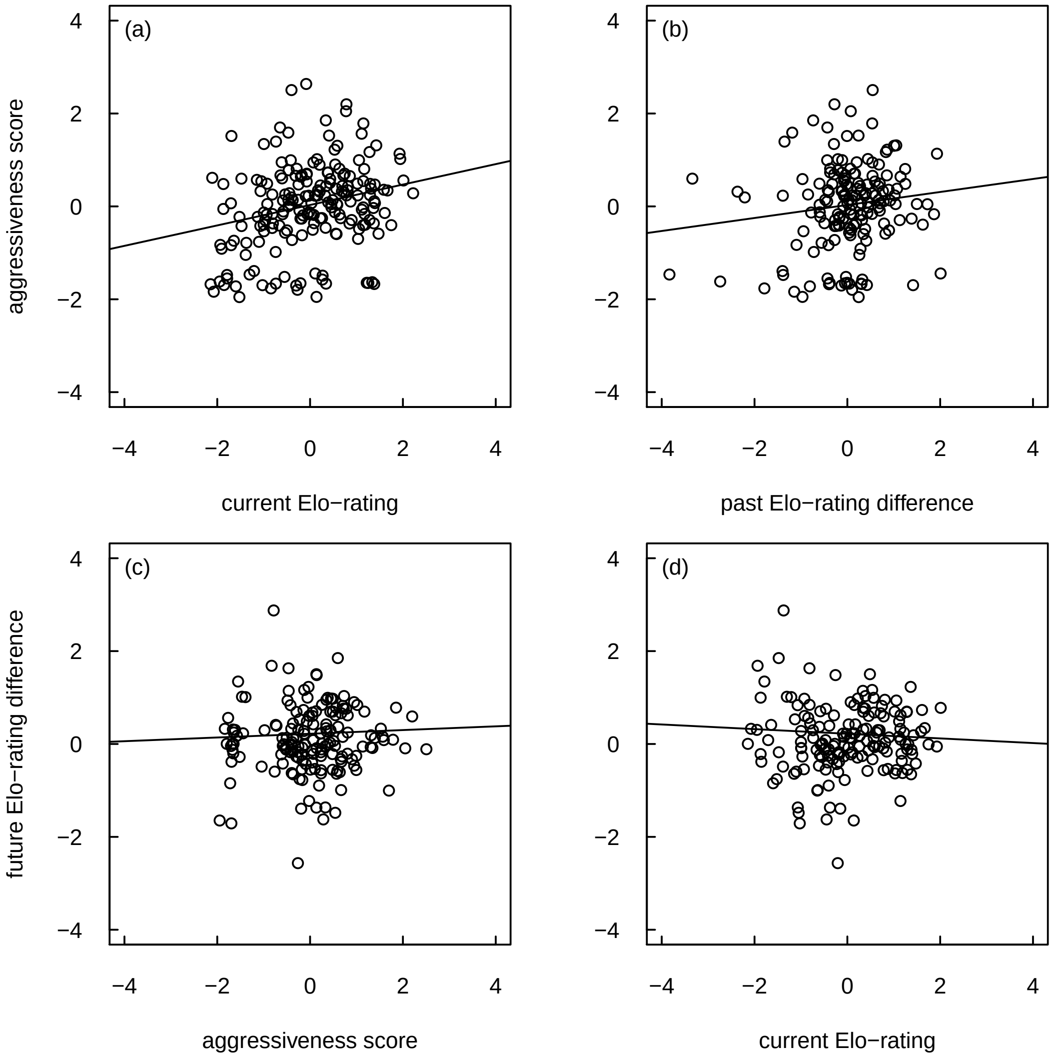


Figure F.3: (a) and (b) depict the relationships between current and past Elo-rating difference and **Aggressiveness** score. (c) and (d) show the relationships between Aggressiveness score and current Elo-rating and future Elo-rating difference.

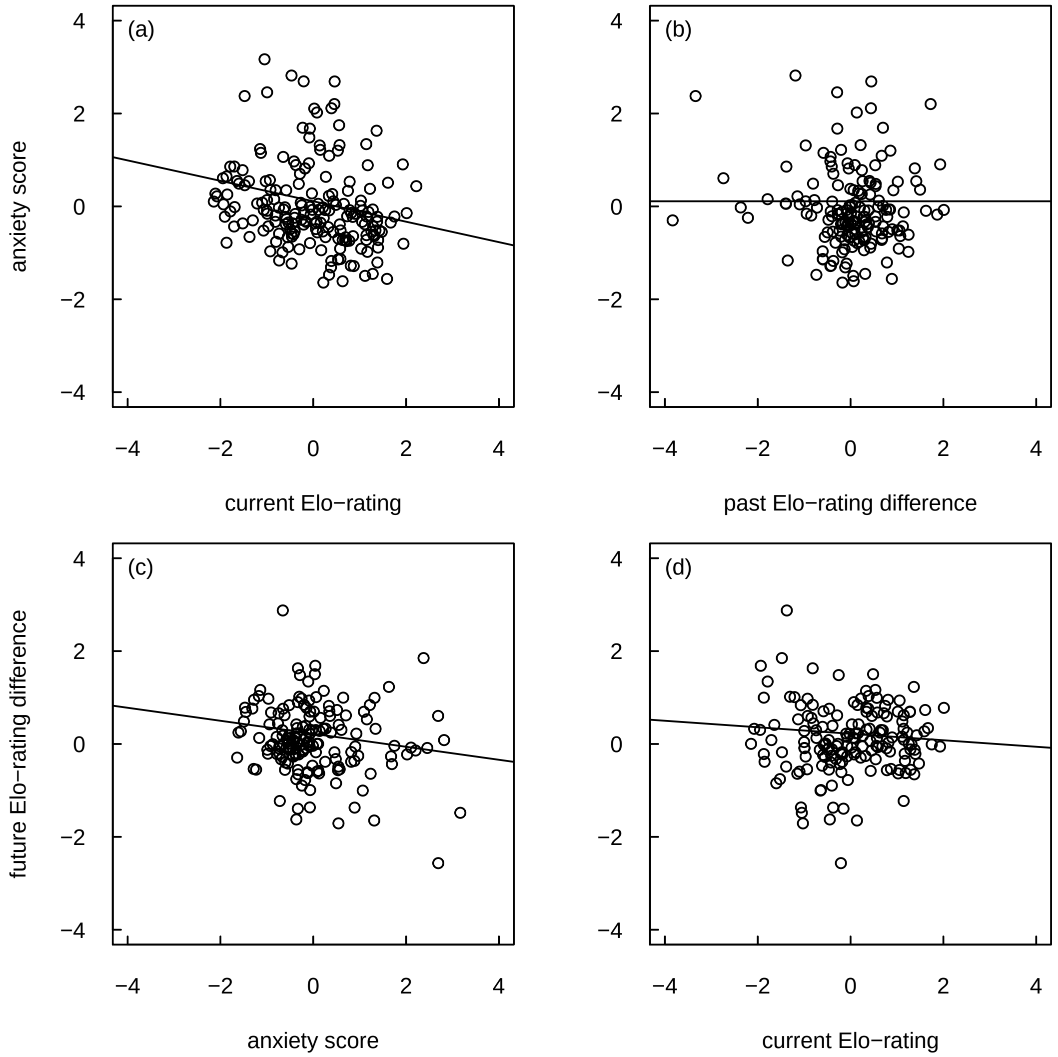


Figure F.4: (a) and (b) depict the relationships between current and past Elo-rating difference and **Anxiety** score. (c) and (d) show the relationships between Anxiety score and current Elo-rating and future Elo-rating difference.

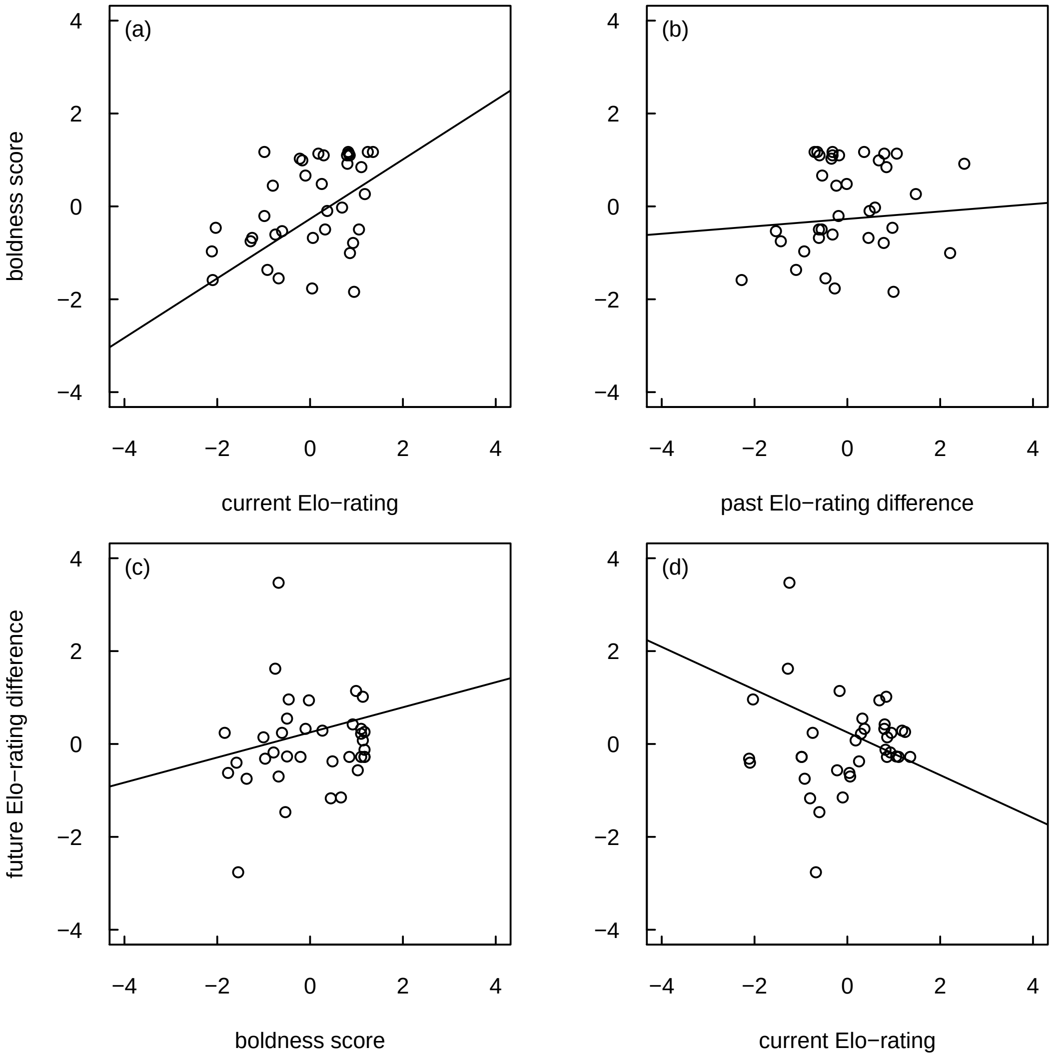


Figure F.5: (a) and (b) depict the relationships between current and past Elo-rating difference and **Boldness** score. (c) and (d) show the relationships between Boldness score and current Elo-rating and future Elo-rating difference.

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Conference contributions

Neumann, C, Heistermann, M, Agil, M, Widdig, A, & Engelhardt, A. Faecal glucocorticoid levels, rank changes and hierarchy dynamics in wild male crested macaques (*Macaca nigra*). (Poster at the 3rd Annual ISWE Conference in Vienna 2012)

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Engelhardt, A, Neumann, C, Heistermann, M, & Perwitasari-Farajallah, D. Sex skin colouration in male Sulawesi crested black macaques (*Macaca nigra*). (Talk at the IPS meeting in Edinburgh 2008)

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Selbstständigkeitserklärung

Hiermit versichere ich, dass ich diese Arbeit selbstständig und nur unter Verwendung der angegebenen Hilfsmittel erstellt habe. Alle wörtlichen und sinngemäßen Zitate aus anderen Werken sind als solche gekennzeichnet.

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