Social tolerance : novel insights from wild female crested macaques, Macaca nigra

Julie Duboscq

▶ **To cite this version:**

Julie Duboscq. Social tolerance : novel insights from wild female crested macaques, Macaca nigra. Vertebrate Zoology. Université de Strasbourg; Georg-August-Universität (Göttingen, Allemagne), 2013. English. NNT : 2013STRAJ040 . tel-01023197

HAL Id: tel-01023197

https://theses.hal.science/tel-01023197

Submitted on 11 Jul 2014

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

UNIVERSITÉ DE STRASBOURG

ÉCOLE DOCTORALE Sciences de la Vie et de la Sante ED414

Ethologie évolutive UMR 7178,

DEPE-IPHC-UdS-CNRS

THÈSE

présentée par :

Julie DUBOSCQ

soutenue le : 05 Septembre 2013

pour obtenir le grade de : **Docteur de l'université de Strasbourg et de l'université de Göttingen**

Discipline/ Spécialité : Sciences de la Vie - Ethologie

Nouvelles perspectives sur la tolérance sociale à travers l'étude des femelles macaques à crête, *Macaca nigra*, dans leur milieu naturel.

THÈSE dirigée par :

Mr. THIERRY Bernard	Directeur de Recherche, université de Strasbourg
Mme FISCHER Julia	Professeure, université de Göttingen, Allemagne

RAPPORTEURS :

Mr. HOFER Heribert	Professeur, Leibniz Institute for Zoo and Wildlife Research, Allemagne
Mr. MAJOLO Bonaventura	Chargé de Recherche, université de Lincoln, Angleterre

---

AUTRES MEMBRES DU JURY :

Mme ENGELHARDT Antje	Chargé de Recherche, Leibniz Institute for Primate Research, Allemagne
Mme PETIT Odile	Directrice de Recherche, université de Strasbourg

Table of Contents

Acknowledgements iii
Résumé v
Summary xiii
Zusammenfassung xv
CHAPTER 1 GENERAL INTRODUCTION 1
1.1 The sociality of female mammals 3
1.2 Consequences of variation in social relationships within a social structure 6
1.3 Models of social evolution 7
1.4 Macaque societies: a study model of variation in social structures 11
1.5 Aims of the thesis 16
CHAPTER 2 SOCIAL TOLERANCE IN WILD FEMALE CRESTED MACAQUES (*MACACA NIGRA*) 19
2.1 Summary 20
2.2 Introduction 21
2.3 Methods 23
2.4 Results 30
2.5 Discussion 37
CHAPTER 3 THE FUNCTION OF POST-CONFLICT INTERACTIONS: NEW PROSPECTS FROM THE STUDY OF A TOLERANT SPECIES OF PRIMATE 43
3.1 Summary 44
3.2 Introduction 45
3.3 Methods 49
3.4 Results 59
3.5 Discussion 63
CHAPTER 4 STRUCTURE AND FUNCTION OF SOCIAL BONDS IN WILD FEMALE CRESTED MACAQUES 69
4.1 Summary 70
4.2 Introduction 71

4.3 Methods 74
4.4 Results 80
4.5 Discussion 85
CHAPTER 5 GENERAL DISCUSSION 93
5.1 Living in a tolerant society 94
5.2 Evolution of different social styles: the potential link between external and internal factors 100
5.4 Outlook and conclusion 106
Bibliography 109
List of figures 135
List of tables 137
Appendices 139
Appendix A – Additional details on the study area and study species 141
Appendix B – Supplementary material to Chapter 2 145
Appendix C – Supplementary material to Chapter 3 149
Appendix D – Supplementary material to Chapter 4 153
Curriculum vitae 157
Publications 159
Conference contributions 160

Acknowledgements

First and foremost, I would like to thank my advisors, Antje Engelhardt, Julia Fischer, and Bernard Thierry. Thank you, Julia, for the inspiration. Thank you, Bernard, for your expertise and experience, your availability and your insightful and open mind. The warmest thanks go to Antje, who trusted me right from the beginning as a volunteer in her field project, and has more than once put the fate of her project in our hands. Thank you for showing me that you can manage a field site, a family and a scientific career all at the same time! Thank you most of all for your guidance and your support, on the professional but also personal side of life!

A special thank goes to Odile, who was also part of my advisory board in Strasbourg, for all the support and friendship across the years. Thanks for the wine and for the second home! In Göttingen, I also would like to thank Julia and Oliver for insightful discussions, Keith especially for his support, advice and very useful contributions, and Jan, Ellen, Kerstin, Christian and Christiane for their invaluable help!!

I am grateful for the financial support of the Volkswagen Foundation and of Primate Conservation, Inc., and for the logistic and administrative support of the Agricultural University of Bogor (IPB), the Mathematics and Natural Sciences Faculty of the University of Manado (UNSRAT), the local office for the Conservation of Protected Area (BKSDA Manado), the Indonesian State Ministry of Research and Technology (RISTEK) and the Directorate General of Forest Protection and Nature Conservation (PHKA).

Thanks to all members of the Macaca Nigra Project and others in Indonesia, for unforgettable memories in North Sulawesi and elsewhere in Indonesia: Daphné, Julian, Antri, Susi and the cook team, Iwan, Meldi, Ugiek, Stephan, Gholib, Ginting, Ade, Deidi, Maria, Nicole, Becky, Pak Jeffrey and Yvon, Samuel and his family, the Mama Ross and the Puri Bali crews, Swen and his family in Bunaken, and the Tasikoki Wildlife Rescue Centre, especially Simon. Special thanks go to Jérôme, Ira and Yandhi for their great work, their patience and commitment!!

Thanks to my colleagues and friends in Strasbourg, especially Cédric, Hélène, and Julien. Warm thanks to my friends, Mathilde, Mary, Anne, Vincent, Anne (Choup), Guigui, Claudie and Jerem for taking the bright side of life, always, for their enthusiasm and optimism!

This thesis would not have been possible without my friends and colleagues in Göttingen, especially Rebecca, Gisi (and the mini!), Chris, Christof, Cédric, Tabby, Matthis, Sally, Marlies, Pascal, Constance, James, Lennart, Peter and Tanja. Thanks for the parties, the BBQs, the animated discussions, the great laughs, and the craziness of it all! Jérôme and Cédric, I cannot thank you enough for all the support, help, fun, friendship and much more. Thank you for being here!!

My family has also always supported me and encouraged me to follow my dreams, even when they brought me far away from them. “Son métier, c’est chercheuse, pas trouveuse! – Oui, mais qui cherche, trouve!” Denis, Danièle, Antoine, Elise and Jules, this thesis is dedicated to you.

Christof… for the sunshine in the morning, the coffee-and-cigarette breaks, the diving, the free spirit, and so much more!!! You rock!!

Résumé

La vie sociale émerge et évolue quand les bénéfices de vivre en groupe l'emportent sur les coûts. Les bénéfices de la vie en groupe comprennent la protection contre les prédateurs, la recherche optimale de ressources et un accès facilité à des partenaires de reproduction alors que les coûts incluent la compétition pour l'accès aux ressources alimentaires et aux partenaires de reproduction ainsi que la transmission de maladies et de parasites. Former des groupes sociaux permanents implique aussi l'exploitation simultanée des ressources et la coordination des activités, ce qui suscite d'inévitables conflits d'intérêts entre individus. La vie sociale est donc un équilibre complexe entre compétition et coopération. Les relations sociales que les individus forment au fur et à mesure de leurs interactions les uns avec les autres sont donc considérées comme des investissements à long-terme améliorant finalement la valeur adaptative des individus. L'analyse des couts et bénéfices de la vie sociale au niveau de la structure sociale, c'est-à-dire au niveau des relations sociales, permets de mettre en lumière comment les individus balancent les coûts (compétition) et les bénéfices (coopération) de la vie en groupe. Chez les animaux sociaux, la diversité des organisations ou structures sociales existantes est grande et différent modèles ont été développés pour expliquer l'évolution de cette diversité. Le modèle socio-écologique favorise l'influence des conditions écologiques sur les organisations et structures sociales, mais la variation dans les comportements sociaux est aussi influencée par des facteurs génétiques, développementaux, et sociaux, ainsi que par l'histoire phylogénétique des espèces. Ces facteurs limitent en effet l'adaptabilité et la flexibilité des systèmes et donc leur évolution. Un point important est aussi que les individus sociaux ne sont pas seulement influencés par leur environnement écologique ou physique mais bien aussi par leur environnement social et le comportement de leurs congénères.

Chez les mammifères, les femelles investissent le plus dans la reproduction (gestation, lactation, apprentissage social). Les modèles théoriques analysant la variation dans les systèmes sociaux partent donc du principe que la ressource importante, et limitante pour la fitness, pour les femelles est l'accès à la nourriture tandis que la ressource limitante pour les males est l'accès à des femelles fertiles. Les femelles forment donc généralement le cœur des groupes. Leurs stratégies sociales devraient œuvrer à maximiser l'accès aux ressources alimentaires soit en réduisant la compétition pour celles-ci ou en développant la coopération pour faciliter leur accès. Les femelles mammifères s'organisent donc au sein de structures sociales selon différent principes, tous destinés à réduire les couts et augmenter les bénéfices de la vie en groupe. Par exemple, l'âge et la taille déterminent l'ordre hiérarchique des femelles chez les éléphants d'Afrique, tandis que l'ordre d'arrivée et la possession organisent l'accès aux carcasses chez les lionnes d'Afrique. Chez les primates cercopithèques, la transmission du rang maternel ainsi que les alliances entre apparentés construisent des hiérarchies linéaires et matrilineaires. La coopération entre individus vivant en groupe est principalement basée sur les associations entre apparentés (la sélection de parentèle) ou sur l'échange réciproque de services ou de biens (l'altruisme réciproque). Les femelles forment donc souvent des relations sociales de dominance et de coopération en lien avec ses stratégies d'accès à

la nourriture. Les femelles établissent aussi souvent des relations sociales fortes, définies comme des interactions sociales fréquentes, positives, stables et équilibrées. Ces relations sociales fortes sont souvent structurées par rapport au patrimoine génétique commun des individus par exemple, ou aux relations de dominance entre les femelles. En effet, établir des relations sociales fortes avec ses apparentes ou avec des individus dominants aide a l'accès aux ressources et donc a l'augmentation de la fitness, directe ou indirecte. La structuration des relations sociales a donc d'importantes conséquences sur la coopération entre individus en général, car les relations sociales fortes apportent des bénéfices à court et long termes. Cependant, les facteurs influençant ces relations sociales au sein des groupes d'animaux sociaux, ainsi que les facteurs jouant sur leur diversité et leur dégrée de force, restent encore peu compris. En particulier, l'effet du type de sociétés dans lesquelles les animaux vivent, par exemple, despotique ou égalitaire, sur les relations sociales des individus est mal connu. Par exemple, le modèle socio-écologique prédit que le besoin de coopération entre femelles pour défendre l'accès aux ressources alimentaires contre d'autres groupes de congénères crée les conditions nécessaires à l'évolution de la tolérance sociale entre femelles, ce qui fait que les apparentés ne sont plus nécessairement les seuls alliés utiles. Cependant, ne considérer que l'influence des conditions écologiques est insuffisant. Par exemple, l'étude des conflits agressifs montre comment les individus préservent la cohésion sociale malgré les conflits d'intérêts. Les agressions en effet perturbent la vie sociale. Les stratégies de résolution de conflits permettent de rétablir la tolérance et la coopération entre individus. Il est désormais bien établi que la fréquence, la forme et la fonction de ces comportements de conciliation sont corrélés au style social de l'espèce, c'est-à-dire au degré de tolérance initiale entre les individus. L'analyse de l'équilibre entre compétition et coopération est donc primordiale.

Pour mieux comprendre la diversité sociale qui existe entre les différences espèces de primates, il est important d'étudier cette variation à différentes échelles, le groupe, l'espèce, le contexte. Les macaques sont un taxon idéal pour adresser ces questions. Les 22 espèces de macaques partagent la même organisation sociale : ils forment des groupes multi-males multi-femelles ; les femelles restent toute leur vie dans leur groupe natal tandis que les males changent de groupe à la maturité sexuelle et plusieurs fois dans leur vie. Les différentes espèces de macaque montrent aussi une variation importante concernant les asymétries de pouvoir entre individus, la fréquence, l'intensité et la directionalité des interactions sociales. Les contraintes sociales liées à la hiérarchie et à la parenté varient aussi entre espèces ou groupes d'espèces. Les différentes espèces de macaque ont donc été classifiées dans plusieurs groupes de style or catégorie sociale selon les modèles, allant des plus despotiques (« Resident-Nepotistic » ou grade 1) au plus tolérants (« Resident-Nepotistic-Tolerant » ou grade 4). Les espèces plus despotiques ont des agressions plus intenses, des affiliations plus rares, une tendance conciliatoire moins élevée et des asymétries de pouvoir plus prononcées que les macaques plus tolérants. Leurs relations sociales sont aussi fortement influencées par leur position dans la hiérarchie et biaisées en faveur de leurs apparentés, un schème bien moins prononcé chez les macaques plus tolérants où les relations et partenaires sociaux sont plus diverses et ouverts.

La majorité des données sur la structure sociale des macaques provient de populations en captivité ou artificiellement nourries, limitant la variation écologique et démographique naturelle. Plus problématique, les espèces despotiques ont été bien plus étudiées au détriment des espèces tolérantes. Les études fondatrices sur les espèces plus tolérantes ont en effet démontré à quel point ces sociétés différent des autres, ce qui a significativement changé le regard porté sur les

interactions entre l'écologie, le comportement et le développement dans ce taxon. Cependant, des résultats contradictoires ont émergé au fur et à mesure de l'accumulation de données sur les espèces tolérantes. Cela apparait principalement dû à de mauvaises conditions d'observation ou à l'oubli de paramètres importants. Notre connaissance et compréhension de la variation dans les relations sociales chez les macaques est donc incomplète.

L'objectif principal de ma thèse est donc d'approfondir notre connaissance et compréhension des sociétés tolérantes de macaques par l'étude approfondie d'une espèce peu étudiée, les macaques a crête de Sulawesi, Macaca nigra, qui plus est dans son milieu naturel. Plus spécifiquement, j'ai pour objectif 1/ d'évaluer le style social des femelles par l'analyse de la fréquence, l'intensité et la directionalité de leurs comportements sociaux (chapitre 1) afin de déterminer leur dégrée de tolérance; 2/ d'examiner les facteurs déterminants et les fonctions des interactions post-agression (chapitre 2), comportements indicatifs du style social des espèces ; et 3/ d'analyser la prévalence et la force des contraintes hiérarchiques et népotistiques (lié à la parenté) sur les relations sociales entre femelles (chapitre 3). Les comportements observés sont ensuite réintégrés dans l'histoire évolutive des espèces en étant comparés à ceux observés chez les macaques plus despotiques en particulier et chez les autres sociétés animales en général.

Les macaques à crête sont endémiques de l'ile de Sulawesi, en Indonésie. La population étudiée habite la réserve naturelle de Tangkoko-Batuangus (1º33'N, 125º10'E), une région de forêt tropicale humide avec variation saisonnière en pluie et en arbres fruitiers à maturité. L'étude fait partie du Macaca Nigra Project (www.macaca-nigra.org), un projet de recherche sur la biologie des macaques à crête. Deux groupes ont été étudiés, comprenant respectivement environ 60 et 80 individus, tous habitués à la présence humaine et identifiables sur la base de caractéristiques physiques. Chaque groupe était suivi chaque jour de l'aube (ca. 5:30 am) au crépuscule (ca. 6:00 pm) entre Octobre 2008 and Mai 2010. Les suivis comportementaux (activité et individus à proximité) duraient jusqu'à la collecte de 30 focal « point-samples ». Toutes les femelles adultes ont été suivies (15 – 18 dans le groupe « PB », 21 – 24 dans le groupe « R1 »). Les comportements sociaux de chaque femelle focal étaient enregistrés continuellement (début et fin des interactions, séquences des comportements et identités des individus interagissant). Au total, j'ai collecté 2 480 heures de données focal data sur 42 femelles (PB: médian = 68 heures par femelle, écart: 65 – 78, N = 18; R1: médian = 66 heures par femelle, écart: 59 – 71, N = 24). De plus, des échantillons de fèces étaient collectés de façon opportuniste pendant les observations pour l'analyse des relations de parenté (N = 140, médian par femelle = 4, range = 3 – 4 ; « two-step ethanol-silica storage method »). Les femelles ont ensuite été génotypées à 12 loci suivant la procédure du "two-step multiplex chain polymerase reaction" et le degré de parenté calculé avec le logiciel COANCESTRY®. L'index « Dyadic Maximum Likelihood » (DML) représente le plus fidèlement le dégrée de parenté r entre les femelles étudiées. Les analyses statistiques comprennent des tests non-paramétriques simples de différences au sein de ou entre groupes et des modèles linéaires généralisés mixtes, permettant l'analyse de l'influence de plusieurs facteurs à la fois sur une même variable dépendante. Toutes les analyses ont été faites avec le logiciel R.

Dans le premier chapitre de la thèse, « Social tolerance in wild female crested macaques, Macaca nigra », j'ai évalué le degré de tolérance des femelles en analysant le contexte, la fréquence, l'intensité, la directionalité et la distribution de leurs interactions agressives et affiliatives. J'ai analysé leur gradient de dominance, leur mimique faciale et leur degré de tendance conciliatoire, tous marqueurs du style social chez les macaques. J'ai également documenté des comportements

qui n'avaient pas encore été analysés chez les macaques tolérants : la réaction à l'approche d'un congénère et la distribution des affiliations entre toutes les femelles du groupe. J'ai confirmé que les femelles macaque a crête ont un style social tolérant avec des conflits de faible intensité, souvent bidirectionnels et réconciliés. L'asymétrie de dominance est modérée et associée à une mimique faciale positive et également bidirectionnelle. De plus, les femelles ont une grande tolérance des autres à leur proximité. Ces observations concordent avec ce qui a été observé chez les autres macaques tolérants en captivité et contrastent avec les macaques despotiques.

Dans le deuxième chapitre de la thèse, "The function of post-conflict interactions: new prospects from the study of a tolerant species of primate", j'ai examiné les relations entre les agressions, et l'occurrence d'interactions post-agression afin de déterminer la fonction de ces dernières. Pour cela, j'ai spécifiquement analysé l'effet des caractéristiques des conflits et des dyades engagées dans les conflits sur leurs conséquences sur l'anxiété des femelles, et l'occurrence des interactions post-agression. Les fonctions des interactions post-agression incluent la réduction de l'anxiété générée par l'agression, la réparation des relations sociales endommagées par l'agression, la protection contre de futures agressions, et le signalement que le conflit est terminé et que les relations peuvent reprendre normalement. Je n'ai pas pu mettre en évidence que les agressions étaient perçues comme anxiogènes, même si l'occurrence d'une agression augmente la probabilité d'agressions secondaires avec d'autres individus. Les agressions entre individus formant des relations sociales fortes ne sont pas non plus génératrices d'anxiété au dessus de la moyenne. En conséquence, les interactions post-agression ne semblent pas fonctionner pour réduire l'anxiété des opposants. Je n'ai pu trouver qu'un support partiel à la théorie selon laquelle les femelles utilisent les interactions post-agression pour réparer leurs relations sociales: les dyades avec une relation forte ou qui se supportent mutuellement ne se réconcilient pas plus que les autres, même si les dyades avec une relation plus stable, mais asymétrique, se réconcilient plus que les autres. L'initiation et la directionalité des interactions post-agression révèlent que la réconciliation pourrait fonctionner comme un signal d'apaisement et d'intention pacifique et que les agressions secondaires initiées contre d'autres individus que les opposants initiaux pourraient fonctionner pour se protéger d'attaques futures ou pour réaffirmer son rang hiérarchique au sein du groupe. Ces résultats sont très distinctes de ce qui est généralement observé chez les autres macaques et animaux sociaux. Ils sont à mettre en relation avec le style social tolérant de cette espèce, où les conflits sont de faible intensité, les asymétries de dominance sont modérées et les réseaux sociaux divers et ouverts. Cela signifie que le type de société dans lesquelles les animaux vivent est à prendre en considération dans l'analyse de la fonction des comportements sociaux. Cela permet une compréhension plus fine des stratégies de résolution des conflits d'intérêt, essentielles à la vie sociale.

Dans le troisième chapitre de la thèse, "Female sociality in a tolerant macaque species: the interplay between dominance, kinship, social bonds and coalitionary support", j'ai analysé les relations entre la dominance, la parenté, l'âge, les liens sociaux et les coalitions. J'ai mis en évidence que les femelles à la fois proches en rang de dominance et apparentées, ainsi que celles appartenant à la même classe d'âge, avaient les liens sociaux les plus forts. En revanche, quand les femelles ne sont pas apparentées, l'effet de dominance est toujours présent, ce qui veut dire que l'effet de la différence en rang est plus important que l'effet de la parenté. Les coalitions sont formées entre femelles appartenant à des classes d'âge différentes ou proches en dominance, mais pas entre apparentées ou entre femelles avec des liens forts. De plus, le support pendant les agressions était

réciproqué mais pas échangé pour du toilettage ou de la tolérance autour des ressources alimentaires. Les effets différents des variables analysées sur deux des plus importants paramètres sociaux censés influencer la valeur adaptative des femelles met en évidence la complexité des relations sociales dans les sociétés tolérantes. Mes résultats démontrent que les femelles tolérantes basent leurs décisions sociales plus en accord avec la compétence ou la disponibilité des partenaires qu'avec les caractéristiques des relations sociales, et qu'elles ont la liberté de décider de façon opportuniste ou situationnelle à quel moment et avec qui s'engager socialement. Cela contraste fortement avec les sociétés plus despotiques.

En combinant des variables comportementales et génétiques, ma thèse apporte de nouvelles perspectives sur les sociétés de macaques tolérants, sur la fonction des comportements et sur les contraintes et adaptations imposées aux individus vivant dans ces sociétés. J'ai confirmé que les femelles macaque à crête ont un style social tolérant, similaire à celui d'autres macaques de Sulawesi et bien distinct de celui des macaques plus despotiques. J'ai aussi montré pour la première fois que les fonctions des interactions post-agression sont différentes chez cette espèce par rapport à d'autres macaques et sociétés animales et qu'elles sont liées au style social tolérant des femelles. De plus, j'ai mis en évidence que les contraintes hiérarchiques et népotistiques étaient modérées, et que les femelles échangent les bénéfices sociaux, comme le support ou le toilettage, selon différent principes que les autres macaques et cercopithèques en général, confirmant le profile tolérant de cette population naturelle de macaques de Sulawesi.

Mon analyse du style social de ces femelles macaque de Sulawesi est la plus complète à ce jour et résume les caractéristiques de la tolérance sociale. Mon analyse descriptive de la variation des caractères sociaux entre les espèces et groupes d'espèces correspond bien aux résultats d'autres chercheurs ayant effectués des analyses plus sophistiquées (meta et phylogénétiques): les styles sociaux peuvent être définis comme des associations de comportements sociaux, variant en degré et niveau autour d'un certain mode, constant au sein des espèces ou groupes d'espèces mais distinct entre espèces ou groupes d'espèces (analogues aux syndromes comportementaux). Un aspect nouveau des sociétés de macaques tolérants est mis en lumière par les résultats de mon étude sur les interactions post-agression, qui contrastent remarquablement avec ce qui a été trouvé chez les autres espèces animales. Les conflits ne semblent pas être anxiogènes et ces interactions ne fonctionnent donc pas pour réduire le stress des individus. Il ne semble pas non plus que les femelles de cette espèce interagissent après les conflits pour réparer leurs relations sociales. Selon mes résultats, il est plus probable que ces affiliations et agressions soient initiées soit pour signaler que l'agression est terminée, soit pour réaffirmer son statut social et prévenir de futures attaques. Mon étude démontre l'importance d'examiner tous les facteurs ensemble, et non séparément, et de considérer le style social de l'espèce dans les analyses, et ce que ça implique pour les coûts et bénéfices des interactions sociales, pour une meilleure compréhension de stratégies de résolution des conflits. En effet, mes résultats ont du sens quand la tolérance sociale des individus est prise en compte. Un autre résultat majeur de ma thèse est l'influence limitée de la dominance ou de la parente dans la vie sociale des femelles. Par exemple, le degré de parenté, un des déterminants majeurs de coopération, n'explique pas la fréquence du support dans les interactions agressives, facteur important pour la valeur adaptative des individus. Les non-apparentées étaient en fait souvent autant les partenaires de coopération que les apparentées. Le rang de dominance n'a aussi aucun effet sur la fréquence des interactions sociales alors que l'âge et la différence en dominance expliquent la variation qui existe dans la force des liens sociaux établis entre femelles et la fréquence

du support dans les agressions. La coopération entre femelles macaque à crête est donc expliquée par d'autres facteurs que ceux mis en évidence dans d'autres espèces, comme la compétence, la motivation ou la disponibilité des partenaires.

Au sein des styles sociaux donc, les différents comportements sont connectés et co-varient les uns avec les autres. En accord avec les recherches précédentes, mes analyses désavouent donc le point de vue selon lequel l'écologie détermine de façon prépondérante la structure sociale des sociétés. En outre, il a démontré les effets maternels (génétiques, et physiologiques entre autres) et les caractéristiques de l'environnement social pendant le développement de l'individu influencent profondément le phénotype comportemental de la progéniture, et donc des futures adultes. Les effets épigénétiques au niveau des gènes, de l'expression des hormones et neurotransmetteurs, et des phénotypes individuels et sociaux interagissent aussi pour façonner et contraindre les organismes à l'intérieur de certaines normes de réactions. Cela ne signifie pas que les organismes ne sont pas flexibles ou ne s'adaptent pas. Cela indique cependant que l'histoire évolutive des espèces, la covariation des caractères et les facteurs épigénétiques et développementaux doivent tous être pris en compte dans les modèles d'évolution sociale, avec les déterminants écologiques. Je propose donc ici un modèle plus complet, qui peut potentiellement prendre en compte non seulement un grand nombre de facteurs mais également les liens qui existent entre eux en m'inspirant de la théorie des syndromes comportementaux. Au niveau individuel, les syndromes comportementaux peuvent expliquer les compromis entre différentes stratégies comportementales et l'évolution de "coping styles" différents mais tout aussi adaptes. Ces syndromes sont influencés par des facteurs, génétiques, sociaux et environnementaux et ont une signification évolutive certaine. Ainsi, si l'on considère les différentes sociétés de macaques comme des stratégies adaptatives, façonnées pour répondre aux mêmes problèmes sociaux et écologiques, un scenario d'évolution sociale globale peut être dessine comme suit. Certaines espèces ont évolué dans des environnements demandant la plus grande prudence et une grande réactivité, comme dans un environnement avec des prédateurs. En combinaison avec une certaine distribution et abondance de ressources alimentaires, ce milieu a sélectionné pour des profiles d'individus réactifs, agressifs, et intolérants à la présence des autres. Ce profile comportemental influence tous les autres caractères sociaux, comme les interactions avec les autres individus du groupe, parce qu'ils sont lies entre eux par des processus régulateurs génétiques et hormonaux. Cela a donc généré des stratégies sociales régulées par des règles strictes, comme des hiérarchies strictes contrôlées par l'agression et de la coopération majoritairement entre des individus ayant des relations stables, fiables et constantes, comme les apparentés. En revanche, dans un milieu plus sûr, où les ressources sont abondantes et/ou dispersées et les prédateurs sont absents par exemple, les individus ont pu se permettre d'évoluer un profile comportemental plus détendu, et ce milieu a pu sélectionner pour des individus curieux et tolérants des autres. Cela a pu générer des stratégies sociales régulées par des règles d'échanges moins strictes et plus ouvertes, réduisant les contraintes hiérarchiques et népotistiques dans la coopération entre individus. Les mêmes systèmes régulateurs ont étendu ce profil comportemental au reste des caractéristiques sociales. En fin de compte, quelle(s) stratégie(s) est la plus adaptée(s) est difficile à déterminer, si nombreux sont les facteurs à prendre en considération. Les processus évolutifs ajustent, régulent et font le lien entre les groupes de traits sociaux. Les fluctuations de l'environnement au cours du temps évolutif peuvent maintenir plusieurs stratégies viables et les corrélations entre comportements peuvent varier si différentes corrélations sont favorables dans différents milieux.

Mes résultats restent à mettre en relation avec l'écologie des femelles, qui est aussi un important facteur pour l'évolution des structures sociales, et le comportement des males. Ils démontrent cependant que la tolérance sociale est bien plus complexe qu'un simple effet de l'écologie et est définie selon l'équilibre entre les processus de compétition et de coopération entre individus. Néanmoins, le portrait des comportements sociaux des femelles macaque à crête établi dans cette thèse diffère substantiellement du modèle traditionnel des primates cercopithecines. Ma thèse constitue un appel à étudier les sociétés animales dans leurs plus divers aspects ensemble et démontre l'importance d'intégrer au sein d'un seul modèle d'évolution sociale à la fois des composants externes (l'environnement) et internes (l'organisme et le système social) pour comprendre la diversité des sociétés animales.

Summary

Sociality is ultimately beneficial for individuals. Social relationships amongst individuals are viewed as long-term investments, influencing individual fitness. Analyses of the costs (competition) and benefits (cooperation) of sociality at this level thus shed light onto individuals' behavioural strategies, which are extremely diverse. To explain the existing social diversity in animal social structures, theoretical models emphasise ecological, genetic, developmental, and social factors as well as the phylogenetic history of species.

In most gregarious mammals, females - being the philopatric sex - often form strong social bonds. Important structural factors of social bonds are dominance and kinship, and this has important implications for cooperation in general. However, it is as yet unclear what drives the variation in strength and quality of bonds, especially in relation to the type of societies individuals live in, for example despotic or egalitarian.

Although all macaque species (genus *Macaca*) share the same social organisation (i.e. multi-male multi-female groups, with female philopatry), variation in social behaviour amongst the different macaque species is striking. These differences have been explained along different lines, from ecology to phylogeny, leading to the classification of their social structures in different categories. A major issue in the study of macaque societies however is a strong bias towards studying some species in detriment of others. This unbalance truly undermines our understanding of the social diversity therein.

The overall aim of my thesis is to foster our knowledge and understanding of the diversity in macaque societies by studying one of the less-known species, the crested macaque, *M. nigra*, for the first time under natural conditions. The first study of my thesis aims at assessing the degree of social tolerance between females. I then examine the structure and function of social bonds between females by investigating post-conflict interactions (second study), and hierarchical and nepotistic influences on social behaviour (third study). Ultimately, this thesis aims at reflecting on the interplay between different factors in a comparative perspective and providing a tentative general framework for the evolution of diverse animal societies.

In the first study, I quantify a comprehensive set of behavioural parameters the expression thereof reflects the social style of the species. I confirm that wild female crested macaques express a tolerant social style, with low intensity, frequently bidirectional, and reconciled conflicts. Dominance asymmetry is moderate, and associated with a bidirectional affiliative bared-teeth display. Females greatly tolerate one another in close proximity. The observed patterns match the profile of other tolerant macaques and are outside the range of patterns of more despotic species.

In the second study, I investigate determinants and function of post-conflict interactions. I analyse the relationship between the occurrence of aggression and behavioural indicators of anxiety, and between the characteristics of conflicts (e.g. intensity, decidedness, or context), the characteristics of dyads involved in conflicts (e.g. strength of the social bond, or frequency of support in the dyad) and the occurrence of three post-conflict interactions in order to study their functions. I find little evidence that aggression affects females' behavioural indicators of anxiety. Consequently, post-conflict interactions do not seem to serve a stress-reduction function. There is also little evidence that females use post-conflict interactions to "repair" their relationships.

Patterns of initiation and directionality of post-conflict interactions rather support the hypotheses that reconciliation constitutes a signal of benign intent and that aggression towards third-parties are used to reassert females' social status. These patterns represent meaningful contrasts compared with findings in other macaques in particular and in other animal species in general, and are related to the females' tolerant social style.

The final study aims at determining the hierarchical and nepotistic influence on social relationships. For this purpose, I investigate links between dominance, kinship, age, social bonds, coalitionary support, and tolerance (feeding in proximity and reconciliation). First, I found that higher-ranking females are not more attractive social partners than lower-ranking ones. Second, kinship does not predict differences in dominance rank. Furthermore, I found that social bonds are strongest between females both kin and close in rank, and similar in age. In contrast, coalitionary support occurs more often amongst females close in rank or across age classes, but not amongst kin or strong affiliates. In addition, tolerance is not influenced by any of the variables tested. The differential effects of the same factors on social bonds, coalitionary support, and tolerance highlight the complexity of social life in tolerant societies, where females form large and diverse affinitive networks.

Through the combination of behavioural and genetic data, my thesis constitutes the first exhaustive study on the social behaviour of females of one of the less-known macaque species under natural conditions, and brings a necessary empirical basis to theoretical frameworks on the evolution of social diversity. The first study supports the idea that social styles are clusters of social behaviour around a certain mode, consistent within but different between species or group of species. I further demonstrate the limited influence of kinship and dominance on social bonds as well as the little importance that strong social bonds have for coalition or social tolerance. These findings raise the question about the adaptive value of the strength of bonds in comparison to their diversity and indicate that these different behavioural strategies can be meaningful in an evolutionary context.

The present theories of social evolution are not entirely satisfactory: major parts of the variation observed in social behaviour remain unexplained. I propose that macaque social styles could be viewed as different coping strategies, or behavioural syndromes, evolved to maximise benefits of sociality. Ultimately, the behavioural syndrome framework not only provides a full account of different behavioural strategies under different contexts and of different individuals from both sexes, but also allows for the examination of proximate mechanisms, ultimate functions and developmental pathways altogether.

The patterns uncovered in this study still remain to be further explained in relation to social (e.g., male influence) and environmental (e.g, competitive regimes) factors. Nevertheless, the picture drawn from crested macaques in this thesis differs substantially from the typical cercopithecine primate model. It also shows the importance of a model of social evolution taking into account all components (the environment, the organism and the social system) to explain fully the diversity of animal societies.

Zusammenfassung

Sozialität ist vorteilhaft für Individuen. Sozialbeziehungen zwischen Individuen können als langfristige Investitionen betrachtet werden, die letztlich individuelle Fitness beeinflussen. Die Analyse der Kosten und Nutzen von Sozialbeziehungen kann daher dazu dienen, herauszufinden wie Individuen mit den Kosten (Wettbewerb) und Vorteilen (Kooperation) vom Gruppenleben umgehen. Theoretische Modelle, die zur Erklärung der existierenden Diversität von Sozialstrukturen im Tierreich dienen, basieren auf der Analyse ökologischer, genetischer, ontogenetischer, phylogenetischer und anderer sozialer Faktoren.

In Säugetieren entwickeln Weibchen häufig intensive soziale Bindungen. Diese Bindungen werden häufig stark von Dominanz- und Verwandtschaftsbeziehungen geprägt, was wiederum Konsequenzen hat für Kooperation im Allgemeinen. Es ist jedoch noch größtenteils unklar, wie Unterschiede in der Stärke und Qualität von solchen sozialen Bindungen auftreten, insbesondere in Bezug auf den Typ der Gesellschaft in der sie auftreten, beispielsweise ob eine Gesellschaft eher despotisch oder egalitär organisiert ist.

Obwohl alle Makakenarten (Gattung *Macaca*) eine gemeinsame Art von sozialer Organisation teilen (Mehrmännchen/Mehrweibchen Gruppen, Philopatrie der Weibchen), treten gleichzeitig markante Unterschiede im Sozialverhalten zwischen den einzelnen Arten auf. Die Unterschiede wurden anhand verschiedener Faktoren erklärt, die von Ökologie bis hin zu Phylogenie reichen, was wiederum zur Klassifizierung der Arten in verschiedene Kategorien führte. Ein Problem dabei ist, jedoch, dass bisher nur einige wenige Makakenarten sehr intensiv erforscht wurden, während viele andere Arten bisher stark vernachlässigt wurden. Diese Unausgeglichenheit unterhöhlt unser Verständnis der Diversität der verschiedenen Sozialsysteme.

Das übergeordnete Ziel dieser Arbeit ist es, durch die Erforschung einer der bisher weniger bekannten Arten, dem Schopfmakaken *M. nigra*, unser Wissen und Verständnis über die Verhaltensdiversität innerhalb der Makaken zu erweitern. Das erste untergeordnete Ziel dieser Arbeit ist es, den Grad sozialer Toleranz zwischen Weibchen zu quantifizieren (Studie 1). Danach erläutere ich die Struktur und Funktion von Sozialbeziehungen zwischen Weibchen. Ich beschreibe die Interaktionen die direkt nach Konflikten stattfinden (Studie 2), und untersuche den Einfluss von Dominanz- und Verwandtschaftsbeziehungen auf Sozialverhalten (Studie 3). Insgesamt können die Ergebnisse dieser Arbeit dazu beitragen, das Zusammenspiel verschiedener Faktoren besser zu verstehen, insbesondere durch den Vergleich der in Schopfmakaken gefundenen Muster mit denen anderer Arten. Darauf aufbauend wird ein theoretischer Rahmen vorgeschlagen, der die Evolution unterschiedlicher Sozialstrukturen im Tierreich zu vereinen sucht.

In der ersten Studie quantifiziere ich eine umfangreiche Reihe von Verhaltensparametern, die dazu geeignet sind den sozialen Stil einer Art zu bestimmen. Die Ergebnisse dieser Studie bestätigen einen toleranten sozialen Stil weiblicher Schopfmakaken, der sich durch Konflikte mit niedriger Intensität, häufiger bidirektionalität, und versöhnung ausdrückt. Asymmetrie in Dominanzbeziehungen ist moderat, was unter anderem durch den bidirektionalen und affiliativen Gebrauch der *bared-teeth* Geste ausgedrückt wird. Weiterhin tolerieren Weibchen gegenseitige räumliche Nähe. Diese Muster stimmen mit denen anderer toleranter Makakenarten überein und liegen außerhalb der für despotische Arten beschriebenen Variation.

In der zweiten Studie untersuche ich die Determinanten und Funktionen von Interaktionen die nach Konflikten stattfinden. Die Kosten von Aggression werden durch Verhaltensindikatoren für Stress gemessen. Weiterhin untersuche ich, ob Charakteristika von Konflikten (z.B. Intensität, Entschiedenheit, Kontext) und der beteiligten Paare (Stärke der sozialen Bande, Häufigkeit von Unterstützung in Konflikten), das Auftreten von Interaktionen *nach* einem Konflikt beeinflussen. Dabei teste ich vier mögliche Funktionen von nach-Konflikt-Interaktionen. Wenig spricht dafür, dass Aggression Kosten beinhaltet, gemessen durch Verhaltensindikatoren für Stress. Es scheint deshalb unwahrscheinlich, dass Interaktionen nach einem Konflikt dazu dienen solchen Stress zu reduzieren. Ebenso unwahrscheinlich scheint es, dass solche Interaktionen dazu dienen die Beziehung zwischen den Tieren zu „reparieren". Im Gegensatz dazu unterstützen die Muster der Initiationen und Richtungen der nach-Konflikt Interaktionen die Hypothese, dass Versöhnung ein Signal für freundliche Intention ist, und dass Interaktionen mit Dritten dem Schutz vor erneuter Aggression dienen. Auch diese Ergebnisse weisen auf den toleranten sozialen Stil von Schopfmakaken hin und kontrastieren mit den Ergebnissen von Studien anderer Makaken- und Tierarten.

Die abschließende Studie beschreibt den Einfluss von Dominanz und Verwandtschaft auf Sozialbeziehungen. Dafür untersuche ich Verbindungen zwischen Dominanz, Verwandtschaft, Alter, sozialen Bindungen, Unterstützung in Konflikten, und soziale Toleranz (Versöhnung und Nahrungsaufnahme in der Nähe anderer Individuen). Die Ergebnisse zeigen, dass hochrangige Weibchen als soziale Partner nicht attraktiver sind als niederrangige Weibchen, und dass Dominanzbeziehungen unabhängig vom Verwandtschaftsgrad sind. Weiterhin kann ich zeigen, dass die stärksten sozialen Bindungen zwischen verwandten Weibchen auftreten, die einen ähnlichen Rang haben und gleichaltrig sind. Im Gegensatz dazu, tritt Unterstützung in Konflikten am häufigsten zwischen Tieren gleichen Ranges und Alters auf, unabhängig vom Verwandtschaftsgrad und der Stärke der sozialen Bindung. Des weiteren konnte keine Beziehung zwischen den getesteten Parametern und sozialer Toleranz gefunden werden. Diese differenzierten Effekte von Beziehungs-Charakteristika unterstreichen die Komplexität des sozialen Lebens in Schopfmakaken. In solch toleranten Gesellschaften formen Weibchen weitreichende und diversifizierte Netzwerke.

Durch die Kombination von Verhaltens- und genetischen Daten, stellt diese Arbeit die erste umfassende Studie über Sozialverhalten unter natürlichen Bedingungen dar, an einer Art über die bisher relativ wenig bekannt ist. Die erste Studie unterstützt die Idee, dass soziale Stile als „Cluster" von sozialen Verhaltensweisen betrachtet werden können. Diese Cluster variieren um einen Modalwert und ähneln sich innerhalb von Arten mehr als zwischen Arten und Gruppen von Arten. Damit können sie auch als *coping* Strategien oder Verhaltenssyndrome betrachtet werden. Weiterhin konnte der geringe Einfluss von Dominanz- und Verwandtschaftsbeziehungen auf die Stärke von sozialen Bindungen nachgewiesen werden, sowie die Abwesenheit eines Effektes der Stärke von sozialen Bindungen auf Koalitionen, Versöhnung, und Nahrungsaufnahme in der Nähe anderer Individuen. Diese Ergebnisse werfen die Frage auf, welchen adaptiven Wert starke soziale Bindungen haben, angesichts ihrer Diversität in Arten in denen soziale Netzwerke gebildet werden. Es kann daher angenommen werden, dass solche Unterschiede zwischen toleranten und despotischen Strategien im evolutionären Kontext bedeutungsvoll waren.

Die vorherrschenden Theorien sozialer Evolution können einen großen Teil der auftretenden Variation im Sozialverhalten nicht ausreichend erklären. Mit dieser Arbeit schlage ich deshalb vor, soziale Stile von Makaken besser als *coping* Strategien oder Verhaltenssyndrome zu betrachten, die sich evolutiv entwickelten, um letztlich die Probleme zu lösen, die mit dem Leben in sozialen

Gruppen einhergehen. Im Rahmen von Verhaltenssyndromen betrachtet können nicht nur verschiedene Verhaltensstrategien in verschiedenen Kontexten und zwischen verschiedenen Individuen erklärt werden, sondern diese erlauben ebenfalls die Integration von Ansätzen um gleichzeitig proximate Mechanismen, ultimate Funktionen, und Ontogenie von Verhalten zu untersuchen.

Die Ergebnisse dieser Arbeit sollten in folgenden Studien durch Quantifizierung weiterer ökologischer (bspw. Wettbewerb um Zugang zur Nahrung) und sozialer Einflussfaktoren (bspw. Männchen) ergänzt werden. Insgesamt weicht das Sozialverhalten von Schopfmakaken, wie ich in dieser Arbeit beschreibe, substantiell von dem ab, was normalerweise als typisch für cercopithecine Primaten angesehen wird. Dies unterstreicht letztlich die Wichtigkeit, sowohl externe (Umwelt), als auch interne Komponenten (Sozialsystem) zu betrachten, um die Diversität von Tiergesellschaften zu erklären.

CHAPTER 1

GENERAL INTRODUCTION

Natural selection should favour the evolution of sociality whenever the benefits of living with conspecifics outweigh the costs (Alexander 1974; Standen & Foley 1989). In this context, social behaviour is adaptive in the sense that behavioural strategies can influence individual fitness. Understanding the emergence and evolution of sociality under its diverse forms and degrees is a major endeavour on the science agenda since Darwin has laid down the theory of natural selection (Darwin 1859).

A group, or social unit, can be defined as a set of individuals of the same species sharing a certain degree of proximity in time and space, and interacting with each other to a greater degree than with other conspecifics (Krause & Ruxton 2002; Wilson 1975). A great diversity of social systems exists. They can be studied at three levels, the social organisation (size, sex and age composition and spatiotemporal association of individuals), the mating system (assortment and mating strategies of the sexes and the consequences of those on the genetic structure of groups), and the social structure (patterning of social relationships between dyads of conspecifics, stemming from their repeated social interactions with each other) (Kappeler & van Schaik 2002). Living with conspecifics can bring better protection against predators, optimal foraging for resources and access to mates, communal rearing of young and information transmission, but it also incurs costs such as heightened competition for access to resources (food, mates and social partners), and increased risk of parasite or disease transmission (Krause & Ruxton 2002; Pulliam & Caraco 1984; Standen & Foley 1989; van Schaik 1983). Furthermore, living in groups involves the simultaneous exploitation of resources and the coordination of activities, which can generate conflicts of interest (Alexander 1974; Krause & Ruxton 2002). As an outcome, individuals form and maintain societies on the basis of a complex combination of cooperation and competition (de Waal 1986; Dunbar 1989). In stable societies, social relationships are considered as investments, buffering individuals against the negative correlates of group-living (Kummer 1978). Variation in the nature and structure of social relationships therefore affects the fitness of individuals (East & Hofer 2010; Silk 2007a; Silk 2012).

To understand the different strategies that individuals develop in order to balance the costs and benefits of living in groups, a major endeavour is to assess how individuals interact with each other, what kind of relationships they form and whom with preferentially, and to investigate the factors influencing these relationships; in other words, it is necessary to study the social structure of groups. In this chapter, since mammals form some of the most complex societies, and females are often at the core of these societies, I will first review the nature, structure and function of social relationships in female mammals in general, and in female primates in particular. I will present

theories aiming to explain social diversity, with an emphasis on social structure. I will introduce macaque societies and highlight the reasons why they constitute a suitable model for the study of variation in social behaviour. The main aim of my thesis is to foster our understanding of this variation through the study of the nature (Chapter 2), structure and function (Chapter 3 and 4) of female social relationships in one of the less-known macaque species. Ultimately, my aim is to provide a better understanding of social variation in a comparative perspective and a framework allowing to link external and internal factors playing a role in the evolution of animal societies.

1.1 The sociality of female mammals

In most gregarious mammals, females are the philopatric sex. They have the potential not only to form dominance hierarchies so as to control access to resources, but also to build enduring cooperative relationships in order to enhance their health and fitness (Silk 2007a). Although fundamental principles regulate and organise the social life of female mammals, a great diversity in social structure exists, at the level of social interactions and relationships, and reflects how females deal with the costs and benefits of sociality.

1.1.1 Nature of social relationships

A social relationship is built from repeated interactions between a dyad of individuals (Hinde 1976). Social interactions can be described in terms of their content, frequency, quality, and patterning (Hinde 1976; Whitehead 2008). Ultimately, these different types of information define the strength and quality of relationships: competitive or cooperative, friendly or agonistic, strong or weak, for example. In general, close or strong social bonds are defined as social relationships in which the exchange of interactions is common, positive, balanced, and stable (Silk 2012). The integration and balance between competitive and cooperative relationships deeply influence the type of society that individuals form - for instance despotic or egalitarian - and shape their communication, cohesion and cooperation patterns. The nature of social relationships is also related to their structure and function in the sense that individuals interact differently with partners of varying qualities to fulfil different goals.

1.1.2 Structure and function of social relationships

1.1.2.1 Dominance

A high dominance status confers multiple advantages. Compared to low-ranking individuals, high-ranking individuals are likely to have better access to resources, to start reproducing earlier, and to produce more offspring that reach high social status, mature earlier and survive better (Alberts 2012; Ellis 1995; Pusey 2012). The determinants of the places that individuals reach in the hierarchies or of their access to resources are numerous: age and size in female African elephants *Loxondota africana* (Archie et al. 2006), arrival order and ownership at carcasses in African lions *Panthera leo* (Packer et al. 2001), or maternal rank inheritance and capacities to recruit allies in cercopithecine primates (Cords 2012) and spotted hyenas, *Crocuta crocuta* (Holekamp et al. 2012). In the latter taxa, and in numerous primates, social power may also outweigh individual power: an individual with low competitive ability but high capacity to recruit allies can enjoy the privileges of being high-ranking (Flack & de Waal 2004; Harcourt 1989). Power asymmetries between individuals can thus be more or less pronounced in relation to ecological or social conditions and benefits of high rank can be limited. The characteristics of a hierarchy thus influence interactions between individuals, in the sense that weak power asymmetries promote negotiation and social exchanges between individuals, whereas strong power asymmetries may limit social exchanges.

1.1.2.2 Cooperation

Traditionally defined as actions providing benefits to recipients while imposing costs on the actors (e.g. Clutton-Brock 2009), cooperative acts can be considered as any assistance, help or support actively provided by individuals to others (Lingon 1991; Noë 2006; van Schaik & Kappeler 2006). Cooperation represents behavioural tactics used by individuals to obtain resources or enhance reproductive success (Dugatkin 1997; Sussman & Garber 2011). Group members can share resources (e.g. vampire bats, *Desmondus rotundus*, Wilkinson 1984a, b), exchange grooming (e.g. non-human primates, Schino & Aureli 2008a), or interchange support and tolerance for resource acquisition and defence (e.g. spotted hyenas, *C. crocuta*, Smith et al. 2007).

The investigation of the determinants of cooperation is an active field and has prompted the development of several frameworks, based on kin selection (Hamilton 1964a, b), reciprocal altruism (Trivers 1971) or biological market (Noë & Hammerstein 1995). Cooperation between non-kin as

well as the exchange of commodities with differential or delayed payoffs especially has generated a wealth of studies (reviewed in Clutton-Brock 2009; Dugatkin 1997, 2002a, b; Kappeler & van Schaik 2006). Although establishing close social bonds is definitely not a prerequisite for cooperation to occur (Clutton-Brock 2009; van Schaik & Kappeler 2006), pairs of close associates cooperate better, exchange goods or services more equitably, and resolve conflict of interest faster or more often than pairs with "weaker" bonds (chacma baboons, *Papio ursinus*, Silk et al. 2006a; macaques, *Macaca sp.*, Petit et al. 1992; ravens, *Corvus corax*, Fraser & Bugnyar 2012; Camargue horses, *Equus cabalus*, Feh 1999; hyenas, *C. crocuta*, Holekamp et al. 2007; Smith et al. 2007; Smith et al. 2011). However, it has also been argued that the patterning of cooperative acts, and the choice and stability of cooperation partners, is contingent on internal, demographic and ecological pressures, rather than on relationship quality between partners. For instance, pregnant or early lactating female chacma baboons are less likely to be involved in coalitions and they would not be reliable cooperation partners, kin or not kin (Barrett & Henzi 2001). Similarly, weak power asymmetries may preclude the interchange of rank-related benefits against other goods or services, whereas strong power asymmetries may facilitate it (Barrett et al. 1999; Noë et al. 1991).

1.1.2.3 Conflict resolution and management

Conflict resolution and management strategies represent the balance between competition and cooperation. They are thus essential for the cohesion and coordination of a society (Aureli & de Waal 2000). Group members cannot always prevent conflicts of interest to escalate into aggression. Aggression is costly and risky and may furthermore jeopardise social bonds and their associated benefits (van Schaik & Aureli 2000). To mitigate the disruptive consequences of aggression, post-conflict mechanisms are powerful social tactics. The function of post-conflict interactions has been investigated predominantly in human and non-human primates. They mainly serve to reduce the stress experienced by opponents and/or bystanders, to re-establish social tolerance, to facilitate subsequent affiliations between individuals, and to lessen the risk of further attack (Aureli et al. 2012). Despite their advantages however, the occurrence, frequency and form of post-conflict interactions vary greatly between individuals or species. These differences have been linked to the degree of power asymmetries and social cohesion between individuals (e.g. macaques, Thierry et al. 2008; spotted hyenas, Hofer & East 2000; Smith et al. 2008), and to conflict and dyad characteristics (e.g. degree of relatedness and strength and/or quality of social bonds in primates, Arnold & Aureli 2006; Aureli et al. 2012).

1.2 Consequences of variation in social relationships within a social structure

As reviewed above, it is well appreciated that social relationships have the potential to provide short-term and long-term benefits. Dyads of individuals forming "valuable" relationships, in terms of degree of relatedness, strength of bonds or frequency of support in aggression, cooperate better, in the largest sense, than others (Aureli et al. 2012; Silk 2007a). Variation in the strength of social bonds can influence reproductive success (bottlenose dolphins, *Tursiops sp.* Frère et al. 2010; feral horses, *Equus caballus* Cameron et al. 2009; Assemese macaques, *M. assamensis* Schülke et al. 2010). It also affects longevity and survival (chacma baboons, *Papio hamadryas ursinus* Silk et al. 2010; Silk et al. 2009; Barbary macaques, *M. sylvanus* McFarland & Majolo 2013). In humans, social support is also related to health and well-being, especially in women (Cohen & Wills 1985; Taylor et al. 2000; Uchino 2006). However, the strength of bonds can be as important as, if not more important than, the diversity of these bonds within a social network. Females in particular may cope better with stress if they have developed a tight network of strong grooming relationships than a more diverse one (Cheney & Seyfarth 2009; Crockford et al. 2008).

The establishment of social bonds of varying strength and quality has thus direct consequences on the costs and benefits of sociality. Nevertheless, it is still unclear what drives these differences. The strength and quality of bonds can vary according to ecological conditions such as the availability of resources or demography fluctuations (Barrett & Henzy 2001; East & Hofer 2010; Sterck et al. 1997; Wrangham & Rubenstein 1986). It may also vary according to the type of societies individuals live in, i.e. with the degree of power asymmetries between individuals, the availability of kin, or the personality of individuals. For example, in macaques, a more relaxed social style, i.e. low intensity conflicts and moderate power asymmetries, fosters the development of large affinitive networks which lessen the importance of dominance and kinship in the choice of social partners (Flack & de Waal 2004; Sueur et al. 2011; Thierry 2013; Thierry et al. 2008). In chacma baboons, females with a "nice" personality have more numerous and stable strong bonds than females with a "loner" personality (Seyfarth et al. 2012). The numerous factors influencing the strength and quality of social bonds within a group highlight the need for a comprehensive theoretical framework of social evolution.

1.3 Models of social evolution

In mammals, females invest heavily into reproduction and the critical resource they should optimise access to is food (Trivers 1972). To this end, favourable traits include competitive skills in order to contest successfully, and social skills in order to establish and maintain alliances, and cooperate effectively (Silk 2007a). Several explanatory models have been proposed to explain the social diversity observed in the patterning of interactions between females.

1.3.1 The ecology of female social relationships

The socioecological model emphasises the role of ecological factors in shaping not only grouping patterns but also social relationships between group members (Alexander 1974; Krause & Ruxton 2002; Krebs & Davies 1997; van Schaik & van Hooff 1983; Wrangham & Rubenstein 1986). In primates, it has been suggested that females form cooperative ("female-bonded" group) or undifferentiated relationships ("non-female-bonded" groups) in relation to the strength of feeding competition, mainly between groups (Wrangham 1980). Since then, this model has been expanded to take into account competition within-groups, as well as competition for safety from predator and from harassing conspecifics. Availability, distribution, abundance and predictability of food resources shape females' social strategies within their group or social unit (Sterck et al. 1997; van Schaik 1989). Depending on the level (within- or between-group), the degree (contest or scramble) and the intensity (high or low) of competition, females disperse from or stay in their natal group, they form more or less linear, nepotistic or individualistic hierarchies, and they cooperate and associate mainly amongst kin or form undifferentiated relationships. Other factors may directly affect female social relationships such as males' reproductive strategies in relation to females' ones (Schülke & Ostner 2012; Sterck et al. 1997).

Although this model has often been successful at explaining grouping patterns, the effect of ecological conditions on social relationships is less clear: there is indeed tremendous intra-species and inter-individual variation, which makes it sometimes difficult to establish general patterns (Lott 1991). In addition, the socioecological models assume great flexibility in the social behaviour of individuals, who should seek to maximise their fitness by constantly adapting their behavioural strategies to local environmental and social conditions (Krebs & Davies 1997).

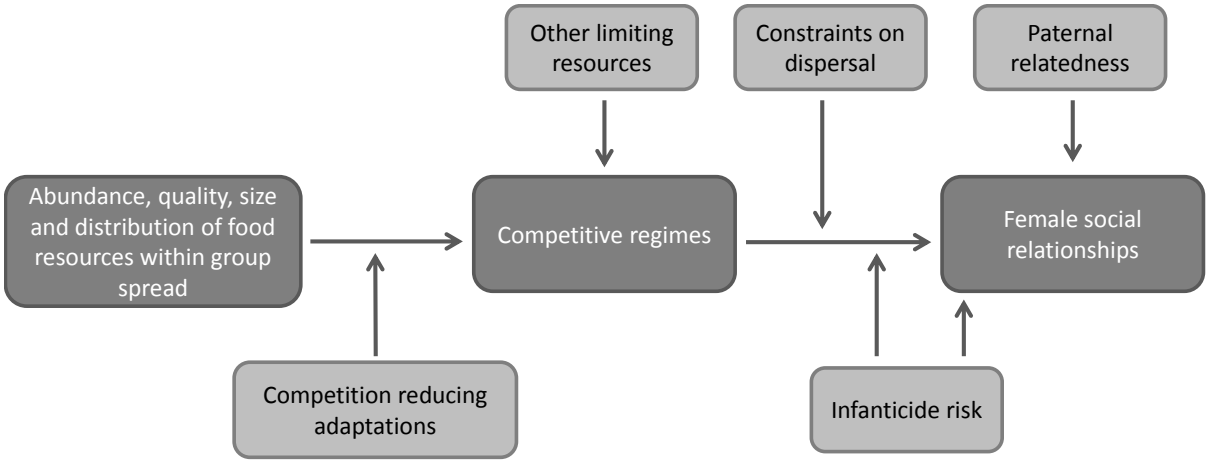

Figure 1.1 Representation of the current socioecological model on the ecology of social relationships amongst female primates (adapted from Schülke & Ostner 2012; see also Sterck et al. 1997; van Schaik 1989).

Although this may be true for some mammals (e.g. Schradin 2013), variation in social behaviour is also influenced and constrained by genetic, developmental, and social factors as well as by the phylogenetic past of species (Clutton-Brock et al. 2009; Holekamp et al. 2013; Kappeler et al. 2013; Sachser et al. 2013; Thierry 2013; Wrangham & Rubenstein 1986). This is especially true in primates at the level of the social structure. Given that social individuals do not live in isolation but are also influenced by the behaviour of their group mates, sociality cannot be understood solely as an adaptation to the physical or ecological environment (Kotrschal et al. 2010).

1.2.2 Theories on the evolution of cooperation

The benefit that individuals get directly from forming social relationships constitutes a major driving force of sociality. The evolution of cooperation between group members has been explained by the benefits of living with kin (kin selection theory; Hamilton 1964a), and of exchanging goods and services regardless of the degree of relatedness (reciprocal altruism theory, Trivers 1971, 2006; biological market theory, Noë & Hammerstein 1994, 1995; mutualism or by-product mutualism; all reviewed in Dugatkin 1997, 2002b; see also Bshary & Bergmüller 2008). As such the choice of cooperation partners is based on the balance between the goods and services that individuals can exchange, the costs and benefits of the exchanges, and the competence of individuals to exchange

them, in terms of willingness or capabilities. Consequently, the choice of cooperation partners varies greatly between societies, in relation both to the characteristics of these societies, despotic and egalitarian for example, and to offer/demand principles (based on the availability of resources for example).

1.2.3 Other constraints on social behaviours

Social behaviours are not isolated from each other. Social traits are linked at different levels, genetic, phenotypic and social, and these linkages shape individual and social profiles.

Although behaviours are flexible traits and reflect the individuals' response to their social and ecological environment, animals are usually consistent in their responses across contexts and situations and thus, they often exhibit limited behavioural plasticity, compared to what would be expected in a given environment (Bergmüller 2010; Sih et al 2004a; Sih 2011). Individuals display robust personalities (also labelled temperaments, behavioural tendencies, behavioural syndromes, etc.; Sih 2011), that have been shown to have evolutionary relevance because they are linked to fitness (e.g. Dingemanse & Reale 2005; Sih et al. 2004a,b; Sih 2011). For example, proactive individuals readily explore the environment and form persistent routines, whereas reactive individuals adjust cautiously to changes in the environment; thus reactive individuals may outcompete proactive ones in stable conditions, but proactive ones may cope better under more unstable conditions (Sih et al. 2004a). At the proximate level, behavioural tendencies are regulated by complex genetic-neurological-physiological pathways and feedback loops (Adkins-Regan 2005; Anestis 2010; Capitanio 2004; Mendoza & Mason 1989; Sih 2011). For example, reactive individuals show higher reactivity of the hypothalamic-pituitary-adrenal (stress) axis and of the sympathetic nervous system, associated with the "flight-or-fight" response, but lower reactivity of the parasympathetic nervous system, associated with maintenance activities, than proactive ones (Koolhaas et al. 1999). These regulation processes are parts of internal systems constraining individual behaviour, especially because they are responsible for important pleiotropic and epigenetic effects which generate correlations between characters (Price &Langen 1992).

Likewise, behaviours are also correlated across contexts. Individuals who are especially aggressive towards conspecifics for example also tend to be bold in front of predators (Sih 2011). Behavioural syndromes, i.e. the "*suite(s) of correlated behaviours reflecting between-individual consistency in behaviour across multiple situations*" can explain trade-offs between behavioural

strategies and the evolution of different equally adaptive coping styles (Sih et al. 2004a (p. 372); Sih 2011). The recognition of this phenomenon has been a real breakthrough in the understanding of the adaptive significance of behavioural flexibility and constraints, and the trade-offs generated thereof, in an evolutionary context, both at the individual and species levels (Sih et al. 2004b). Indeed, conspecifics or individuals of the same populations are more similar to each other than others, which create species-specific "modal tendencies" contributing to inter-specific variations (primates, Capitanio 2004; Mendoza & Mason 1989). Maternal effects and characteristics of the social environment during development have also been shown to affect strongly offspring, and consequently adult, behavioural phenotypes, which to some extent are genetically and socially inherited (Kappeler et al. 2013; Sachser et al. 2013). Another level of constraints on social behaviour is the tendency for phylogenetically close species to resemble each other more than they resemble others. The implication is that it may limit the variation of traits through a limited responsiveness of an ancestral trait to new selection pressures or a similar response to different ecological problems (Kamilar & Cooper 2013). By case, species-specific behavioural syndromes are viewed as an important aspect of speciation (Sih et al. 2004a).

The interaction of individuals at the social level adds a further layer of complexity in the regulation of social behaviour. Within a social structure, social traits are linked in ways that make some combination of traits more likely than others. For example, when aggression is risky or costly - with high risk of injury or high likelihood of losing the contested resources - the weaker individuals are better off avoiding direct confrontation, and acknowledging their lower status (Maynard-Smith 1974; Pope & de Vore 1979). As an outcome, this ultimately generates strong dominance hierarchies accompanied with signals of lower social status (Preuschoft and van Schaik 2000). In turn, strong dominance hierarchies regulate interactions between individuals, who display a strong preference for their kin as cooperation partners (Chapais 2004; Emlen 1997; Flack & de Waal 2004). Linkages between traits mean that a change in one character can introduce a chain of changes in others. However, some changes may occur at some costs, or with some resistance from the system if, for example, a change in a correlated trait that is not the target of selection would be deleterious (Bergmüller 2010; Price & Langen 1992; Sih et al. 2004a).

Thus, individuals can retain some behavioural flexibility while being constrained within a species-specific reaction norm (Dingemanse et al. 2010; Mendoza & Mason 1989; Mendoza et al. 2002). Understanding how individuals interact with each other, what kind of relationships they form, and which factors influence these relationships requires the account of a broad range of mechanisms and processes together with a comparative perspective allowing to contrast different societies with each other.

1.4 Macaque societies: a study model of variation in social structures

1.4.1 Socioecology of macaques

The genus *Macaca* (Mammalia: Cercopithecidea) is at the same time a homogenous and diverse taxon. It is a monophyletic group belonging to the sub-family cercopithecinae and one of the most widespread non-human primate genera, ranging from Morocco to Japan. The genus emerged about seven million years ago and diversified five to six million years ago into different phyletic groups while colonising Eurasia (Fooden 1980). Twenty two species of macaques are presently recognised and three lineages have been identified, corresponding to three waves of colonisation of Asia (Abegg & Thierry 2002; Delson 1980; Fooden 1980, 1982; Thierry 2007). Macaques are ubiquitous and live in a wide range of habitats, from equatorial to temperate ecosystems, to primary rain forests and grassland. Group size varies from a dozen individuals up to some hundred in anthropogenic habitats. Most macaques are frugivorous but their diet can be highly flexible, depending on species, and includes seeds, roots, leaves, grass, flowers, insects, fungi, and small vertebrates, such as snakes, birds or bats (Ménard 2004).

On the one hand, macaques share the same social organisation: they live in multi-male multi-female groups, where females are philopatric, i.e. they stay in the group they were born in, and live with both kin and non-kin partners, whereas males migrate upon reaching sexual maturity and throughout their lives (Pusey & Packer 1987; Thierry 2011). On the other hand, the different species of macaques show great variation in their social structures. In some species, females form strict linear matrilineal hierarchies, where daughters assume the hierarchical rank just below the one of their mother, and they preferentially interact, associate and support with kin throughout their life (Cords 2012; Thierry 2011). Other species show variation around this theme, with, at the extreme, weak power asymmetries and little kin bias in social interactions (Thierry 2007). These differences have been explained along different lines, from ecology to phylogeny, which are not exclusive from each other, and which I will review in the next paragraphs.

1.4.2 Variation in macaque societies

1.4.2.1 The concept of social tolerance

Living in a group is a form of social tolerance as individuals have to contend with the presence, proximity and interference of conspecifics. Theories on the evolution of cooperation in animal societies indeed provide frameworks to understand how individuals deal with each other in the context of group living (Axelrod & Hamilton 1981; Dugatkin et al. 1992; Hamilton 1964a, b; Maynard Smith 1976; Trivers 1971; Vehrencamp 1983). Vehrencamp (1983)'s reference to despotic vs. egalitarian systems describes the balance "*between the forces of cooperation and competition*", leading to a bias in fitness benefits between group members: "*In egalitarian societies, benefits are divided roughly equally or in proportion to the risk or effort taken. In despotic societies, on the other hand, benefits accrue disproportionately to a few individuals in the group at the expense of others*." (p. 667).

In the socioecological model, egalitarianism or tolerance refers to shallow hierarchies in which dominant individuals do not fully restrain subordinates' access to resources. de Waal (1989a) was one of the first to explicitly define social tolerance as a "*low competitive tendency especially by dominants towards subordinates*" (p. 245) and states that "*in addition to dominance, social tolerance and variations in motivation determine the outcome of competition*." (p. 247). To explain contrasts between macaque species, Thierry (2013) brings a more general view of social tolerance that does not only focus on competition. Varying degrees of social tolerance reflect "*stable clusters of behavioural traits connected by numerous links*" (p. 6): these sets of interrelated behavioural traits are consistent within but different between species or group of species (Thierry 2000, 2007, 2013). Such a perspective is germane to the concept of behavioural syndromes proposed at the personality level (Sih et al. 2004a). This broader line of thought can encompass all components of a social system, as well as the variation within. In this section, I will review the existing variation in macaques' social behaviour and link it to the various conceptions of social tolerance.

1.4.2.2 Variation related to feeding competition

In the model about the ecology of females' social relationships, macaques have been divided into two social categories: the "Resident-Nepotistic" category (RN; all macaques but the Sulawesi-macaque group) and the "Resident-Nepotistic-Tolerant" category (RNT; the Sulawesi-macaque group; Sterck et al. 1997). The model assumes that RN category evolved under high predation

pressure and strong within-group feeding competition, leading to female philopatry, strict linear matrilineal hierarchies and cooperation predominantly amongst kin. With regard to the RNT category, it would have evolved under low predator vulnerability, strong between-group, and possibly within-group, feeding competition, leading to female philopatry, linear hierarchies but "tolerant" dominance relationships between females: higher-ranking females are thought to allow lower-ranking ones access to resources, be they ecological or social, in exchange for their participation in resource defence against other groups (Sterck et al. 1997).

Several studies on the feeding ecology of macaques have been carried out, most of them aiming at testing the relation between feeding competition and female social relationships (e.g. Cooper 2004; Hanya et al. 2008; Heesen et al. 2013; Ménard 2004; van Noordwijk & van Schaik 1987; van Schaik & van Noordwijk 1988). These studies have found patterns that are not always consistent with the predictions of the socioecological model. Furthermore, a comparison of the patterns of between-group competition - through observable intergroup encounters - across macaque species contradicted the female resource defence hypothesis (Cooper 2004). Thus, the impact of between-group competition on the within-group tolerance of females is unclear. Most importantly, few studies have been carried out on RNT species under natural conditions; thus knowledge of their social behaviour in relation to ecological and social factors is incomplete.

1.4.2.3 Variation related to kinship

According to the socioecological model, females live with kin because the cost of dispersal outweighs the cost of competing with kin (Sterck et al. 1997). "Alliances" amongst kin are thus preferred, and hierarchies are usually matrilineal because closely genetically related females support each other in aggression (Cords 2012). Indeed, females show higher frequencies of grooming, co-feeding, and reconciliatory behaviour amongst kin than non-kin (reviewed in Silk 2006 and Chapais & Berman 2004), creating a clear differentiation between matrilines (Chapais 1992; Chapais & Berman 2004). However, this is only one side of the picture. In some macaque species, such as Barbary macaques or the Sulawesi-macaque group, kin bias in social interactions is less pronounced (Thierry 2007). The socioecological model relates this difference to increasing between-group competition (see above), which would favour cooperation between kin and non-kin alike, although tests of this hypothesis in relation to ecological conditions are inconsistent (see above). Similarly, the "strength of competition model" relates the strength of direct competition for food to the degree of rank-related fitness differentials (strong competition = high rank-related fitness differential). "Alliances"

with kin or with non-kin are consequently more or less advantageous, which leads to the evolution of different "dominance style" (despotic vs. egalitarian) and, concurrently, to more or less nepotistic hierarchies (Chapais 2004). This model also remains to be properly tested.

Male reproductive skew and its consequence on the degree of relatedness between females have recently been proposed as an important factor explaining the difference in "social tolerance" between macaque species (Schülke & Ostner 2008). Indeed, a high male reproductive skew increases the overall degree of relatedness of the group by generating cohorts of age peers that are paternally related. This higher degree of relatedness could thus increase cooperative relationships between related females, both from the maternal and paternal lines. Studies on kin bias usually account only for maternal relatives, and may thus have mistaken an absence thereof because paternal relatives bridge matrilines (Schülke & Ostner 2008). Since competition amongst males for fertilisation is dependent on female cycle synchrony itself related to environmental seasonality, the degree of male reproductive skew has not been thought to be related to the patterning of social relationships between females (Thierry 2004). A recent analysis, although preliminary, indicates that it may nevertheless be the case (Schülke & Ostner 2008).

1.4.2.4 Variation related to social behaviour

Knowledge on macaque social structures is heavily biased towards a few species, such as rhesus, *M. mulatta*, or Japanese, *M. fuscata*, macaques. It is mainly based on studies in captive or provisioned settings. Variation in social structure was recognised when comparisons between different species were carried out: amongst other characteristics, rhesus and Japanese macaques engage in conflicts of high intensity (i.e. with biting), mainly unidirectional and seldom reconciled (Chaffin et al. 1995; de Waal & Luttrell 1989). There is pronounced dominance asymmetry between individuals, and the silent bared-teeth display serves as a formal submissive signal (de Waal & Luttrell 1985; Preuschoft & van Schaik 2000). In addition, dominance rank and kinship markedly constrain social interactions (Chapais 1983). In contrast, species such as Barbary (*M. sylvanus*) and Tonkean macaques (*M. tonkeana*) display mild, often bidirectional and frequently reconciled conflicts (Demaria & Thierry 2001; Petit et al. 1997; Thierry 1985). Dominance asymmetries seem less pronounced, and the silent bared-teeth display appears to be an appeasement signal (Petit & Thierry 1992; Thierry et al. 2000a). Affiliation occurs with limited influence of dominance and kinship relationships (Matsumura & Okamoto 1997; Thierry et al. 1994).

The variation observed between the social styles of macaque societies gave rise to the formulation of the covariation model which states that the social relationships of macaques range within a socio-space defined by linkages between traits (Thierry 2004, 2013). Contrary to the socio-ecological model which is based on the action of ecological factors (i.e. external determinants), the covariation model emphasises the interconnection between traits and the action of self-organizing principles (i.e. internal determinants) (Hemelrijk 1999; Thierry 2004, 2013). Correlations between social styles and phylogenetic relatedness have also been found (Thierry et al 2000, 2008; Balasubramaniam et al. 2012a). Based on behavioural differences between species, macaques have been arranged along a four-grade scale of social styles, ranging from despotic (grade 1) to tolerant (grade 4; Table 1.1). This classification resembles to some extent, but in more details, the classification of the socioecological model (Sterck et al. 1997).

Table 1.1 Tentative scaling of macaque social styles (grade 1: despotic, grade 4: tolerant; from Thierry 2007).

Grade 1	Grade 2	Grade 3	Grade 4
M. mulatta Rhesus macaques	*M. fascicularis* Longtailed macaques	*M. arctoides* Stumptailed macaques	*M. tonkeana* Tonkean macaques
M. fuscata Japanese macaques	*M. nemestrina* Pigtailed macaques	*M. sylvanus* Barbary macaques	*M. maurus* Moor macaques
M. cyclopis Taiwan macaques	*M. assamensis* Assamese macaques	*M. silenus* Liontailed macaques	*M. nigra* Crested macaques
	M. thibetana Tibetan macaques	*M. radiata* Bonnet macaques	*M. brunnescens* Muna-Butung macaques
		M. sinica Toque macaques	*M. ochreata* Booted macaques
			M. hecki Heck's macaques
			M. nigrescens Gorontalo macaques
			M. siberu Siberut macaques

The social behaviour of the grade-4, or RNT, macaque species has been far less studied than the one of its grade-1 or 2, or RN, counterparts, especially under natural conditions. Most of the data come from a patchwork of captive and provisioned populations, where variation in demography and environment is limited or constrained. Furthermore, divergent results have been found between studies of grade-4 macaques' social structure. For example, the sole study on a

natural, but provisioned, population of Moor macaques, classified as grade-4, showed an absence of counter-aggression in conflicts, which is utterly unexpected (Matsumura 1998). Related to kin bias, while some captive studies found that kinship and dominance had limited influence on grooming (Bernstein & Baker 1988; Thierry et al. 1990), others on several captive and one wild populations showed that kinship was a good predictor of associations and interventions in conflicts between individuals (Baker & Estep 1985; Matsumura & Okamoto 1997; Petit & Thierry 1994a). It is thus unclear whether these discrepancies reflect intra-species variability within a species-specific reaction norm, or depend on demographic and environmental conditions, or whether they constitute meaningful inter-species differences (Hill 2004; Thierry 2000).

1.5 Aims of the thesis

Our knowledge of macaque societies thus appears biased: the lack of studies at one end of the variation continuum seriously undermines our understanding of the social diversity therein. The specificities of grade-4 macaque social behaviour as we know it so far raise interesting questions about the nature, structure and function of social relationships between females of these species with respect to the costs and benefits of sociality.

The overall aim of my thesis is thus to foster our knowledge and understanding of the diversity in macaque societies by studying one of the less-known ones, the crested macaque, *Macaca nigra*, provisionally classified as RNT/grade-4, under natural conditions. A particular objective of my thesis is to assess the degree of social tolerance between females as this has never been done under completely natural conditions.

In the first study (Chapter 2), I investigate a whole set of behavioural variables the expression thereof is suggested to reflect the social style of the species. I specifically analyse the degree of power asymmetries, the directionality and context of the silent bared-teeth display, and the conciliatory tendency. I also look at the distribution of grooming and approach in close proximity amongst group females to determine the diversity of their social networks.

I then more specifically tackle the study of the structure and function of social relationships between females by investigating two important social patterns linked to social style, post-conflict interactions (Chapter 3) and hierarchical and nepotistic influences on social behaviour (Chapter 4). In Chapter 3, I study the determinants and functions of post-conflict interactions. I analyse the “costs” of aggression, and its influence on behavioural indicators of anxiety. I then investigate the relationship between the characteristics of conflicts (e.g. intensity, decidedness, or context), the

characteristics of dyads involved in conflicts (e.g. strength of the social bond, or frequency of support in the dyad), and the occurrence of post-conflict interactions in order to analyse their potential functions. Finally, in Chapter 4, I analyse the strength of hierarchical and nepotistic influences on social relationships. I specifically investigate the strength of social bonds, the frequency of coalitionary support, of tolerance around resources and of reconciliation. I particularly confront my results with the different predictions of the socioecological and covariation models.

The ultimate aim of my thesis, through the provision of novel insights on a supposedly different species, is to reflect on the interplay between different factors in a comparative perspective and to provide a framework tentatively encompassing them all for a better understanding of the evolution of diverse animal societies.

.

CHAPTER 2

SOCIAL TOLERANCE IN WILD FEMALE CRESTED MACAQUES (*MACACA NIGRA*)

Julie Duboscq, Jérôme Micheletta, Muhammad Agil, J. Keith Hodges, Bernard Thierry & Antje Engelhardt.

American Journal of Primatology (2013), 75, 361-375.

doi: 10.1002/ajp.22114

2.1 Summary

In primates, females typically drive the evolution of the social system and present a wide diversity of social structures. To understand this diversity, it is necessary to document the consistency and/or flexibility of female social structures across and within species, contexts and environments. Macaques (*Macaca* sp.) are an ideal taxon for such comparative study, showing both consistency and variation in their social relations. Their social styles, constituting robust sets of social traits, can be classified in four grades, from despotic to tolerant. However, tolerant species are still understudied, especially in the wild. To foster our understanding of tolerant societies and to assess the validity of the concept of social style, we studied female crested macaques, *Macaca nigra*, under entirely natural conditions. We assessed their degree of social tolerance by analysing the frequency, intensity and distribution of agonistic and affiliative behaviours, their dominance gradient, their bared-teeth display and their level of conciliatory tendency. We also analysed previously undocumented behavioural patterns in grade 4 macaques: reaction upon approach and distribution of affiliative behaviour across partners. We compared the observed patterns to data from other populations of grade 4 macaques and from species of other grades. Overall, female crested macaques expressed a tolerant social style, with low intensity, frequently bidirectional and reconciled conflicts. Dominance asymmetry was moderate, associated with an affiliative bared-teeth display. Females greatly tolerated one another in close proximity. The observed patterns matched the profile of other tolerant macaques and were outside the range of patterns of more despotic species. This study is the first comprehensive analysis of females' social behaviour in a tolerant macaque species under natural conditions and as such, contributes to a better understanding of macaque societies. It also highlights the relevance of the social style concept in the assessment of the degree of tolerance/despotism in social systems.

2.2 Introduction

In non-human primates, females typically drive the evolution of the social system, highlighting the importance of focusing on females when studying primate social evolution (Clutton-Brock & Lukas 2012; Lindenfors et al. 2004). Female primate social structures vary greatly between species, ranging from females forming loose and changing associations, to females establishing stable bonds with a subset of partners (Wrangham 1980). Different conceptual frameworks exist to explain the evolution of this social diversity. Variation in social structures may reflect ecological pressures – mainly predation and food abundance and distribution – which would shape not only the grouping patterns of females (i.e. dispersal vs. philopatry) but also their social relationships (Koenig 2002; Sterck et al. 1997; van Schaik 1989). Alternatively or additionally, relations between behavioural traits, phylogenetic constraints and/or self-organizing principles may limit the flexibility and plasticity of social structures, and thus constrain their evolution (Hemelrijk 1999; Thierry 2007). Quantifying the consistency and/or flexibility of female social relationships across contexts and environments, within and across species, is a necessary strategy in understanding their evolution.

Female primate social structures result from a complex combination of cooperative and competitive interactions (Hinde 1976). Furthermore, an individual's social behaviour is influenced both by ecological and social pressures, that is, the strategies of conspecifics (Wrangham 1987). Thus, previous studies on female-bonded groups (i.e. with female philopatry) have not only investigated ecological factors influencing female social relationships (Koenig 2002), they also have looked at the various social trade-offs faced by females in terms of cooperation and competition. One such trade-off is exemplified by the degree of social tolerance between dominant and subordinate individuals, which has shaped alternative conflict management strategies (de Waal 1986), tightly linked to sociality, and potentially, differential access to resources, whether social or ecological (van Schaik 1989).

Macaques (*Macaca* sp.) are an ideal taxon in which to investigate the determinants of social behaviour because they show both consistency and variation in their social relations. They also live in a great variety of environments (Fooden 1982). Most macaques form multi-male multi-female groups. Males emigrate upon reaching sexual maturity, whereas philopatric females organize themselves into matrilines, i.e. subgroups of maternal kin (Pusey & Packer 1987). However, patterns of aggressive, submissive and affiliative behaviours, the degree of intensity and symmetry in social interactions, and conciliatory tendencies vary considerably among species (Thierry 2007). Distinctive social styles, i.e. sets of interrelated social traits, are discernible and categorized into four social grades, ranging from despotic to more tolerant (de Waal 1989a; Thierry 2000, 2007). Despotic

species such as rhesus and Japanese macaques (*Macaca mulatta* and *M. fuscata*) engage in conflicts of high intensity, mainly unidirectional and seldom reconciled (Chaffin et al. 1995; de Waal & Luttrell 1989). There is pronounced dominance asymmetry between individuals and the silent bared-teeth display serves as a formal submissive signal (de Waal & Luttrell 1985; Preuschoft & van Schaik 2000). In these species, dominance rank and kinship markedly constrain social interactions (Chapais 1983). In contrast, more tolerant species such as Tonkean and moor macaques (*M. tonkeana* and *M. maurus*) display less severe, more bidirectional and more frequently reconciled conflicts (Demaria & Thierry 2001; Petit et al. 1997; Thierry 1985). Dominance asymmetry is less pronounced, and the silent bared-teeth display is mainly used in affiliative interactions (Petit & Thierry 1992; Thierry et al. 2000a). Affiliation occurs in an extended network of partners with limited influence of dominance and kinship relationships (Matsumura & Okamoto 1997; Thierry et al. 1994).

The concept of an evolved grade-specific social style implies that within a species, interrelated social traits are robust despite variation in the environment. It also implies that social variation within a grade is less pronounced than between grades. So far, most of the knowledge accumulated on macaque societies has come from studies conducted either in captive or provisioned settings, where behaviours and/or the dynamic of interactions may be altered (Asquith 1989; Judge 2000). Furthermore, most studies to date have focused on the despotic end of the social style spectrum (grades 1 and 2) whereas the most tolerant one, grade 4, is the least studied grade (Thierry 2007). Research in captive settings has shown that the behavioural profile of tolerant macaques differs substantially from that of the more despotic rhesus and Japanese macaques for example (Petit et al. 1997; Thierry 1985). Information on wild tolerant macaques is however limited to few studies on the same group of provisioned moor macaques, which showed differences relative to captive populations. Counter-aggression, for instance, was, unexpectedly, not observed (Matsumura 1996, 1998; Matsumura & Okamoto 1997). Whether counter-aggression is really absent in this species or whether this finding is related to difficult observation conditions or to the inadequacy of the dataset is unknown. More information on tolerant macaques under natural conditions in the wild is clearly needed.

To extend our knowledge of social behaviours of tolerant macaque species in the wild, we studied female social behaviours in two wild, habituated but not provisioned groups of crested macaque, *M. nigra* (Fooden 1969), a member of grade 4, in Sulawesi, Indonesia. We first investigated female aggressive and affiliative behavioural patterns to assess social tolerance focusing on the frequency, intensity and distribution of agonistic and affiliative behaviour among females, their dominance gradient, and their level of conciliatory tendency. We studied the context and directionality of the silent bared-teeth display to verify that it constitutes an affiliative rather than a

submissive signal in this species. We also analysed further behavioural patterns that have not yet been assessed in grade 4 macaques, although researchers have used them to characterize social tolerance in other grades: responses to others' approach, and distribution of affiliative behaviour across partners. We then examined whether the patterns observed in the wild population were consistent with those reported in captivity. Finally, to evaluate our results in the framework of macaque social styles, we compared them to data from other grade 4 macaques and from other species of other grades. We expected the wild population's behavioural profile to be consistent with captive conspecifics and other grade 4 macaque populations but substantially different from macaques of other grades.

2.3 Methods

2.3.1 Study site and groups

Crested macaques are endemic to the island of Sulawesi, Indonesia (Sugardjito et al. 1989). The study population inhabits the Tangkoko-Batuangus Nature Reserve (1˚33'N, 125˚10'E; e.g. Duboscq et al. 2008), broadly classified as a lowland rainforest with seasonal variation in rainfall and fruit abundance (O'Brien & Kinnaird 1997). The research area is a mix of primary and secondary forest as well as old regenerating gardens (O'Brien & Kinnaird 1997). The study was part of the Macaca Nigra Project (www.macaca-nigra.org), a long-term field project focusing on the biology of crested macaques (for more details see Appendix A).

We studied two groups, "PB" and "R1", comprising about 60 and 80 individuals respectively. The monkeys were well habituated to human observers, but not provisioned, and spent around 60% of their time on the ground (O'Brien & Kinnaird 1997). We could individually identify all adults based on physical characteristics (shape and colour of the anogenital region, wrinkles and special facial features, or scars).

2.3.2 Data collection

JD, JM and another field assistant followed each study group from dawn (*ca.* 5:30 am) to dusk (*ca.* 6:00 pm) every day between October 2008 and May 2010. We collected behavioural data on all adult females (15 – 18 in PB, 21 – 24 in R1) using focal animal sampling (Martin & Bateson 1993; inter-observer reliability: Cohen's kappa = 0.69 – 0.90, correlation coefficients between

behavioural variables = 0.79 – 0.98, all $P < 0.05$). Each day, we selected females for observation in a predetermined random order, balancing observations across 4 periods of the day (early and late morning and early and late afternoon). For each subject on a given day, we aimed at collecting 30 consecutive point samples for her activity. Sometimes, we could not accurately monitor the focal female's activity (e.g. she was temporarily out of sight). In such cases, we extended the observation protocol as long as necessary to achieve 30 data-points of activity monitoring. We also extended protocols to get post-conflict observation periods of sufficient length (see Conciliatory tendency section). We included all focal protocols lasting more than two minutes in the analyses. Focal follows in the final dataset had the subject in sight (whether her activity was visible or not) for a median of 32 minutes (range: 2-100 minutes, including one outlier that lasted almost 2 hours when we monitored a female about to give birth); these records included a median of 30 activity point samples (range = 2 – 84). We recorded the subject's activity (feeding, foraging, socializing, traveling, resting) every minute and the identity of neighbours (in body contact, within 1 body length, and within 5 body lengths) every alternate minute. We recorded focal social events continuously, including start and end time of the interactions, the sequence of all of the subject's behaviours (see next section), as well as identity and behaviours of all social partners. In addition, every ten minutes, we recorded the identity and general activity of neighbours up to ten body lengths away, and every 30 minutes, we noted the general activity of the majority of visible individuals around the focal female (usually up to 20 meters).

During the study, several females reached adulthood (gave birth to a live infant for the first time) and one disappeared. For greater clarity, we excluded these females from our analysis. Thus, in total, our study included 2,480 hours of focal data from 36 subjects (PB: median = 68 hours per female (range: 65 – 78, N=15); R1: median = 66 hours per female (range: 59 – 71, N=21)).

2.3.3 Behavioural definitions

We defined an *aggressive interaction* as the display of an aggressive behaviour of any intensity followed by an aggressive or non-aggressive response. Aggressive acts ignored by the receiver contributed only to our analysis of responses to aggression (see below). Aggressive behaviours included *threat*: aggressive vocalizations (bark, grunt, rattle, scream) and/or facial expressions (half-open mouth, open-mouth bared-teeth, stare, jaw movement); *attack*: aggressive behaviours exceeding the threat intensity but excluding bite, further divided into *contact attacks* (hit, missed hit, grab and push) and *non-contact attacks* (chase, lunge and stamp); and *bite* (Thierry et al. 2000a). We defined a *displacement*, or *approach-retreat interaction*, as a female approaching

without provocation, usually within 5 body lengths, another female who simultaneously moved away (Thierry et al. 2000a). Displacements did not involve any aggressive component. Affiliative interactions included grooming, non-aggressive body contact, embrace, tail grasp/rub, soft grunt, and affiliative facial expressions such as lipsmack (Thierry et al. 2000a). We counted as one grooming bout any continuous episode of grooming, by one or both partners, with breaks not exceeding 10 sec. We also recorded *approach* to one body length of another female, as long as the two stayed within this distance for at least 5 sec. Only *non-agonistic approaches*, where the approaching female did not direct aggression to her partner while coming near, were used when evaluating the response of an approached individual (de Waal & Luttrell 1989). Finally, we recorded *silent bared-teeth display,* a facial expression, where the upper lip or both lips are vertically retracted, exposing the teeth and sometimes the gums (Thierry et al. 2000a).

2.3.4 Data analysis

Analyses were limited to dyadic interactions involving focal females. When more than two individuals were involved sequentially or simultaneously with the focal female, we broke down polyadic interactions into dyadic ones or we prioritized interactions according to the intensity of behaviours used: agonistic interactions were prioritized over affiliative ones and interactions involving body contact were prioritized over those involving only displays. We calculated frequencies (per hour of observation time, i.e. total number of minutes across all focal protocols, divided by 60, the focal female was visible, with or without the possibility of monitoring her activity) and percentages (of behaviour as a proportion of interactions) per focal female, and then computed medians and ranges as well as means ± SDs across all females in each group.

2.3.4.1 Agonism

To assess the intensity of aggression, we calculated median percentages of specific aggressive behaviours (threat, non-contact attack, contact attack and bite) as a proportion of all aggressive interactions for each female. If an interaction included several aggressive elements, we categorized it by the most intense aggression shown (bite > contact attack > non-contact attack > threat). To analyse response to aggression, we categorized the responses as *leave* (move away from the aggressor from any proximity category to a larger distance), *retaliate* (respond aggressively to the aggressor), *affiliate (*respond with a friendly behaviour) or *ignore (*no reaction or change in

activity). We quantified counter-aggression as the proportion of aggressive interactions with counter-aggression (any aggressive response, including aggressive screams).

2.3.4.2 Affiliation and other behaviours

To assess the intensity of affiliation, we calculated the median percentage of affiliative interactions with body contact (e.g. touch, embrace, tail grasp/rub, grooming) as a proportion of all affiliative interactions for each female. If a given interaction included several affiliative elements, we prioritized body contact over other behaviour.

To assess the degree of tolerance among females, we grouped responses to non-agonistic approach as having a *negative outcome* if the approached female retreated, aggressed, or screamed at the approaching female, a *positive outcome* if the two females engaged in affiliation, and a *neutral outcome* if there was no action/reaction from either female (Cooper & Bernstein 2008; de Waal & Luttrell 1989). To measure how evenly females distributed their grooming bouts and approaches among adult female group-mates, we used the standardized Shannon-Wiener diversity index H / H_{max} (Cheney 1992; Shannon & Weaver 1949). This index is calculated as follows:

$$H / H_{max} = - \sum_{s=1}^{s} p_i ln\,(p_i) / ln\ (N-1)$$

where s is the number of actual interaction partners, p_i the relative proportion of behaviour exchanged (i.e. proportion of total grooming bouts, or proportion of total approaches) between the i^{th} focal female and other females and N the total number of potential female partners, i.e. the number of females in the group. This index ranges from 0 (very uneven distribution of the behaviour) to 1 (even distribution across female group-mates).

2.3.4.3 Conciliatory tendency

Post-conflict observations (PC) were extracted from focal protocols and did not differ from a normal protocol in terms of data collected. PCs started right after the last exchange of aggressive behaviours between the focal female and her opponent and lasted ideally ten minutes (range: 2 – 11 min). Usually, matched-control observations (MC) are conducted at the same time the next possible observation day after the aggressive interactions de Waal & Yoshihara 1983. Because this procedure did not guarantee ideal matching conditions, we chose MCs *a posteriori* (Aureli 1992) from focal protocols conducted within a month before or after the protocol in which the particular aggressive interaction was recorded (median number of days between PC and MC: 17.4 (range: 1 – 32)). To qualify as MC, the same two opponents as in the PC had to be in proximity (<10 body lengths), and

the group's general activity had to be the same in the MC as in the PC. In addition, neither of the two opponents should have been involved in aggressive interactions within 2 min prior to or after the beginning of the MC, nor should they be engaged in affiliation with each other. We compared the occurrence of the first affiliation between opponents between PC and MC periods: we classified pairs as "attracted" when the first affiliation occurred sooner in the PC compared to the MC, "dispersed" when the first affiliation occurred sooner in the MC compared to the PC or "neutral" when the first affiliation occurred at the same time in both periods or no affiliation occurred in either period. We computed the corrected conciliatory tendency (CCT) as the number of attracted minus dispersed pairs divided by the total number of pairs (Veenema et al. 1994), first per individual, then across females (median). The CCT was calculated separately for contact affiliations only and for all affiliations together to ensure valid comparisons with other studies.

2.3.4.4 Dominance hierarchy

Interaction matrices used for calculating hierarchy parameters were based on two types of dyadic interactions extracted from focal protocols: *displacements* and *winner – loser interactions*; the latter were "decided" aggressive interactions with a clear outcome, mainly interactions in which one of the opponents left (this species has no obvious submissive signals; Thierry et al. 1994; Thierry et al. 2000a). If other responses occurred, such as affiliation or retaliation, we coded the interaction as undecided. Displacements were always decided interactions. We assessed hierarchy linearity with the *linearity index h'* (corrected for unknown relationships, de Vries 1995), which ranges between 0 (not linear) and 1 (strictly linear). To assess power asymmetries among females, we calculated the *Directional Consistency Index (DCI)*, which represents how often a particular behaviour is given in the most frequent direction and ranges from 0 (equal exchange) to 1 (unidirectional) (van Hooff & van Wensing 1987). We also calculated *steepness*, based on normalized David's scores (Gammell et al. 2003), which measures the degree to which individuals differ in their ability to win contests (de Vries et al. 2006): steepness can vary from 0 (no average difference) to 1 (maximum average difference). We report steepness calculations based on both D_{ij} indices, which take into account the frequency of interactions, and P_{ij} indices, which do not (de Vries et al. 2006). The displacement matrices served as the basis for calculating female ranks according to the I&SI method (Matman 1.1; de Vries 1998; de Vries et al. 1993). As 54% of aggressive interactions were "undecided", we also derived a hierarchy (I&SI method) and calculated DCI and steepness based on *all initiated aggressive acts*, i.e. all aggressive acts given, regardless of the response of the receiver but excluding ignored aggressive acts. We compared the two indices and the rank order obtained to those based on displacement and

winner-loser interactions to explore the effect of undecided interactions on power asymmetries and to assess the reliability of displacement interactions in building hierarchies in this species (de Waal 1989a; Thierry et al. 1994). We also give information on some descriptive attributes of the matrices (Appendix B, Tables B1-B6), such as number of interactions recorded, percentage of unknown relationships (dyads with no interaction) and percentage of two-way relationships (each dyad member both won and lost contests against her opponent).

2.3.4.5 Silent bared-teeth display

To analyse the context in which silent bared-teeth displays occurred, we categorized the occurrences of this facial expression into three mutually exclusive contexts, according to how the two females interacted 10 sec before and/or after the display: *negative* (aggression), *positive* (affiliation) or *neutral context* (approach or sit in proximity, without further social exchange). We assessed the distribution of the bared-teeth display across partners with the standardized Shannon-Wiener diversity index (see above). To test the directionality of the display relative to females' dominance rank, we calculated the *up/down index*, which measures how consistently a behaviour is directed up or down the hierarchy (Castles et al. 1996; de Waal & Luttrell 1989). The up/down index was computed as follows for each individual: $\frac{u}{(u+d)}$, where u is the proportion of displays given up the hierarchy, and d the proportion given down the hierarchy. An index of 0.5 indicates no bias and constitutes the reference point; an index lower than 0.5 indicates a tendency to express the behaviour down the hierarchy, and vice versa (Castles et al. 1996).

2.3.5 Comparative perspective within the macaque genus

We evaluated our results in the context of variation among macaque societies by contrasting them with data on a specific set of behavioural variables from other macaque populations. We first assessed the degree of tolerance of the study females relative to other grade 4 macaque species. In this comparative dataset, a single research team conducted all but one study (on moor macaques) ensuring comparable definitions and data collection methods (Petit et al. 1997; Petit & Thierry 1994b; Thierry 1985; Thierry et al. 1994). For the comparison with macaque species of other grades, we mainly selected studies conducted under natural conditions, but also included those in which provisioning occurred to increase our sample size. We included studies that matched behavioural definitions to ours as much as possible, and included focal female data only.

2.3.6 Statistical analyses

We based statistical analyses on individual data for each group separately. We tested for group differences in rates and percentages of behaviours and interactions. When groups did not differ statistically, we combined the results for subjects in both groups to simplify presentation, but still report the group-wise statistics. When groups showed significant differences, we present the results separately for each group. For indices of distribution (Shannon-Wiener and up/down indices), indices of dominance gradient (DCI and steepness) and conciliatory tendency, we always report results for each group separately. We ran most analyses in R 2.14.2 (R Development Core Team 2011). All tests were non-parametric, exact (package "exactRankTests", Hothorn & Hornik 2011) and two-tailed. We analysed differences across outcomes of approaches and across contexts of silent bared-teeth occurrences based on frequencies of each outcome or context per observation time. More specifically, we tested whether each outcome of an approach was equally likely and whether females showed silent bared-teeth in each context equally. When the difference between the three outcomes or contexts was significant, we ran post-hoc tests with the function friedmanmc (package "pgirmess" Giraudoux 2012) to determine which outcome of approaches was more likely or which context the silent bared-teeth was more likely associated with. We give the observed difference and the critical difference. When the former is higher than the latter, the difference between the two categories compared is considered significant (Siegel & Castellan 1988). We used Matman 1.1 with 2000 permutations to calculate the linearity index h', DCI and percentages of unknown and two-ways relationships (Noldus, Wagenigen, de Vries et al. 1993). Steepness was calculated and tested in R (package "steepness", Leiva & de Vries 2011) with 2000 permutations. All significance levels were set to 0.05.

2.4 Results

Table 2.1 Summary of behavioural data in the two study groups

	groups			
	PB		**R1**	
	median (range)	**mean ± SD**	**median (range)**	**mean ± SD**
AGONISM:				
aggressive interaction (nb / h)	0.26 (0.18 - 0.58)	0.31 ± 0.12	0.38 (0.20 - 0.95)	0.43 ± 0.19
displacement (nb / h)	0.28 (0 - 1.22)	0.34 ± 0.33	0.48 (0.27 - 1.09)	0.50 ± 0.21
aggressive behaviour (% of all aggressive interactions)				
threat	67 (44 – 91)	68 ± 16	61 (20 – 89)	61 ± 19
non-contact attack	20 (0 – 44)	18 ± 13	25 (5 – 50)	27 ± 14
contact attack	11 (0 – 50)	12 ± 13	8 (0 – 30)	10 ± 9
bite	0 (0 – 9)	2 ± 3	0 (0 – 13)	3 ± 5
response to aggression (% of all aggressive interactions)				
avoid	36 (0 – 87)	24 ± 17	56 (0 – 90)	46 ± 27
retaliate	20 (4 – 36)	20 ± 9	14 (0 – 63)	21 ± 17
affiliate	11 (0 – 38)	15 ± 14	10 (0 – 39)	14 ± 13
ignore	21 (0 – 60)	24 ± 17	20 (0 – 63)	19 ± 14
counter-aggression	30 (4 – 50)	28 ± 15	21 (0 – 71)	26 ± 19
AFFILIATION AND OTHER:				
affiliative interaction (nb / h)	2.19 (1.30 – 3.33)	2.25 ± 0.60	2.95 (0.98 – 4.24)	2.73 ± 0.76
contact affiliation	63 (20 – 56)	64.54 ± 5.89	63 (48 – 72)	62.30 ± 7.21
grooming bout (nb / h)	1.25 (0.65 – 1.89)	1.10 ± 0.55	1.22 (0.22 – 2.50)	1.25 ± 0.63
grooming H'/H_{max}	0.86 (0.77 – 0.94)	0.86 ± 0.05	0.85 (0.67 – 0.92)	0.84 ± 0.07
approach (nb / h)	4.95 (3.11 – 7.90)	5.28 ± 0.35	5.00 (2.48 – 8.88)	5.67 ± 0.43
approach H'/H_{max}	0.94 (0.93 – 0.97)	0.95 ± 0.01	0.92 (0.87 – 0.97)	0.92 ± 0.02
outcome of approach (% of all non-agonistic approaches)				
negative	7 (1 – 24)	9 ± 3	13 (6 – 23)	13 ± 3
positive	28 (21 – 42)	30 ± 5	29 (21 – 40)	30 ± 3
neutral	63 (49 – 71)	62 ± 6	58 (44 – 66)	57 ± 4
silent bared-teeth (nb / h)	0.15 (0.05 – 0.49)	0.17 ± 0.02	0.12 (0.05 – 0.32)	0.16 ± 0.02
silent bared-teeth H'/H_{max}	0.63 (0.24 – 0.83)	0.68 ± 0.03	0.52 (0 - 0.79)	0.49 ± 0.23
context of occurrence of silent bared-teeth (% of all occurrences)				
negative	9 (0 – 40)	13 ± 14	13 (0 – 53)	15 ± 16
positive	45 (20 – 87)	49 ± 19	59 (25 – 100)	57 ± 23
neutral	36 (9 – 80)	36 ± 19	29 (0 – 63)	28 ± 19
silent bared-teeth up/down index	0.50 (0.14 – 1)	0.56 ± 0.28	0.50 (0 – 1)	0.49 ± 0.36

hourly frequencies (nb / h), percentages as proportion of specific interactions/behaviours considered, Shannon-Wiener diversity index H'/H_{max} and up/down index (median (range) and mean ± SD, N_{PB} = 15, N_{R1} = 21).

2.4.1. Agonism

Females were involved in an aggressive interaction with another female about once every 3 hours (Table 2.1). Displacements and aggressive interactions occurred at similar rates (Table 2.1). Most aggressive interactions involved only threats (Table 2.1, Figure 2.1a). Non-contact attacks occurred more frequently than contact ones (Table 2.1, Figure 2.1a). Females rarely bit each other (Table 2.1, Figure 2. 1a).

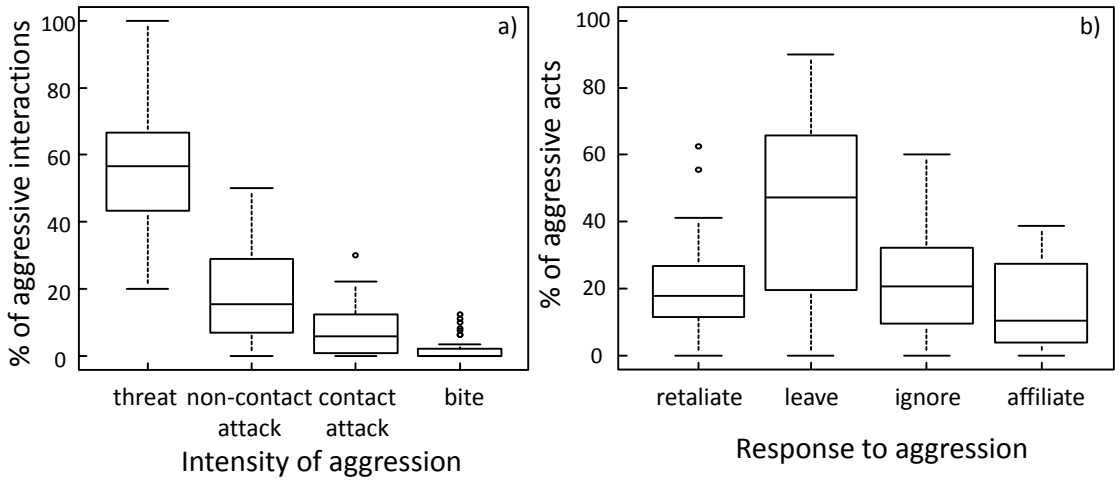

Figure 2.1 Detailed characteristics of agonistic interactions (see definition in text): intensity of aggression as a proportion of all agonistic interactions (a) and response to aggression as a proportion of all aggressive acts (b) across the two groups combined (median, interquartiles and 1.5 interquartile range, N = 36 females).

Recipients of aggression usually responded by leaving the aggressor's proximity (Table 2.1, Figure 2.1b). Less frequently, they retaliated, ignored their aggressor or attempted to appease her with friendly behaviour (Table 2.1, Figure 2.1b). Females counter-attacked their opponents in 27% of aggressive interactions (median; range = 0 – 71%, mean = 27% ± 17 SD, N = 36; Table 2.1).

2.4.2 Affiliation and approach

Females had affiliative interactions 2.5 times per hour and more than 60% of these interactions involved body contact (including grooming; Table 2.1). Females were involved in a

grooming bout with another female about once an hour and they closely approached female partners approximately five times per hour (Table 2.1).

Females in R1 group approached each other significantly more frequently than females in PB group (Mann-Whitney test: N_{PB} = 15, N_{R1} = 21, U = 245, *P* = 0.005; Table 2.1). Non-agonistic approaches significantly led to different outcomes (Friedman chi-square test: PB: χ^2 = 30, d.f. = 2, N = 15, P < 0.001; R1: χ^2 = 42, d.f. = 2, N = 21, P < 0.001): most approaches did not result in any observable response (Figure 2.2a-b; post-hoc tests: PB: N = 15, neutral/negative: observed difference = 30, critical difference = 13, neutral/positive: observed difference = 15, critical difference = 13; R1: N = 21, neutral/negative: observed difference = 42, critical difference = 16, neutral/positive: observed difference = 21, critical difference = 16). In addition, when females reacted to a close proximity approach, it was significantly more often positively than negatively (Figure 2.2a-b; post-hoc tests: PB: N = 15, observed difference = 15, critical difference= 13; R1: N = 21, observed difference = 21, critical difference= 16; Table 2.1).

Grooming and approach diversity indices were both close to 1 in both groups (Table 2.1), indicating that females distributed their grooming bouts and approaches evenly across all female partners.

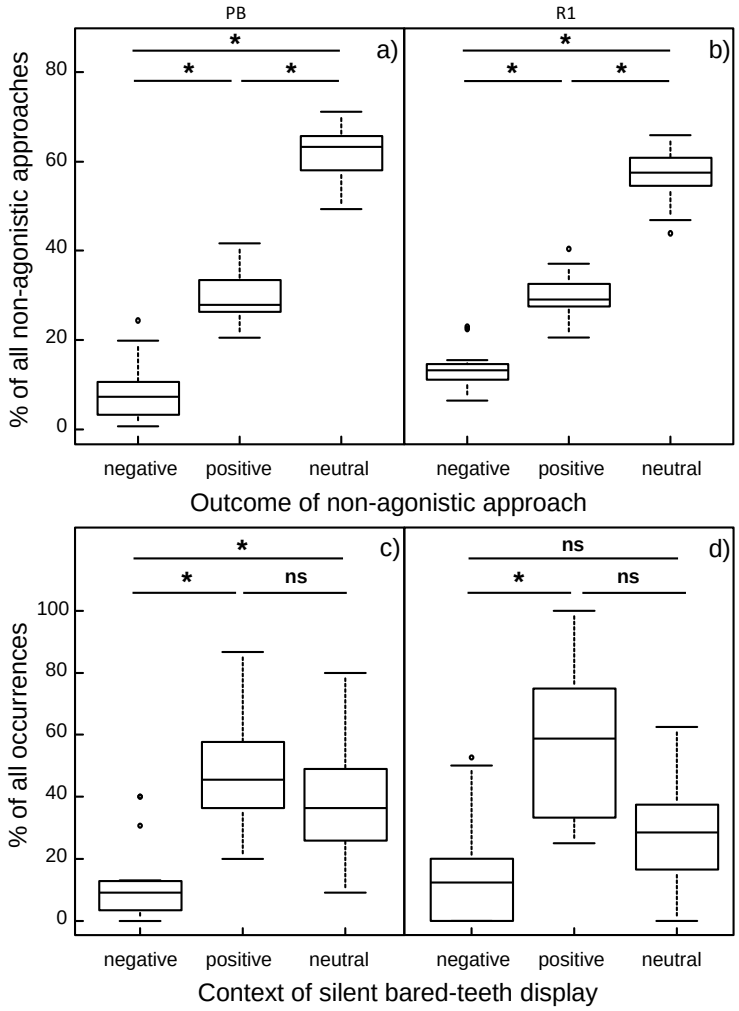

Figure 2.2 Two of the behavioural parameters indicators of social tolerance in macaques: outcome of approach (a – b) as a proportion of non-agonistic approaches and context of occurrence of silent bared-teeth display (c – d) as a proportion of all occurrences in PB (a and c panels) (N = 15) and R1 (b and d panels) (N = 21) groups (median, interquartiles and 1.5 interquartile range; post-hoc tests after Friedman, * = observed difference > critical difference, ns = observed difference < critical difference).

2.4.3 Conciliatory tendency

In total, we examined 285 PC-MC pairs (PB: 127, median per female = 8, range: 4 – 15; R1: 158, median per female = 7, range: 3 – 14). The median corrected conciliatory tendency (CCT) with all affiliation (contact and non-contact) was 41% (median, range = 13 – 75%) in PB (4% dispersed, 45% attracted, 52% neutral) and 47% (median, range = 0 – 100%) in R1 (4% dispersed, 51% attracted, 46% neutral) (see Table III for mean contact CCT).

2.4.4 Dominance hierarchies

Hierarchies in both groups were significantly linear (PB: h' = 0.54 – 0.94, R1: h' = 0.43 – 0.74, depending on the type of interactions, all Ps < 0.01). In both groups and with all 3 types of agonistic interaction, all hierarchies were moderately but significantly steep (Table 2.2, Appendix A Table A1 – A6). Directional Consistency Indices were high for winner-loser and displacement interactions, indicating a high directionality of those dominance-related interactions (Table 2.2). With all initiated aggressive acts, hierarchies were shallower compared to displacement interactions but rather similar to winner-loser interactions (Table 2.2). DCIs were substantially lower however (Table 2.2), indicating that, within a dyad, aggressive interactions could often be initiated by both members. Rank orders obtained with displacements and winner-loser interactions were similar (15 out of 21 ranks in R1 and 10 out of 15 ranks in PB). In contrast, with all initiated aggressions, only 3 out of 21 ranks in R1 and 3 to 4 out 15 ranks in PB matched those established with decided interactions. Given that the displacement interaction matrices had the least number of unknown dyads, there were considered most reliable to establish rank orders.

Table 2.2 Parameters of hierarchies considering two types of dominance-related interactions: *winner – loser* interactions and *displacement* interactions, as well as *all initiated* aggressive acts (see text for definitions). Number of interactions recorded (N interactions), percentage of unknown relationships (% unknown) and of two-way relationships in the matrices (% two-ways) (see text for definition), steepness values with *Dij* and *Pij* indices (all significant) and Directional Consistency Indices (DCI) are also given.

group	interaction types	N interactions	% unknown	% two-ways	steepness D_{ij} / P_{ij}	DCI
PB (N = 15)	*winner - loser*	207	23	2	0.420 / 0.631	98
	displacement	561	4	18	0.693 / 0.895	89
	all initiated	360	10	42	0.398 / 0.576	62
R1 (N = 21)	*winner - loser*	283	36	3	0.281 / 0.455	94
	displacement	732	11	11	0.563 / 0.785	93
	all initiated	639	12	35	0.333 / 0.483	64

2.4.5 Silent bared-teeth display

Females in PB group showed silent bared-teeth displays significantly more frequently than females in R1 group (Mann-Whitney test: U = 228, N_{PB} = 15, N_{R1} = 21, P = 0.022; Table 2.1). In both groups, females did not display this facial expression equally across interaction contexts (Figure 2.2c-

d; Friedman chi-square test: PB: χ^2 = 13, d.f. = 2, N = 15, P = 0.001; R1: χ^2 = 19, d.f. = 2, N = 21, P < 0.001). In PB group, females expressed silent bared-teeth least often in the negative context (post-hoc test: N = 15, neutral/negative: observed difference = 15, critical difference = 13, positive/negative: observed difference = 18, critical difference = 13). In R1 group, however, displays occurred similarly often in negative or positive contexts as compared to neutral contexts (post-hoc tests: N = 21, neutral/negative: observed difference = 13, critical difference = 16; neutral/positive: observed difference = 14, critical difference = 16), but occurred more often in a positive context than a negative one (post-hoc tests: positive/negative: observed difference = 28, critical difference = 16; Table 2.1).

Diversity indices for the bared-teeth display were rather low (Table 2.1), indicating that females showed this display to a specific set of female partners. Up/down indices for this behaviour were not significantly different from 0.5 (value indicating no bias; Wilcoxon one-sample test: PB: T = 49, N = 15, P = 0.482; R1: T = 84, N = 21, P = 0.653), showing that females did not direct displays selectively up or down the hierarchy.

Table 2.3 Summary of social variables within grade 4 social style: mean percentages of bite, contact attack, counter-aggression, mean corrected conciliatory tendency (CCT) with contact affiliation and steepness (with D_{ij} indices) in females of different grade 4 macaque species: captive *M. nigra*, captive *M. tonkeana* and captive and provisioned *M. maurus*, as compared to the studied crested macaques (*M. nigra*, wild). Whether data have been published for non-related individuals only (non-kin) or all individuals (all) is indicated in the first line. Steepness was computed regardless of kin relationships (all).

Variables	***M.nigra*** **(wild)** [1]	*M. nigra* (captive) [2]	*M.tonkeana* (captive) [3]	*M.maurus* (captive/provisioned) [4]
kin/non-kin	**all**	non-kin	non-kin	all
bite (%)	**2 – 3**	8.9	0	2.6
contact attack (%)	**8 – 11**	51.5	11.5	33.3
counter-aggression (%)	**26 – 28**	50.8 - 56.1	59.6	0
CCT (contact) (%)	**27 – 29**	22.2	47.9	42.3
steepness	**0.281 – 0.693**	0.257 - 0.817	0.332 - 0.653	0.397 - 0.545

References: [1] this study; [2] Petit et al 1997, Petit unp.data, Micheletta unp.data, Balasubramaniam et al. 2012a ; [3] Thierry 1985, Desportes and Thierry unp.data, Demaria and Thierry 2001; [4] Matsumura 1996, 1998, Petit and Thierry 1992

2.4.6 Comparison within the macaque genus

Overall, most of the variables we measured fell within the range of data reported for captive or provisioned grade 4 female macaques (Table 2.3).

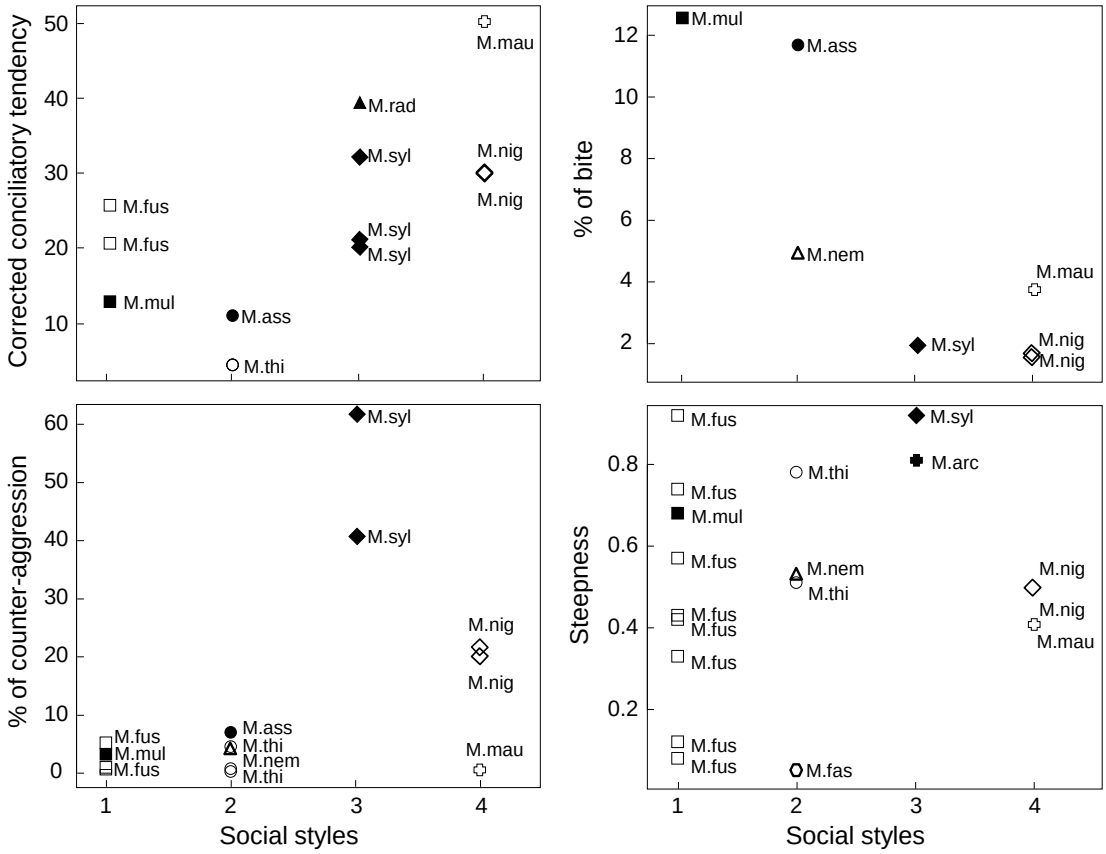

Figure 2.3 Variation of four social parameters according to social style grades, summarized across studies conducted on females under natural conditions. Means of corrected conciliatory tendency (upper left), percentage of agonistic interactions involving bites (upper right) or counter-aggression (lower left) and steepness values (lower right) are represented. The four variables were extracted from published studies or calculated from (un)published data. The dataset includes only studies of adult females, followed as focal individuals, under natural conditions, with or without provisioning. Data points within one grade represent means in different studies and/or different groups of the same or different species, abbreviated next to the data point. Different species have different symbols. Several data points may overlap when means are similar. (References: *M. fuscata* (M.fus, empty square): Furuichi 1983; Hanya et al. 2008; Hill & Okayasu 1995; Koyama 2003; Kutsukake 2000; Majolo et al. 2009c; Mori et al. 1989; Nakamichi 2003; Nakamichi & Shizawa 2003; Oi 1988; Schino & Aureli 2008b; *M. mulatta* (M.mul, full square): Cooper & Bernstein 2008; Sade 1972; *M. assamensis* (M. ass, full circle): Cooper & Bernstein 2008; *M. fascicularis* (M.fas, empty hexagone): Gumert 2000; *M. thibetana* (M.thi, empty circle): Berman et al. 2004; Berman et al. 2008; *M. arctoides* (M.arc, full cross): Estrada et al. 1977; *M. nemestrina* (M.nem, empty triangle): Oi 1990; *M. radiata* (M.rad, full triangle): Cooper et al. 2007;; *M. sylvanus* (M.syl, full diamond): Fa 1985; Kuester & Paul 1996; Patzelt et al. 2009; Thierry & Aureli 2006; Thierry et al. 2008; *M. maurus* (M.mau, empty cross): Matsumura 1996, 1998; *M. nigra* (M.nig, empty diamond): this study, PB and R1 groups separately)

The behavioural patterns we observed also fell within the range of data from other tolerant female macaques (grades 3 and 4, Figure 2.3), and generally outside the range reported for more despotic ones (grades 1 and 2, Figure 2.3). In contrast to females in more despotic species, aggressive interactions among the study females were of notably low intensity, frequently

bidirectional and often reconciled. There is variation within grade and species, however. Compared to other populations of grade 4 macaques, the percentage of counter-aggression and the CCT with contact affiliation in the study groups were low. Compared to some groups belonging to grade 3 (two groups of *M. sylvanus*, one of *M. radiata*), the study subjects also showed seemingly less counter-aggression and fewer reconciled conflicts. Lastly, steepness values, which were expected to be lower in tolerant species compared to more despotic ones, varied too greatly within grade and even within species to show any clear relationship with the social style graded scale (Figure 2.3).

2.5 Discussion

This study is the first comprehensive analysis of social behaviours of female crested macaques under natural conditions. We studied two wild groups and analysed an extensive body of behavioural data on female social behaviour; some of the variables were previously undocumented for grade 4 macaques. By focusing on the less studied tolerant end of the macaque social style spectrum, this study contributes to a better understanding of macaque societies.

Behavioural patterns observed in wild female crested macaques generally fit the definition of a tolerant social style: aggressive interactions are of low intensity, often bidirectional and reconciled. The consistency of the observed patterns found in both study groups indicates the robustness of the results. We also found that much aggression was ignored or appeased and that affiliative interactions and approaches were frequent and evenly distributed among female partners. Power asymmetries between females were moderate. Displacement interactions were as frequent as aggressive interactions, seemed to be most reliable for computing hierarchy parameters and constitute a valid substitute to decided aggressive interactions to build hierarchies. Thus, social power appeared to be reinforced more commonly through weak rather than severe agonism. Since the occurrence of the silent bared-teeth display was linked neither to agonistic context nor to dominance rank, this facial expression did not constitute a signal of submission.

The degree of social tolerance in a society is best appreciated in comparison with other societies. Behavioural patterns of wild female crested macaques were very similar to those of captive conspecifics in particular, and of other grade 4 species in general, and substantially different from species in other grades. In addition, wild female crested macaques exchanged approaches and grooming evenly among a large network of female social partners, suggesting a low clustering in affiliation. This result is consistent with the work of Sueur and collaborators (2011), showing differences of affiliation network size and composition between tolerant and despotic social styles. This result would also be consistent with the usually less pronounced kin bias in affiliation

characterizing other grade 4 macaques (Thierry et al. 1994; Thierry et al. 1990). Three variables, namely, approach and grooming distribution and proportion of negative reaction upon approach, revealed a dimension of social tolerance that has never been quantified in macaques from grade 4 (for other grades see Castles et al. 1996; Cooper & Bernstein 2008; de Waal & Luttrell 1989). In comparison with female rhesus (grade 1) and Assamese (*M. assamensis*: grade 2) macaques, mean values of grooming diversity and percentage of negative reaction upon approach appear respectively higher and lower in the crested macaque females studied here (Cooper & Bernstein 2008). These measures of social tolerance thus seem to vary according to the species' social style grade, and could provide reliable tools in the assessment of the degree of social tolerance.

Consistent with a high degree of social tolerance, female crested macaques expressed moderate power asymmetries. In this study, power asymmetries were more or less pronounced dependent on the type of interactions. Initiated aggressive acts yielded the same steepness values as winner-loser interactions but with a much lower DCI, showing that power asymmetries amongst females in those groups were not entirely due to capabilities of winning contests. Also, displacement interactions, more frequent and unidirectional than the two other types of interactions, pictured stronger asymmetries than decided aggressive interactions, indicating that power may be better asserted with low intensity display than direct aggression. Similarly, Thierry and colleagues (1994) found that different agonistic variables yielded different hierarchical orders in captive Tonkean macaques. Such inconsistencies, evidenced both in captive and wild populations of grade 4 macaques and independent of observational effort, highlight the difficulty of reliably assessing hierarchical variables when a large proportion of aggressive interactions are represented by interactions with undecided outcome. Yet, those interactions may bear essential information about the dynamics of dyadic dominance relationships, perhaps representing negotiation interactions instead of or in addition to dominance interactions. Low to moderate power asymmetries, usually associated with an absence of formal submissive signals (Preuschoft & van Schaik 2000), a pattern also found in this study, leave room for the negotiation of conflicts. Social negotiation may occur through the exchange of aggressive and affiliative signals within the same interaction, as we observed, or through the balance of aggressive and affiliative components in dominance relationships (de Waal 1986). These results suggest that it could be important to take these inconsistencies into account when analysing further dyadic dominance relationships and how females deal with conflicts of interest.

The comparisons we carried out also highlighted intra-species and intra-grade variation. For example, counter-aggression seemed to occur twice as frequently in captive populations of grade 4 macaques as compared to wild crested macaques, and was apparently absent in a provisioned group

of moor macaques. These differences could reflect species differences or variation in demographic structure and/or living conditions. First, comparative studies showed that variation within species or grade is less pronounced than between species or grades, but species differences do exist (Balasubramaniam et al. 2012b; Thierry et al. 2008). Second, even though the percentage of dyads without observed agonistic interactions was similar in all groups, groups of wild crested macaques were up to three times larger than groups of captive and provisioned populations, which could have resulted in different interaction dynamics. Moreover, in contrast to the other studies, our analyses were carried out disregarding kinship, information currently not available. Although the influence of kinship on social interactions appears relatively weak in grade 4 species (Demaria & Thierry 2001; Matsumura & Okamoto 1997), it may still be that the number of related individuals, and thus of potential allies, influenced the outcome of social interactions. Lastly, it has been shown that captivity or provisioning influence the rates, distribution and intensity of contests through alteration of space available and/or food distribution (Asquith 1989; Judge 2000; Southwick et al. 1976; Wrangham 1974). Individuals subject to different degrees of competition would need to adapt their competition and conflict management strategies accordingly, albeit within their reaction norm. The extended choice of options of wild crested macaque females when responding to aggression (avoiding, ignoring, and affiliating) may constitute alternative tactics to retaliation and may better balance conflicts of interest. These results show that detailed analyses of responses to aggression can also help to reach a finer understanding of conflict management strategies, which have been shown to be tightly linked to social styles (Thierry et al. 2008).

Our comparative perspective is only descriptive and would need to incorporate formal phylogenetic analyses to be complete. We aimed here at scaling our data to the observed behavioural variation within the macaque genus, and not at testing differences between grades or species. Our conclusion is nevertheless consistent with other comparative studies, almost all controlling for phylogeny (de Waal 1989a; Thierry 2000; Thierry et al. 2008; Thierry et al. 2000b). Those studies showed, as is also illustrated in Figure 2.3, that the percentage of bites decreases with the social style grade whereas the percentage of counter-aggression and the conciliatory tendency increase. However, high intra-specific and intra-grade variation in steepness values, even among our study groups, prevents us from drawing any clear conclusion regarding their distributions along the gradient of social styles. Power asymmetries were expected to decrease from despotic to more tolerant species (Flack & de Waal 2004; Thierry et al. 2008; van Schaik 1989), a relationship confirmed in recent studies (Balasubramaniam et al. 2012b; Richter et al. 2009) using the steepness index developed by de Vries and colleagues (2006). Our contradictory observation may indicate limitations of the steepness index when used to compare groups or species (e.g. influence of the

proportion of unknown relationships in the matrix on the steepness value: Klass & Cords 2011). Alternatively, the expected pattern may be revealed if data were controlled for phylogeny (Balasubramaniam et al. 2012a). Our contradictory observation may also reflect the inclusion of different kind of agonistic interactions, for example only unidirectional (i.e. without counter-aggression) or uni- and bidirectional (Balasubramaniam et al. 2012a).

Our comparative perspective also identified intra-species variability, an issue which has puzzled animal behaviour researchers for decades (Lott 1991). Our study groups, for example, also differed in their approach and silent bared-teeth rates, which may reveal different social dynamics, for example differences in group size or group cohesion. This intraspecific variation is particularly well illustrated in the Japanese macaques, more variable in the degree of their interactions' intensity and symmetry than expected (Nakagawa 2010). It is also now well appreciated that whereas the differences between the extreme ends of the social style gradient (grades 1 and 4) are clear-cut, the boundaries between and within the middle grades (2 and 3) are less distinct (Balasubramaniam et al. 2012b; Thierry 2007).

Our study illustrates how consistent interrelated behavioural patterns are despite variation in environmental conditions. The social style concept thus seems to be valid and robust. The social style of wild female crested macaques now needs further investigation at the levels of social relationships and networks. We presently know that females exhibit a high degree of tolerance towards female conspecifics, and that they seem to form large social networks. This suggests that females presumably have more freedom to interact with social partners of their choice, regardless of dominance and kinship. However, dominance and kinship are two preponderant components of macaque societies, and the extent to which they influence these tolerant relationships in the wild is still unknown. It is also not known how tolerant females balance their levels of competition and cooperation in regard to ecological and demographic changes. Even though social styles and environmental conditions appear uncorrelated (Ménard 2004), demographic and ecological factors may still participate in shaping the intensity, symmetry, distribution and timing of social relationships between females in ways that are presently ill-understood (Henzi & Barrett 2007; Henzi et al. 2009). In macaque societies, the phylogenetic signal appears to be strong (Balasubramaniam et al. 2012a; Thierry et al. 2008; Thierry et al. 2000b), which suggests that internal constraints and phylogenetic history play an important role in their evolution. Nevertheless, investigating the different factors mentioned above as potential selection pressures on the evolution of different social styles is an important next step. Finally, the concept of social tolerance/despotism may be a feature that is not restricted to macaque societies but may be extended to other primate genera (e.g. Hare et al. 2012; Leca et al. 2002). This concept could help to unravel competitive and

cooperative trade-offs faced by group members, shedding light onto the evolution of primate societies more generally.

CHAPTER 3

THE FUNCTION OF POST-CONFLICT INTERACTIONS: NEW PROSPECTS FROM THE STUDY OF A TOLERANT SPECIES OF PRIMATE

Julie Duboscq, Muhammad Agil, Antje Engelhardt, Bernard Thierry.
Accepted, Animal Behaviour.

3.1 Summary

Aggression can generate anxiety, create uncertainty about its aftermath and jeopardise social relationships. Post-conflict interactions serve as conflict management strategies to mitigate those consequences. Whereas characteristics of post-conflict interactions have been well studied in many animals, their functions are still insufficiently investigated. Four functional hypotheses have been proposed: stress-reduction, relationship-repair, self-protection and benign-intent. We aimed to test these hypotheses in females of a tolerant macaque species, the crested macaque, *Macaca nigra*, under natural conditions, for three post-conflict interactions: reconciliation, affiliation and aggression with third-parties. Our results bring meaningful contrasts compared with findings in other animal species. We found no evidence that aggression had consequences on individuals' behavioural indicators of anxiety, although it increased the likelihood of secondary aggression with third-parties. There was little evidence for the stress-reduction hypothesis as the occurrence of any of the three post-conflict interactions investigated had little effect of the behavioural indicators of anxiety measured. Conflict and dyad characteristics also had a limited influence on anxiety. The relationship-repair function was only partly validated because dyads with stronger bonds or exchanging more support did not reconcile more often, but dyads with attributes related to the symmetry, stability and predictability (i.e. security) in relationships did. Patterns of initiation and directionality of post-conflict interactions in this study population suggest that reconciliation may constitute a signal of appeasement and benign intent and that aggression towards third-parties may function for self-protection and for reassertion of the females' social status. The distinctive pattern of post-conflict management strategies revealed in wild female crested macaques appears related to their typical tolerant social style. These results outline the usefulness of concomitantly studying aggression, post-conflict interactions and their functions while taking into account the level of social tolerance characterising the society under study for a more comprehensive understanding of conflict management strategies.

3.2 Introduction

A correlate of group-living is the occurrence of conflicts of interests between group members, their most conspicuous expression being overt aggression (Alexander 1974). Aggression incurs costs such as being injured or becoming the target of coalitions from other individuals (Hand 1986). Aggression increases anxiety, manifested through elevated scratching, restlessness, heart rate and stress hormone levels (non-human primates, Arnold & Aureli 2006; mammals, Schino 2000; king penguin, *Aptenodytes patagonicus*, Viblanc et al. 2012; goose, *Anes anes* Wascher et al. 2008). Aggression furthermore creates "uncertainty" about the social situation directly following conflict in the sense that opponents are uncertain as to whether aggression will flare up again (Arnold & Aureli 2006; Schino 2000). Aggression may ultimately jeopardise the benefits of the relationship between the two opponents (van Schaik & Aureli 2000), all of which may be additional sources of anxiety. In gregarious animals, conflict management strategies to mitigate the consequences of aggression thus have adaptive value for individuals; they are also necessary for social cohesion (de Waal 1989b, 2000). Investigating the determinants and functions of post-conflict strategies is thus essential to understand better how individuals deal with conflicts of interest and maximise the benefits of group-living.

To alleviate the consequences of aggression, both for the aggressor and the recipient, different post-conflict management strategies are possible. Reconciliation is the exchange of positive behaviour between former opponents soon after the end of aggression (de Waal & van Roosmalen 1979); secondary aggression is the reoccurrence of aggression, either between former opponents (renewed aggression) or between a non-involved third-party and one of the opponents (secondary aggression; Clutton-Brock & Parker 1995; Kazem & Aureli 2005); and affiliation with third-parties, or more generally, mediation by a third-party, is the exchange of positive behaviour between a non-involved third-party and one of the previous opponents (Das 2000; Watts et al. 2000; Yarn 2000). Not all conflicts are followed by post-conflict interactions however, even within the same dyad of individuals. Researchers have thus shifted their attention from the characteristics of post-conflict events towards their potential functions and the factors influencing their occurrence. Although a variety of post-conflict interactions occurs in a large range of gregarious animals, so far, their functions have been investigated predominantly in primates (Aureli et al. 2012; Schino 2000 but see Kutsukake & Clutton-Brock 2008). Interestingly, different interactions do not necessarily have different functions. The differences in function are inherent to the identity of the initiator and receiver of the behaviour, and to their role, or absence of a role, in the previous conflict, i.e.

aggressor, recipient or a third-party (Table 23.1 in Aureli et al. 2012). This study investigates the function of post-conflict interactions from the opponents' point of view.

Four main non-exclusive functional hypotheses have been formulated and tested. Under the stress reduction hypothesis, post-conflict interactions, notably reconciliation, affiliation with third-parties and redirection of aggression (i.e. from the recipient to an uninvolved third-party), serve to lower the anxiety of opponents generated by the previous conflicts (Aureli 1997; Aureli et al. 2012). According to this hypothesis, conflicts that are more "stressful", because they are more intense, longer or undecided, should increase the likelihood of post-conflict interactions (Arnold & Aureli 2006). The relationship repair hypothesis postulates that post-conflict interactions, especially reconciliation, function to preserve the strength and quality of the relationship between partners (Aureli 1997; Aureli et al. 2012). These two functions have been further integrated into the "integrated hypothesis" on the ground that the quality of a relationship influences the degree of anxiety experienced by interacting partners (higher relationship quality generates heightened anxiety). Hence, repairing relationships also helps to decrease anxiety (non-human primates, Aureli 1997; Koski et al. 2007b; McFarland & Majolo 2012; humans, Worthington Jr 2006; Worthington Jr 2004). In this context, Cords and Aureli (2000) distinguished three components of a social relationship: value (in terms of fitness benefits), security (i.e. how predictable or stable the relationship is), and compatibility (i.e. the general tenor of a relationship). This framework allowed the influence of the relationship characteristics on the occurrence of reconciliation to be investigated in more details. It could hence be shown that more "valuable" partners such as kin or friends reconcile more often than less "valuable" partners (Aureli et al. 2012; Cords & Aureli 2000). Another potential function, the "self-protection" hypothesis, traditionally focuses on third-party individuals' strategies to protect themselves against receiving secondary aggression from previous opponents, for example by being proactive and initiating social interactions (Aureli et al. 2012). We nevertheless investigate this function from the previous opponents' point of view since it could be strategic as well for them to initiate interactions: for example, to reduce the likelihood of further hostility, or to reassert themselves in the social order of the group. This may not however directly decrease the anxiety or stress that opponents experience. Finally, the benign intent hypothesis views reconciliation as a signal that the conflict has ended, thereby facilitating further social exchange between opponents (Silk 1996). Researchers have argued that this function is similar to the "integrated hypothesis" (Cords & Aureli 1996), but it is worth considering it as a fully valid functional hypothesis because opponents may reconcile following more immediate motivations than mending relationships, for example to get groomed (Silk et al. 1996).

Amongst primates, macaque societies are well studied with respect to conflict management strategies and their functions (Aureli et al. 1994; Aureli et al. 1993; de Waal & Aureli 1996; de Waal & Aureli 1997; Demaria & Thierry 2001; Judge 1991; Majolo et al. 2009a; Patzelt et al. 2009; Thierry et al. 2008). Females being the philopatric sex, they form the core of the group, and they develop long-lasting relationships, which makes them suitable to understand mechanisms and functions of conflict management strategies. More interestingly, the different macaque species show differences in conciliatory tendencies, degree of power asymmetries, kin bias in social interactions, and level of social tolerance between individuals (Thierry et al. 2008). Macaques that are said to be tolerant display higher conciliatory tendencies and more demonstrative forms of reconciliatory behaviours than macaques that are said to be more despotic (Thierry et al. 2008). Social interactions in tolerant macaques seem also less constrained by dominance and kinship and individuals can form large and diverse affiliative networks. In contrast, more despotic species form highly clustered social networks with a substantial preference for kin (Sueur et al. 2011; Thierry 2007). Furthermore, in tolerant macaques, on the one hand, conflicts are mainly of low intensity, theoretically inducing little stress, but on the other hand, they include a high amount of counter-aggression, theoretically inducing significant costs or stress (Petit et al. 1997; Thierry 1985; Thierry et al. 2008; Chapter 2). We can therefore expect tolerant macaques to contrast with more despotic ones in the functions of post-conflict interactions: for example, some assumptions, such as the influence of conflict characteristics on anxiety, may not fit to their tolerant social style. However, tolerant macaque species remain largely understudied in comparison to more despotic ones, especially under natural conditions. The potential functions of post-conflict interactions in particular have never been fully investigated in the most tolerant species, the Sulawesi macaques. For instance, we have no information on the costs and consequences of aggression that would help to infer the functions of post-conflict interactions from the nature of the conflicts preceding those interactions (e.g. intense conflicts or conflicts between strong associates). In addition, the different strategies of post-conflict management are often addressed separately in a given species (but see Call et al. 1999; Koski et al. 2007a; Logan et al. 2012; Wittig & Boesch 2003), although different post-conflict interactions may not be independent of each other and may even occur concurrently (Koski et al. 2007a).

The aims of this study were two-fold: (1) to analyse the consequences of aggression in general and in relation to conflict and dyad characteristics, and (2) to test hypotheses regarding the functions of three post-conflict interactions, in wild female crested macaques (*Macaca nigra*), a species characterised by a tolerant style of social relationships (Petit et al. 1997; Chapter 2). For this purpose, we investigated relations between characteristics of conflicts and interacting dyads, behavioural indicators of anxiety (hereafter anxiety), and the occurrence of three post-conflict

interactions: reconciliation, affiliation and aggression with third-parties. The following general predictions, which can overlap between hypotheses, can be drawn from the four functional hypotheses presented above and from the extensive literature on primate post-conflict interactions (more specific ones are listed in Table 3.1):

(1) Consequences of aggression: (a) in general, the occurrence of aggression should increase the opponents' anxiety and the likelihood of further aggression; (b) conflict and dyad characteristics should influence the degree of anxiety experienced by opponents.

(2) Stress reduction hypothesis: (a) affiliative post-conflict interactions, either between opponents or with a third-party, should decrease the opponents' anxiety and the likelihood of further aggression; (b) redirection (i.e. aggression form the initial recipient to a third-party) should decrease the anxiety of the initiator of redirection; (c) if certain conflict characteristics generate more anxiety, conflicts with these characteristics should be more often followed by post-conflict interactions to alleviate this anxiety.

(3) Relationship repair hypothesis: we formulate predictions in the specific framework of this hypothesis only for affiliative interactions between adult females as we presently do not have the kin relationships of all individuals in the group, and could not identify all the juveniles involved in third-party interactions. Affiliations should be more likely amongst dyads with particular relationships, i.e. between individuals that are strongly bonded and/or that benefit particularly from being associated.

(4) Self-protection hypothesis: (a) the initial recipients of aggression should initiate post-conflict interactions more often than aggressors, because they are theoretically more at risk of receiving new bouts of aggression; (b) the occurrence of post-conflict affiliation between any parties should lower the risk of further aggression to/from any parties; (c) secondary aggression between opponents and third-parties should target mainly lower-ranking individuals, such as lower-ranking females and juveniles, in order to reassert the opponents' social status.

(5) Benign intent hypothesis: (a) the opponent with a higher motivation to signal the end of the conflict (e.g. the one more likely to escalate aggression by retaliating or the one more "stressed" by the event, most likely the recipient) should be the one to initiate the first interaction; (b) non-contact affiliative behaviours should precede contact ones as a signal that re-establishing contact with the former opponent will have no immediate negative consequences

3.3 Methods

3.3.1 Data collection

Crested macaques are endemic to the island of Sulawesi, Indonesia (Sugardjito et al. 1989). The study population inhabits the Tangkoko-Batuangus Nature Reserve (1˚33'N, 125˚10'E; e.g. Duboscq et al. 2008; Higham et al. 2012), broadly classified as a lowland rainforest with seasonal variation in rainfall and fruit abundance (O'Brien & Kinnaird 1997). We studied two well-habituated non-provisioned groups, "PB" and "R1", comprising about 60 and 80 individuals respectively. All adults could be individually identified based on physical characteristics. Observation conditions were excellent because the monkeys are semi-terrestrial, spending approximately 60% of their time on the ground (O'Brien & Kinnaird 1997). This research adheres to all legal requirements and guidelines of the German and Indonesian governments and institutions and to the ASAB/ASB guidelines for the treatment of animals in behavioural research and teaching.

Each study group was followed from dawn (*ca.* 5:30 am) to dusk (*ca.* 6:00 pm) every day between October 2008 and May 2010. We collected behavioural data on all adult females (15 – 18 in PB, 21 – 24 in R1) using focal animal sampling (Martin & Bateson 1993). We observed focal females until 30 activity point-samples were collected. We recorded her activity (feeding, foraging, socializing, traveling, resting, self-grooming) every minute and the identity of neighbours (in body contact, within 1 body length, and within 5 body lengths) every second minute. We also counted scratching bouts per minute (Table 3.2). We recorded focal social events continuously, including start and end time of interactions, sequence of all of the female's behaviours, with identity and behaviours of all social partners. In the course of the study, the adult female cohort slightly changed as one old female disappeared, and six young females reached adulthood. For clarity and simplicity, we only included in the analyses adult females that were continuously present in the groups across the whole study. In total, this study included 2 480 hours of focal data from 36 females (PB, N = 15: median = 68 hours per female, range: 65 – 78; R1, N = 21: median = 66 hours per female, range: 59 – 71). Inter-observer reliability was calculated with Cohen's kappa for categorical data and a set of Pearson's correlations for continuous data (Martin & Bateson 1993). Overall, reliability was good to excellent ($\kappa = 0.69 – 0.90$, correlation coefficients between behavioural variables = 0.79 – 0.98, all Ps < 0.05).

Table 3.1 Details of predictions and summary of results on the four potential functions of three post-conflict interactions.

Predictions	**Results**
Consequences of aggression:	
The occurrence of aggression increases:	
scratching	no
restlessness	no
secondary aggression	yes
Conflicts generate more scratching and higher restlessness when they are:	
more intense	scratching: no – restlessness: no
longer	scratching: no – restlessness: no
undecided	scratching: no – restlessness: yes
Conflicts generate more scratching and higher restlessness when within:	
dyads with higher CSI	scratching: no – restlessness: no
dyads with more frequent support	scratching: no – restlessness: no
dyads with more symmetric relationships	scratching: no – restlessness: no
dyads with more constant temporal exchange of grooming	scratching: no – restlessness: no
dyads with less counter-aggression	scratching: no – restlessness: no
dyads with less aggression	scratching: no – restlessness: no
dyads with a smaller rank difference	scratching: no – restlessness: no

Table 3.1 (continued)

Functions:	**Aggression with 3rd-party**	**Affiliation with 3rd-party**	**Reconciliation**
Stress-reduction			
Interaction decreases			
scratching	no	yes	no
restlessness	no	no	no
renewed and secondary aggression		no	no
Interaction occurs more often after			
intense conflicts	no	no	no
undecided conflicts	no	no	yes
longer conflicts	no	no	no
social context conflicts	no	yes	yes
unexpected direction conflicts	no	no	trend
Repair of relationships			
Affiliation occurs more often after conflicts within			
dyads with higher CSI		no	no
dyads with more frequent support		no	no
dyads with more symmetric relationships		no	opposite
dyads with more constant temporal exchange of grooming		no	yes
dyads with less counter-aggression		no	yes
dyads with less aggression		no	no
dyads with a smaller rank difference		yes	no
Self-protection			
Recipients initiate more interaction than aggressors	no (30%)	no (53%)	no (59%)
Interactions initiated by opponents target more often lower-ranking individuals	yes (83%)	yes (81%)	
Aggression with third-parties occurs less often with reconciliation or affiliation	no		
Benign intent (reconciliation)			
Recipients initiate more often reconciliation			no (41%)
Higher-ranking females initiate more often			yes (64%)
Affiliative non-contact affiliations precede contact ones			yes (69%)

3.3.2 Data processing

We defined and recognised an aggression, or conflict, whenever an individual displayed an aggressive behaviour (threat, hit, grab, push, bite; Chapter 2) towards another one, who responded either by an aggressive or non-aggressive behaviour (e.g. avoidance; Chapter 2). An aggression was terminated when females had stopped exchanging aggressive behaviour for more than a minute (Petit et al. 1997). Similarly, an affiliation was defined and recognised as any active affiliative behaviour (e.g. groom, embrace, touch, lipsmack, or grunt), directed at an observable target (Thierry et al. 2000a, Chapter 2). The individual starting the behaviour was the initiator of the interaction and the target of this behaviour was the recipient.

3.3.2.1 Post-conflict observation periods

Post-conflict observations (PC) were extracted *a posteriori* from focal protocols. PCs started right after the last exchange of aggressive behaviours between the focal female and her opponent, and lasted ideally ten minutes (median: 10 min, range: 2 – 10 min). If aggression flared up again within a minute of the start of a PC, the PC was postponed until the aggression had definitely stopped or discarded if it was not possible to postpone it. Traditionally, PCs are subsequently paired with matched-control observation periods (MC), which are standard observation protocols often conducted the day after, or according to observation conditions, as soon as possible after, the specific aggression has occurred, controlling for opponents' proximity, group's activity and/or period of the day (de Waal & Yoshihara 1983). However, this procedure was traditionally designed for captive studies where group composition and activity is more stable and predictable throughout the day than under natural conditions. Using this method substantially reduced our dataset (285 PC-MC against 450 PCs in total) because we did not always find suitable MCs to match PCs (e.g. previous opponents were not found in proximity within a fixed timeline after the specific aggression). In order to be able to analyse our complete dataset, we followed the procedure of Patzelt and colleagues (2009), who applied a derivative of the time-rule method (Aureli et al. 1989). Females in this study affiliated with each other on average 2.5 times per hour and aggressed each other on average 0.4 times per hour (Chapter 2), meaning that an interaction occurring within 10 min was above the average probability of interacting (24 min for affiliation and 150 min for aggression) and was therefore counted as a post-conflict interaction. When calculating frequencies of interactions in PC and baseline (i.e. the entire observation period), we nevertheless controlled for the number of scans

the dyad spent in proximity, (see Data analyses). The results based on this definition of post-conflict interactions and those obtained through the PC-MC method were identical.

3.3.2.2 Behavioural variables and indices

Definitions of variables are summarised in Table 3.2 (see Chapter 2 for more details).

Restlessness and *scratching* were used as behavioural indicators of anxiety. Restlessness is the rate of changes in activity or behaviour, the higher the value the more restless the individual is. It is part of the generalised anxiety disorder diagnosis in humans (e.g. Kavan et al. 2009). It was positively correlated to scratching in rhesus macaques (Higham et al. 2011) and also in females of this study (Pearson's correlation: $r_p = 0.625$, $N = 36$, $P < 0.001$). We based our index on feeding, foraging, resting, travelling and self-grooming activities. For each minute scan of observation, we coded 1 when a change in activity occurred (for example, the female foraged then rested) or 0 when no change occurred (the female kept foraging). We then calculated the number of changes (i.e. number of 1s) per scans, i.e. the total number of 1s and 0s, per focal, in PCs and baseline (i.e. the entire observation period or 19 months).

To account for differences in dominance between females, we used *Elo rating*, a recently developed index which reflects individuals' success in agonistic interactions (Albers & de Vries 2001; Neumann et al. 2011). Calculations were based on sequences of agonistic interactions with clear winner and loser (aggressive interactions where the recipient leaves or displacement interactions; see Neumann et al. 2011; Chapter 2). Basically, at the beginning of the observation period, each individual in a group starts with a rating of 1 000, which is updated after each agonistic interaction an individual is involved in. The updating process increases or decreases the Elo rating of each individual according to the outcome of the interaction and a determined factor, *k* (here k = 100 as in Neumann and colleagues (2011)): the winner increases its Elo rating, the loser decreases it. An expected outcome (higher-rated individual wins) brings smaller changes in individual Elo ratings than an unexpected one (lower-rated individual wins). One of the advantages of this method is that ratings are updated continuously and can be extracted at any point in time. Since Elo rating is a new method in behavioural ecology and biology, we ordered females according to their Elo ratings (higher Elo rating first) and verified that this order was identical to the one obtained through the I&SI method which establishes the optimal rank order fitting a linear hierarchy (de Vries 1998). We calculated Elo ratings of the aggressor and the recipient retrospectively the day before the conflict occurred. We then subtracted the Elo rating of the recipient of aggression from the Elo rating of the aggressor to have the absolute difference in Elo ratings between the two opponents. We tabulated

the sign of the difference as an extra variable (e.g. higher-ranking female as the initiator = positive difference).

Relationships can be described by three components representing different relationship qualities: value, i.e. the benefits partners bring to each other (e.g. support in aggression), security, i.e. how stable or symmetric or predictable the exchange of social behaviour is, and compatibility, i.e. the general tenor of relationships (Cords & Aureli 2000). Researchers have operationally defined these three components by reducing a pool of dyadic variables into the three relationship components through Principal Component Analysis (Fraser & Bugnyar 2010; Fraser et al. 2008; Majolo et al. 2010; McFarland & Majolo 2011). However, our data were not adequate for this procedure (low Kaiser-Meyer-Olkin index of sampling adequacy, low communalities and variables loading on different factors difficult to interpret). To study the influence of dyadic relationship characteristics, we therefore selected a set of variables most representative of social relationships (see Table 3.2) consistent with the framework of Cords and Aureli (2000) and with those used by other researchers (e.g. Fraser & Bugnyar 2011; Majolo et al. 2009b; McFarland & Majolo 2012).

To quantify the strength of the social bond of a dyad, we pooled different affinitive behaviours into a single index, the *Composite Sociality Index* (CSI, Silk et al. 2006b). This index measures the extent to which a dyad deviates from the average dyad in the group and is built on matrices of correlated social behaviours, here grooming duration, frequency of approach in close proximity and percentage of positive approaches (Table 3.2). High values represent dyads that had stronger social bonds than the average dyad in their group. Although the strength of bonds may be related to fitness components in female mammals (primates, Silk 2007b; mammals, Silk 2007a), we have no evidence of this pattern in our study population yet. Thus, this index together with the frequency of aggression represented the general tenor of relationships, or their compatibility (Cords & Aureli 2000; Fraser & Bugnyar 2010; Fraser et al. 2008; McFarland & Majolo 2011; Table 3.2). Using Elo ratings (see above), we also controlled for rank difference, which can influence the frequency of social exchanges such as females closer in rank interact more often with each other than females further in rank in the hierarchy (Schino 2001; Seyfarth 1977). This variable thus also represented compatibility of a relationship. The sign of the difference was included because lower-ranking females can also initiate aggression against higher-ranking ones (Chapter 2; Table 3.2), a particular feature of tolerant macaque species potentially having an influence on post-conflict events.

Table 3.2 Summary of behavioural variables, their definitions, units and scales

Variables	Definitions	Unit / Scale
Consequences of aggression		
scratching bout	one episode of scratching the same body area. A new bout started with changes in body area or breaks of more than 5s.	number per minute
aggression	aggression between a 3rd-party and one of the opponents (secondary aggression) or between the two opponents again (renewed aggression, only if > 1min after PC started).	number per minute
restlessness	an index of changes in activity (see text). The higher the index the more restless the individual.	continuous
Post-conflict interaction characteristics		
affiliation	frequency of affiliation between opponents or with third-parties, controlling for proximity scans (< 5 body-length)	number per dyadic proximity scans
presence in proximity	frequency of proximity scan with opponent present	number per focal proximity scans
aggression	frequency of aggression between opponents or with third-parties, controlling for proximity scans (< 5 body-length)	number per dyadic proximity scans
initiation	initiation of reconciliation, affiliation and aggression with a 3rd-party	by aggressor / by recipient or by opponent / by a third-party
Conflict characteristics		
intensity	occurrence of physical contact (hit, grab, push, bite)	yes / no
duration	difference between the onset and offset of the aggressive interaction	second
decidedness	identification of a clear winner (e.g. recipient avoids aggressor)	yes / no
polyadic	involvement of other individuals than the two original opponents	yes / no
redirection	the recipient directs aggressive behaviour(s) towards third-party individual(s) within less than 30s after the original conflict.	yes / no
context	divided in food-related: conflict occurring during feeding or foraging, and socially-related: conflict occurring over access to an infant, a grooming or mating partner or consisting of an aggressive intervention.	food / social
Dyadic characteristics		
grooming	duration of grooming given and received	min. / dyad obs. hours
approach frequency	frequency of approaches in close proximity (≤ 1 body-length)	number / dyad obs. hours
positive approach	frequency of close proximity approaches followed by affiliation	number / dyad obs. hours
grooming variation	coefficient of variation of grooming duration across the 19 months of the study (see text)	continuous
absolute Elo difference	difference in Elo ratings of the aggressor and recipient (see text)	continuous
sign rank difference	sign of the difference in Elo ratings (see text)	positive / negative
affiliation symmetry index	average symmetry index in grooming and approach (see text)	continuous
CSI scores	based on grooming, approach within-one-body-length and positive approach (see text)	continuous
support	mean frequency of support and peaceful intervention (see text)	number / dyad obs. hours
aggression	frequency of aggressive interactions	number / dyad obs. hours
counter-aggression	frequency of bidirectional aggressive interactions	number / dyad obs. hours
Components of a relationship		
value	support	
security	affiliation asymmetry index, grooming variation, counter-aggression frequency	
compatibility	CSI, aggression frequency, Elo difference	

We furthermore selected diverse indices or interactions measuring symmetry (ASI, see below and Table 3.2), stability (CV, see below and Table 3.2) and predictability (counter-aggression because it is related to undecided outcomes in aggression, Table 3.2) in behavioural exchanges, which together represented the security in relationships (Cords & Aureli 2000; Fraser & Bugnyar 2010; McFarland & Majolo 2011; Table 3.2). The *affiliation symmetry index* (ASI) shows how much each member of the dyad contributes to the relationship. A value of 0 indicates complete symmetry (equal exchange between individuals within the dyad), 1 complete asymmetry. The index is based on the absolute difference between what is given by individual A to individual B and what is given by individual B to individual A over the sum of what is exchanged between A and B (Majolo et al. 2010). In order to take into account a more substantial part of females' relationships and because one dyad was never observed grooming, we calculated the ASI both for grooming duration and for number of approaches in close proximity. The two were highly correlated. We then averaged the two indices to compute a mean dyadic ASI. The *grooming variation index* (CV) measures the temporal variation in grooming duration exchanged within a dyad (Majolo et al. 2010). Grooming duration within a dyad was calculated for each month (range = 0 – 3011s). The grooming variation index was then computed by dividing the standard deviation by the mean of the 19 months of the study for each dyad. A small coefficient of variation indicates that within a dyad, grooming was exchanged consistently month after month.

Finally, value was represented by *support in aggressive interactions* (Cords & Aureli 2000; Fraser & Bugnyar 2010; Majolo et al. 2010) as it is often related to fitness advantages through rank-related benefits and access to resources (Harcourt 1989; Harcourt & de Waal 1992), and it was reciprocated amongst our study females (Duboscq et al. in preparation). Support in aggression included instances of aggressive support in favour of a female and peaceful interventions (Petit & Thierry 1994a). In the former, the focal female either gave or received support to/from another female in an on-going aggressive interaction. In the latter, the focal female directed affiliation to one or both of the opponents, at least one being female, or the focal female received affiliation from another female during an aggressive interaction. Their frequencies were calculated over the total number of aggressive interactions each member of the dyad was separately involved in to account for opportunity to support.

3.3.3 Data analyses

We calculated baseline behaviour frequencies per minute of focal observation time per female over the duration of the entire observation period and PC frequencies over the duration of

PCs. Although PCs' events were not excluded from baseline calculations, they only represent 2.7% of the total observation time; thus baseline calculations were conservative. We computed dyadic frequencies over total dyadic observation time and focal frequencies over focal observation time.

3.3.3.1 Consequences of aggression (Appendix C, Table C.1, Models 1a-c)

We compared the level of scratching and restlessness between PC periods without interaction of any kind and baseline to assess the general influence of the occurrence of aggression on anxiety. To investigate more directly the consequences of aggression, we studied the effect of conflict and fighting dyad characteristics altogether on restlessness, scratching, and occurrence of renewed and secondary aggression together because renewed aggression was rare (see Results). Redirection of aggression also occurred infrequently so we only compared focal restlessness, frequency of scratching, frequency of secondary aggression and frequency of affiliation with opponent depending on whether redirected aggression occurred or not.

3.3.3.2 Occurrence of post-conflict interactions (Appendix C, Table C.1, Models 2a-c)

To show that post-conflict interactions were specific to post-conflict periods, we compared frequencies of specific interactions (affiliations between opponents, affiliations between one of the opponents and third-parties and aggression between one of the opponents and third-parties) between PC periods and baseline. We also report the attributes of actors and receivers of the first interaction of the PC (opponents' role in the previous conflict, relative rank and strength of the dyadic bond between opponent and interaction partner when possible).

3.3.3.3 Functions of post-conflict interactions

Stress reduction hypothesis (Appendix C, Table C.1, Models 1a-c; Models 3a-b): We investigated the effect of post-conflict interactions on scratching, restlessness and occurrence of secondary aggression, while taking into account, amongst other variables, conflict and fighting dyad characteristics.

Relationship repair hypothesis (Appendix C, Table C.1, Models 3a and 4): We first tested the effect of fighting dyad characteristics on the occurrence of post-conflict affiliation between opponents at the conflict level. We then investigated the influence of dyadic characteristics on the general dyadic propensity to reconcile. Since we could not calculate Veenema's corrected conciliatory tendency reliably for each dyad due to a too low number of conflict per dyads (minimum

necessary = 3; Veenema et al. 1994), we analysed the dyadic number of conflicts followed by affiliation between opponents, controlled for the total number of conflicts the dyad had over the observation period.

Self-protection hypothesis (Appendix C, Table C.1, Models 1c and Models 3a-b): We tested whether recipients initiated or received post-conflict interactions more often than aggressors. We also investigated whether affiliative post-conflict interactions reduced the likelihood of secondary aggression. When possible, we looked at the relative rank of targets of secondary aggression compared to the initiator to determine whether lower-ranking individuals were more often targeted than not.

Benign intent hypothesis (Appendix C, Table C.1, Model 3a): We analysed the initiation of reconciliation in regard to the opponents' role in the previous conflict. We also investigated whether the initiator of reconciliatory affiliation used in majority non-contact behaviours before contact behaviours as a signal of peaceful intention.

3.3.4 Statistical analyses

All analyses were done in R version 2.14.1 (R Development Core Team 2011). Alpha was set at 0.05. Wilcoxon tests were executed with the package "exactRankTests" (Hothorn & Hornik 2011). To test the effects of post-conflict interactions, and conflict and dyadic characteristics, we ran Generalised Linear Mixed Models (GLMMs) (Bolker et al. 2008) as they allow taking single conflict as the basis of analysis while accounting for repeated measurements. Random factors included aggressor, recipient or focal female, and group, depending on models. In Model 4, an "offset" term was introduced to take into account the total number of conflicts each dyad had (Appendix C, Table C.1). We also included various interactions between our different variables, especially between different conflict characteristics, between role of opponent and conflict characteristics or between dyadic characteristics. None of the interactions tested contributed significantly to our models (likelihood ratio tests (LRT), full versus reduced model, all Ps > 0.05), so we finally excluded them all from the analyses. We transformed continuous variables to improve normality whenever necessary and standardised them to a mean of 0 and a standard deviation of 1 to make estimates comparable. GLMMs, with Gaussian, binomial or Poisson error structures, were implemented with the function "lmer" from the package "lme4" (Bates et al. 2011). For all models, we checked that the assumptions of normally distributed and/or homogeneous residuals were fulfilled by visually inspecting plots of the residuals and of the residuals against fitted values (Field et al. 2012). We also checked for model stability by excluding data points one by one and comparing the estimates derived in this way with

those obtained from the full model (Field et al. 2012). Variance Inflation Factors were derived using the function "vif.mer" and were considered acceptable below 4 (Field et al. 2012). Since we tested general hypotheses about the influence of a set of predictor variables, and not which one had more influence on the response variable, we then tested the full model (including all fixed effects and random effects) against a null model (including only the intercept and random factors, control factors too when specified) using a likelihood ratio test (function "anova" with argument test "Chisq"). P values from GLMMs with Gaussian error structure were calculated based on Markov Chain Monte Carlo sampling and derived using the function "pvals.fnc" of the package "languageR" (Baayen 2007). Whenever the full model was not statistically different from the null model, we report the estimates and standard errors but omit the P values. Details of the different models (Appendix C, Table C.1) as well as their full results (Appendix C, Table C.2 & C.3) are given in the supplementary material.

3.4 Results

We based our analyses on 450 conflicts (PB: 173, median per female = 7, range: 6 – 20; R1: 277, median per female = 12, range: 6 – 24) on 207 out of 315 dyads (PB: 76, median per dyad = 2, range: 1 – 8; R1: 141, median per dyad = 2, range: 1 – 9). In half of the cases (N = 226), the focal female was the recipient of aggression. Results are summarised in Table 3.1.

3.4.1 Consequences of aggression

We found no statistically significant difference in mean restlessness, scratching frequency and secondary aggression frequency in regard to the females' role in conflicts, aggressor or recipient (Wilcoxon signed-rank tests: N = 32, restlessness: V = 237, P = 0.625; scratching: V = 245, P = 0.733; aggression: V = 190, P = 0.258, Figure 3.1a).

There was no significant difference in female mean restlessness between PC periods and baseline (Wilcoxon test, V = 276, N = 36, P = 0.380). Scratching frequency in PCs with no interaction were lower than during baseline (Wilcoxon test: V = 441, N = 32, P < 0.001, Figure 3.1b). There was no significant difference between mean scratching frequencies in PCs with interactions (of any kind) and PCs without (Wilcoxon test: V = 177, N = 32, P = 0.168). Female mean aggression frequency was higher in PCs compared to baseline (Wilcoxon test: V = 10, N = 36, P < 0.001, Figure 3.1b).

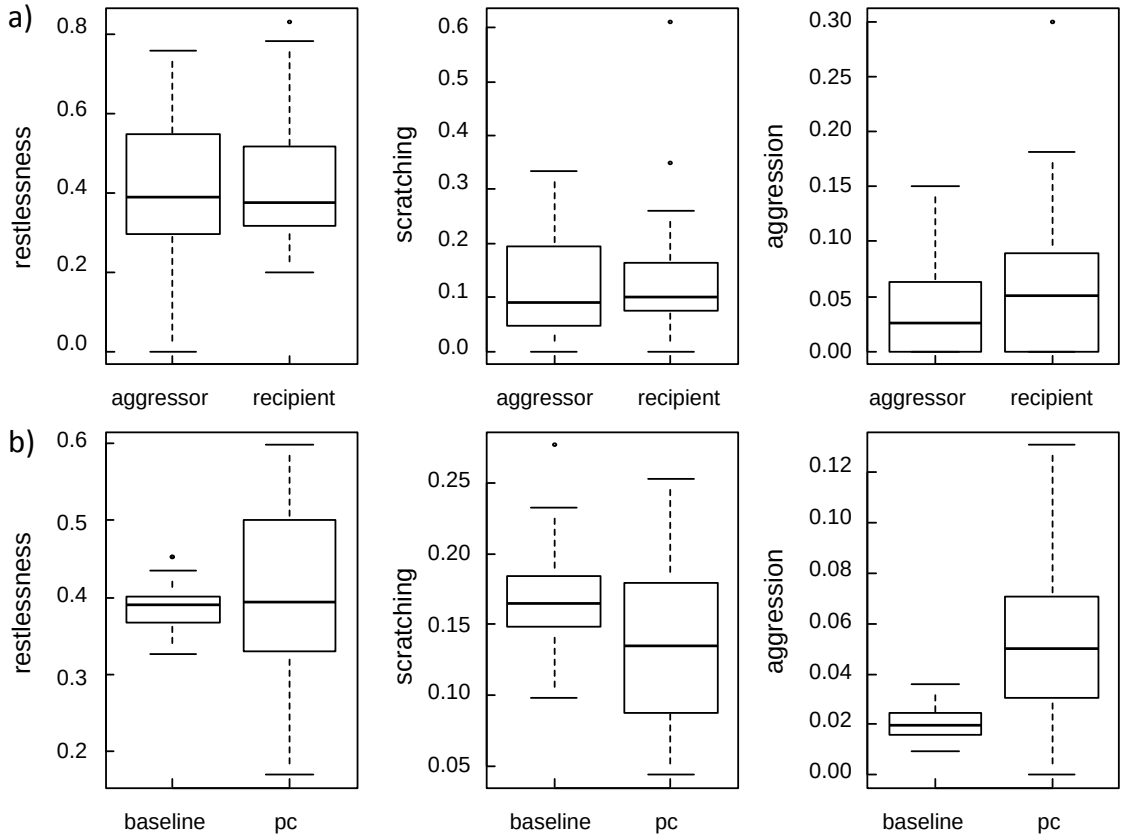

Figure 3.1 Restlessness, scratching frequency (number per minute) and secondary aggression frequency (number per hour) a) according to role of focal female in initial aggression, aggressor or recipient, and b) in post-conflict periods (pc) and baseline (median and inter-quartiles, N = 36, see text for test results).

Females were more likely to scratch after low intensity conflicts, and were more restless when conflicts were undecided (Appendix C, Table C.2a, Models 1a-b). None of the conflict characteristics had a significant influence on the occurrence of secondary aggression (Appendix C, Table C.2a, Model 1c). Similarly, there was no evidence that fighting within a specific dyad had any effect on anxiety and likelihood of secondary aggression (Appendix C, Table C.2a, Models 1a-c).

3.4.2 Occurrence of post-conflict interactions

3.4.2.1 Affiliation between opponents

Females affiliated with their opponent in 47% of PC periods. Female opponents affiliated and stayed in proximity of each other significantly more often during PC than baseline (Appendix C, Table C.2b, Models 2a-b).

3.4.2.2 Affiliation between opponents and third-parties

Female opponents affiliated with a third-party individual in 62% of PCs. The overall frequency of affiliation with third-party individuals in PCs was significantly higher than baseline affiliation levels (Appendix C, Table C.2b, Model 2c). However, females gave and received affiliations equally often in PCs and baseline (Wilcoxon tests: N = 36, affiliation given: PC = 0.07 ± 0.09 per min, baseline = 0.06 ± 0.05, V = 304, P = 0.658; affiliation received: PC = 0.05 ± 0.06, baseline = 0.04 ± 0.04; V = 341, P = 0.907). 57% of affiliations with third-parties were initiated by the previous opponents. Females were more likely to affiliate with a third-party when they had previously affiliated with their opponent (73% vs. 54%; Appendix C, Table C.3a, Models 3a-b).

3.4.2.3 Post-conflict aggression between opponents and between opponents and third-parties

We observed a total of 205 bouts of all secondary aggression occurring in 36% of PC periods. Aggression occurred more frequently in PCs than overall aggression during baseline (Wilcoxon test: V = 10, N = 36, P < 0.001). Females both gave and received more aggression in PCs than baseline (Wilcoxon tests, N = 36: $PC_{(given)}$ = 0.05 ± 0.03 per minute, $baseline_{(given)}$ = 0.02 ± 0.01, V = 83, , P < 0.001; $PC_{(received)}$ = 0.04 ± 0.03, $baseline_{(received)}$ = 0.01 ± 0.00, V = 55, P < 0.001). Aggression flared up again between the two previous opponents in only 8% of all cases (renewed aggression, N = 15); in half of these cases, renewed aggression occurred although reconciliation had already taken place. Recipients redirected aggression in 13% of PCs (redirection, N = 58). In 56% of these cases, females simultaneously left the proximity of their aggressor, which indicated the end of the initial conflict. 56% of secondary aggressions other than renewed aggression and redirection (N = 132) were initiated by one of the opponents.

3.4.3 Functions of post-conflict interactions

3.4.3.1 Stress reduction hypothesis

Females were not less likely to scratch or to be less restless when reconciliation occurred than when reconciliation did not occur (Appendix C, Table C.2a, Models 1a-c). Females affiliating with third-party individuals scratched less, but were not less restless (Appendix C, Table C.2a, Models 1a-c). Scratching and restlessness were not influenced by the reoccurrence of aggression (Appendix C, Table C.2a, Models 1a-b; for redirected aggression: Wilcoxon tests: N = 20, restlessness: V = 82, P = 0.409; scratching: V = 108, P = 0.352; secondary aggression: V = 190, P = 0.257).

Females reconciled significantly more often when conflicts occurred in a social context (58% vs. 21%), when conflicts were undecided (70% vs. 30%) or shorter (35% of above-mean duration vs. 51% of below-mean duration) and when redirected aggression did not occur (48% vs. 36%; Table S3a, Model 3a). Females affiliated with third-party individuals significantly more often when conflicts occurred in social contexts (73% vs. 37%; Appendix C, Table C.3a, Model 3b). There was no evidence that conflict characteristics influenced the occurrence of secondary aggression (Appendix C, Table C.2a, Model 1c).

3.4.3.2 Relationship repair hypothesis

There was a large variation in dyadic proportion of reconciled conflicts: 20% of dyads that had conflicts (N = 207/315) never reconciled and 23% always reconciled. Overall, dyads reconciled 45% of their conflicts. At the conflict level, we found that dyads with a higher asymmetry in affiliation (48% for dyads with an above mean symmetry vs. 46%) or exchanging less counter-aggression (51% for dyads with a below-mean counter-aggression frequency vs. 46%) were more likely to reconcile compared to other dyads (Appendix C, Table C.3a, Model 3a). In addition, in general, dyads with a higher asymmetry in affiliation, a lower variation in grooming duration across time and a smaller frequency of aggressive interactions showed a higher number of reconciled conflicts (Appendix C, Table C.3b, Model 4).

Females did not affiliate more often with female third-parties with which they had a higher-than-average CSI score (mean $CSI_{(3rd\text{-}party)}$ = 1.81 ± 0.95, mean $CSI_{(baseline)}$ = 1.58 ± 0.97; one-sample Wilcoxon signed-rank tests: V = 2534, N = 92, P = 0.124), but they did affiliate more often with female third-parties closer in Elo rating than the average difference (mean $Elo_{(3rd\text{-}party)}$ = 641 ± 471, mean $Elo_{(baseline)}$ = 849 ± 576; one-sample Wilcoxon tests: V = 1033, N = 92, P < 0.001).

3.4.3.3 Self-protection hypothesis

Overall, the role of the focal female in the initial aggression did not significantly influence the occurrence of reconciliation, of third-party affiliation, or of secondary aggression (Appendix C, Table C.2a, Model 1c, Table C.3a, Models 3a-b). Recipients did not initiate significantly more affiliation with third-parties than aggressors (Wilcoxon test: V = 211, N = 36, P = 0.657). Aggressors initiated significantly more aggression towards third-parties than recipients (Wilcoxon test: V = 409, N = 36, P < 0.001).

Female recipients redirected aggression towards lower-ranking individuals in 98% of all instances (juveniles: 75% of cases, females: 23% of cases (all lower-ranking than the recipient), males 2% of cases). Secondary aggressions from opponents to third-parties were generally directed down the hierarchy (83% of instances directed at lower-ranking individuals than the opponents).

The occurrence of post-conflict affiliations did not significantly lower the likelihood of secondary aggression (Appendix C, Table C.2a, Model 1c). Reconciliation was less likely when redirection occurred (Appendix C, Table C.3a, Model 3a). Females were more likely to affiliate with a third-party when they also redirected aggression (67% vs. 62%) or in general, when they were involved in secondary aggression (70% vs. 59%; Appendix C, Table C.3a, Model 3b).

3.4.3.4 Benign intent hypothesis

Recipients did not significantly initiate more reconciliation than aggressors (59% of reconciliations initiated by recipients; Wilcoxon test: V = 259, N = 36, P = 0.930). Higher-ranking females initiated significantly more reconciliation than lower-ranking females (64% initiated by the higher-ranking female; Wilcoxon test: V = 419, N = 36, P < 0.001). Reconciliation tended to be more likely when lower-ranking females had initiated the previous conflict (77% vs. 40%; Table S3a, Model 3a). 59% of first contact affiliations, significantly higher than by chance (Proportion test: $N_{initiator}$ = 75, N_{total} = 127, 95% CI = 0.50 – 0.68, P = 0.051), were preceded by a non-contact affiliative behaviour such as lipsmacking or grunting.

3.5 Discussion

The study of post-conflict interactions in females of a wild population of tolerant macaques brings a novel perspective on the function of these interactions. The occurrence of aggression did not increase the measured level of anxiety of opponents, but it increased the likelihood of further

aggression occurring in the period right after. Conflict and fighting dyad characteristics had little influence either on the behavioural indicators of anxiety tested or on the occurrence of any of the three post-conflict interactions investigated. The patterns uncovered in wild female crested macaques thus indicate different functions of post-conflict interactions in this population compared to other macaques in particular and, to our knowledge, animal societies in general.

The fact that the occurrence of aggression did not increase behavioural indicators of anxiety, neither in aggressors nor in recipients, stands in stark contrast with what was generally found in other animals. Thus, although scratching has been linked to anxiety in numerous species, including humans (Maestripieri et al. 1992; Schino et al. 1996), it could be that scratching and anxiety levels are weakly correlated in tolerant species (see De Marco et al. 2010, 2011, but also Aureli & Yates 2010). Recording of other displacement activities and/or physiological parameters such as heart rate, blood pressure or stress hormones could provide a more detailed anxiety profile. Another possible explanation for this pattern could be that females were "too busy to scratch" given that post-conflict interactions occurred overall in 63% of PCs, and happened quickly and in rapid succession. In contrast, in more despotic macaques, affiliation after conflicts is rarer, leaving room for the expression of anxiety (Cooper & Bernstein 2008; Majolo et al. 2009a; Thierry et al. 2008). More significantly, since conflict characteristics had little influence on behavioural indicators of anxiety, it seems that conflicts between females of this wild population of crested macaques were not significantly costly or were not perceived as risky. In comparison to despotic species, conflicts were indeed of lower intensity (i.e. with less biting) so the risk of being wounded was low (Thierry et al. 2008; Chapter 2). Since crested macaque females also showed high rates of counter-aggression (Chapter 2), a fair amount of aggressive interactions were undecided, i.e. without a clear winner and a loser, and power asymmetries were moderate (Chapter 2). The combination of these conflict characteristics makes it plausible that social exchanges are less stressful (Aureli & Schaffner 2006; de Waal 1986, 1996). These patterns are mostly consistent with existing data from captive crested macaques (Petit et al. 1997; Petit & Thierry 1994b) and other tolerant Sulawesi macaques (semi-free ranging Tonkean macaques, *M. tonkeana*, Demaria & Thierry 2001; wild Moor macaques, *M. maurus*, Matsumura 1996), suggesting that the function of post-conflict interactions depends on the social style of species.

Our results show not only contrasting patterns with regard to the consequences of aggression, but also with regard to our predictions about the functions of post-conflict events. The occurrence of post-conflict interactions had little effect on opponents' behavioural indicators of anxiety. The occurrence of positive post-conflict interactions also did not seem to prevent the reoccurrence of aggressive ones. Based on these results, there was therefore little evidence for the

stress-reduction hypothesis. This is at odds with the majority of the literature in non-human primates (Arnold & Aureli 2006; Aureli et al. 2012) and other mammals (e.g. domestic goat, *Capra hircus*, Schino 1998). Nonetheless, these particular findings are understandable given that aggression had no effect on behavioural indicators of anxiety in the first place, and in the light of crested macaques' conflict characteristics (i.e. low intensity and high frequency of bidirectional aggression).

Again contrary to what we expected, and to what was reported in many other animal species (non-human primates: Arnold & Aureli 2006; Aureli et al. 2012; canids: Cools et al. 2008; Cordoni & Palagi 2008; common raven, *Corvus corax*, Fraser & Bugnyar 2011) and in humans (Fry 2000), partners with a higher CSI ("friends", i.e. dyads that associated and groomed frequently), a lower rank difference (potential kin) and a higher frequency of support ("valuable" partners) did not reconcile more often than those with "weaker" relationships. These findings may be related to the large affinitive networks these females form, where they largely distribute their grooming and approaches amongst their partners (Chapter 2). Thus, in contrast with the relationship repair hypothesis, female crested macaques may work at mending a majority of their relationships, and not only the stronger, more compatible or more valuable ones in the sense of Cords and Aureli (2000). However, we did not investigate long-term benefits of post-conflict interactions on social relationships and it is possible that reconciliation promotes reciprocity in grooming or lowers the probability of aggression in future interactions (Koyama 2001; Silk et al. 1996). Alternatively, our results shed light on other relationship characteristics that female crested macaques may value: dyads with more asymmetric affinitive interactions but less aggression and more consistent duration of grooming across months were more likely to reconcile. This may seem paradoxical at first glance. On the one hand, a predictable and stable relationship, however asymmetric, should be worth preserving. On the other hand, regardless of the stability/predictability of the relationship, reconciling asymmetrical relationships may underlie the high motivation of both dyad members, the one most responsible of maintaining the relationship, and the one getting the benefits of this relationship. Altogether, these results stress the importance of considering all aspects of a relationship, as the different components may indeed have different weights for the individuals, especially in species forming large balanced affinitive networks.

Since the two major functions of post-conflict interactions could not be readily confirmed in females of this population of crested macaques, the self-protection and benign intent hypotheses remain as potential explanatory functions. Related to a self-protection function, aggressors were more often the initiators of secondary aggression towards third-parties, and they also received, although not significantly, more affiliation from third-parties than recipients, suggesting that third-parties could intervene to appease aggressors. However, affiliation with third-parties was not

associated with less secondary aggression from/to third-parties, making an appeasing effect unlikely. Aggression towards third-parties was mainly directed at lower-ranking individuals, especially redirected aggression, which is consistent with a majority of findings in other animals (Kazem & Aureli 2005). From the recipient's perspective, these results support a self-protection effect of aggression towards third-parties in the sense that redirection may serve to reverse a "loser-effect", thereby helping to re-establish social status or to "score psychological victories" (Aureli et al. 2012; Watts et al. 2000). Additionally, given that redirection stopped the initial conflict in more than half of the cases, initial recipients may also initiate secondary aggression when it is less costly or more beneficial to leave the conflict, for example to avoid escalating aggression (Thierry 1985). From the aggressor's perspective, directing aggression to third-parties, especially lower-ranking ones, may function to reinforce a "winner-effect" (Aureli et al. 2012). This makes sense in crested macaques considering that there is no obvious signal of submission females can rely on to assess their social status (Petit et al. 1997; Thierry et al. 2000a; Chapter 2).

Lastly, consistent with a benign intent function, more than half of the first reconciliatory affiliations with contact started with a non-contact affiliative behaviour such as lipsmacking. Similarly, in chacma baboons (*Papio ursinus*) and chimpanzees (*Pan troglodytes schweinfurthii*), opponents were more successful at engaging in reconciliation when "signalling" their peaceful intentions with vocalisations while or before initiating affiliative body contact than without (Arnold & Whiten 2001; Cheney et al. 1995; Silk et al. 1996). In addition, first, higher-ranking females initiated reconciliation more frequently than lower-ranking ones. Second, reconciliation was more likely to follow aggression with unexpected direction, i.e. from lower- to higher-ranking females. The elevated risk of counter-aggression in crested macaques could indeed produce a strong incentive for higher-ranking individuals to being conciliatory in order to avoid escalation and potential coalition formation or long harmful conflicts as consequences. This is also in line with the benign intent hypothesis, which predicts that when retaliation is likely to happen, such as in female crested macaques, recipients should initiate post-conflict contact to signal their peaceful intention and their willingness to avoid escalating (Silk 1996).

Finally, the co-occurrence of different types of post-conflict interactions was not explained by the sequence of interactions: affiliation with a third-party did not necessarily follow a secondary aggression and thus did not constitute a reconciliation episode between one of the opponents and the third-party themselves. Also, on average, secondary aggression occurred later than affiliation with a third-party and the partners involved were rarely the same. This co-occurrence of different kind of interactions with different partners could reflect a general response to the arousal induced by the initial conflict. This explanation has been proposed for instance to account for the occurrence

of quadratic affiliations, that is, affiliative interactions arising between bystanders right after a conflict they were not involved in (De Marco et al. 2010; Judge & Mullen 2005). This finding is consistent with the idea that the occurrence of post-conflict interactions is driven by emotional arousal, which would trigger mechanisms to restore tolerance and to re-establish cooperation between partners (Aureli & Schaffner 2013; Aureli & Schino 2004).

Overall, post-conflict interactions in wild female crested macaques show a different profile from a majority of other macaque and primate species. From the opponents' point of view, our results do not substantiate the stress reduction hypothesis and only partly support the relationship repair one. This does not however undermine the value of these hypotheses for other species. The patterns uncovered in this population make sense in light of its tolerant social style. Individuals from tolerant species, in contrast to more despotic ones, are subjected to weaker hierarchical and nepotistic constraints and interact with more numerous and diverse partners (Sueur et al. 2011; Chapter 2). These dense social networks may allow individuals of tolerant species to maintain group cohesion and to enhance information transmission at low cost through elaborate and efficient social exchanges (de Waal 1986).

The present conclusions, although drawn from the study of a single population of wild crested macaques, highlights the need for further systematic investigations, especially in non-primate species, to achieve a more comprehensive understanding of conflict management strategies in animal societies. Many taxa form social units with permanent, or recurrent, membership, with individualised relationships and where aggressive conflicts occur (Aureli et al. 2002). In gregarious animals, individuals thus benefit of having mechanisms to maintain or restore tolerance between group-members and ultimately, to preserve the benefits of sociality (e.g. spotted hyenas, *Crocuta crocuta*, Hofer & East 2000; toothed whales, Samuels & Flaherty 2000). In such a prospect, factoring in the level of despotism vs. tolerance in social structure appears as a valuable analytic tool to unravel the full range of mechanisms and functions of conflict management strategies in animal societies.

CHAPTER 4

STRUCTURE AND FUNCTION OF SOCIAL BONDS IN WILD FEMALE CRESTED MACAQUES

Julie Duboscq, Muhammad Agil, Dyah Perwitasari-Farajallah, Bernard Thierry, Antje Engelhardt
Prepared for submission

4.1 Summary

A driving force of sociality is the benefits individuals get directly from forming social relationships, which are viewed as investments influencing individual fitness. Favourable traits include competitive skills in order to contest successfully, and social skills in order to establish and maintain alliances for effective cooperation. Important structural factors of social bonds are dominance and kinship, and this has important implications for cooperation in general: kin or individuals adjacent in ranks form the strongest bonds and groom, support or reconcile more often with each other than other dyads. However, how much dominance and kinship influence social life greatly differ between species. In macaques, variation in the hierarchical and nepotistic influences on social relationships between females has been explained along different lines, from ecology to covariation of characters, leading to the classification of their social relationships along an axis despotic - tolerant. A major issue in the study of macaque societies however is a strong bias towards studying despotic species in detriment of tolerant ones. This unbalance truly undermines our understanding of the relationships between the strength of bonds, patterns of coalitionary support and levels of social tolerance according to different degrees of power asymmetries and nepotism. To foster our knowledge in this respect, we aimed at investigating social bonds in relation to dominance, kinship and age, and their function in relation to coalitionary support and levels of social tolerance, in wild female crested macaques, *Macaca nigra*, one of the less-known tolerant macaques. We related our findings to assumptions from the socioecological model and from the covariation model. First, we found no evidence that higher-ranking females are more attractive social partners than lower-ranking ones. Second, kinship does not predict rank relationships. Furthermore, social bonds were strongest between females both kin and close in rank, and also similar in age. In contrast, coalitionary support occurred more often amongst females close in rank or across age classes, but not amongst kin or strong affiliates. In addition, feeding in proximity and reconciliation were not influenced by any of the parameters tested. These results are overall more consistent with a covariation of social traits than with a purely ecological explanation. The differential effects of the same factors on social bonds, coalitionary support, and levels of social tolerance highlight the complexity of social life in tolerant societies, where females form large and diverse affinitive networks.

4.2 Introduction

A driving force of sociality is the benefits individuals get from associating with each other, such as protection against predators or optimal foraging (Krause & Ruxton 2002), but also the benefits they get directly from forming social relationships. The evolution of cooperation between group members has been explained by the benefits of living with kin (kin selection theory; Hamilton 1964) and of exchanging goods and services (reciprocal altruism theory, Trivers 1971, 2006; biological market theory, Noë & Hammerstein 1994, 1995; mutualism or by-product mutualism; all reviewed in Dugatkin 1997, 2002b; see also Bshary & Bergmüller 2008). Social relationships are viewed as investments influencing individual fitness (Kummer 1978) and buffering individuals against the negative consequences of group-living such as increased competition for resources (Silk 2007a; Wrangham & Rubenstein 1986). Looking for the determinant factors of social relationships, competitive and cooperative, is a major task in behavioural ecology and sociobiology.

In mammals, females invest heavily into reproduction, and the critical resource they should optimise access to is food (Trivers 1972). To this end, favourable traits include competitive skills in order to contest successfully, and social skills in order to establish and maintain alliances, and cooperate effectively (Silk 2007a). In permanent stable societies, hierarchical dominance is an important structuring factor of female social relationships because forming hierarchies regulates access to resources without resorting to costly fighting (Preuschoft & van Schaik 2000). High dominance rank can confer multiple privileges, such as greater access to resources and better reproduction (Ellis 1995). Cooperating with kin also provides advantages, not only in terms of fitness by common descent, but also because kin are more familiar and reliable individuals to cooperate with (Chapais 2006; Emlen 1995). Thus, from an evolutionary point of view, high-ranking individuals and kin should be preferred social partners. Female close kin indeed groom, support, reconcile, or help each other more than non-kin (Hirsch et al. 2012; Holekamp et al. 2012; Silk 2007b; Smith et al. 2010). Females also exchange rank-related benefits such as tolerance around resources or support in aggression against other social commodities such as grooming or participation in hunting (Schino 2007; Smith et al. 2007). The greater attractiveness of higher-ranking individuals as social partners can additionally structure social relationships: as a result of the competition to associate with higher-ranking individuals, females form stronger bonds with others close to their own rank, and exchanges are directed up the hierarchy (Schino 2001; Seyfarth 1977; Smith et al. 2007). In female-philopatric, matrilineal, societies, kinship and dominance have cumulative effects on social bonds, and consequently social bonds between dyads of individuals both kin and close in rank are often the strongest.

However, the extent to which dominance and kinship influence females' social life greatly differs between species in relation to social and ecological competitive regimes (Barrett & Henzi 2001; Berman & Thierry 2010; Kapsalis 2004; Schülke & Ostner 2012; Silk 2007a; Thierry 2006). The need for cooperation in collective action problems such as in resource defence as well as the degree of availability in resources can reduce both power asymmetries and nepotism between individuals (Barrett et al. 2002; van Schaik 1989). The benefits of associating with higher-ranking individuals also require, as in any trading, that these individuals provide benefits (e.g. support) and that other individuals trade them against something else (e.g. grooming) (Noë & Hammerstein 1994). Researchers have also argued that individuals may associate and cooperate with others based on familiarity, competence or energetic needs, instead of competition with each other (Chapais 2006; de Waal & Luttrell 1986; Harcourt 1989). As a result, kin or higher-ranking individuals are not necessarily the best partners to cooperate with (Chapais 2006; Clutton-Brock 2009; Harcourt 1989). Cooperation amongst non-kin is actually substantial in some societies; it is sustained because both partners get mutual benefits although they have selfish motives (Chapais 2006; Clutton-Brock 2002, 2009).

Amongst non-human primates, the genus *Macaca* provides an ideal setting to test hypotheses about variation in social bonds according to different degrees of power asymmetries and nepotism. Although they share the same social organisation, i.e. multi-male multi-female groups, with female philopatry and male dispersal (Pusey & Packer 1987), the different macaque species vary greatly in patterns of aggression and affiliation and in the strength of hierarchical and nepotistic influences on social interactions (Koenig 2002; Sterck et al. 1997; Thierry 2007). These differences are currently explained by two models based on different lines of reasoning: whereas the socioecological model mostly relies on the action of ecological factors (van Schaik 1989), the "covariation model" emphasises the role of constraints internal to the social organisation (Thierry 2013). The socioecological model divides macaques species into two categories, Resident-Nepotistic (all but the Sulawesi-macaque group) and Resident-Nepotistic-Tolerant (the Sulawesi-macaque group), based on the strength of between-group (BGC) and within-group (WGC) contest competition for access to food (Sterck et al. 1997; van Schaik 1989). The covariation model classifies macaque species along a four-grade scale of social styles, from despotic (grade 1) to tolerant (grade 4), defined as stable sets of interrelated behaviours (Thierry 2007, 2013). Thus, although the determinants of such diversity are different between the two classifications (see Clutton-Brock & Janson 2012; Janson 2000; Koenig & Borries 2009; Koenig et al. 2013; Thierry 2008), the resulting contrast between both social structures, i.e. tolerant vs. despotic, appear similar. Species classified as RN or despotic, such as rhesus, *Macaca mulatta*, or Japanese, *M. fuscata*, macaques form strict

linear nepotistic and despotic hierarchies, based on coalitionary support amongst kin. Power asymmetries are pronounced. Dominance and kinship strictly regulate social interactions (Koenig 2002; Sterck et al. 1997; Thierry 2007). Species classified as RNT or tolerant, such as Tonkean macaques, *M. tonkeana*, also establish linear hierarchies but power asymmetries are moderate (Koenig 2002; Sterck et al. 1997; Thierry 2007) and the influence of dominance and kinship on social interactions is somewhat limited (Thierry 2007). While the social behaviour and ecology of despotic species have been well characterised (e.g. Chaffin et al. 1995; Cooper & Bernstein 2008; de Waal & Luttrell 1989; Hanya et al. 2008; Heesen et al. 2013; Majolo et al. 2009; van Noordwijk & van Schaik 1987; van Schaik & van Noordwijk 1988), the information available remain scarce under natural conditions for more tolerant ones, such as the Sulawesi macaque species group (Matsumura 1998; Matsumura & Okamoto 1997; Okamoto & Matsumura 2002). This lack of empirical data at one end of the variation continuum prevents to evaluate accurately the theoretical assumptions made by the socioecological and covariation models about the evolution of female social relationships.

To foster our knowledge in this respect, we investigated social bonds according to dominance, kinship and age, and their function in relation to coalitionary support and tolerance levels, in wild female crested macaques (*Macaca nigra*), a species classified as RNT/grade-4. A previous study showed that the crested macaque females indeed express a grade-4, or tolerant, social style: they display linear hierarchies but moderate power asymmetries. They also form large and balanced affinitive networks, and a large proportion of their conflicts is bidirectional and reconciled (Chapter 2). This profile is similar to those reported in other grade-4 macaques (Matsumura 1998; Thierry et al. 1994). A pending question is thus to what extent dominance and kinship shape social relationships and whether we can relate these patterns to the assumptions made by the socioecological model about competitive regimes, and/or to Thierry's most recent classification of social behaviours (2013). Although the socioecological model (Koenig 2002; Sterck et al. 1997; van Schaik 1989) and the covariation model (Thierry 2013) give similar behavioural profiles of tolerant Sulawesi macaques, they make contrasting predictions regarding the extent of kin or dominance biases in the patterning of social interactions. In what follows, italics highlight these differences.

The socioecological model states that hierarchies are established and maintained by coalitions of relatives. In such a view, females form matrilineal hierarchies, meaning that *genetically related females occupy adjacent ranks*. Also, *the degree of relatedness should be related to the strength of cooperative relationships (i.e. social bonds), the frequency of coalitionary support, and levels of social tolerance*. In contrast, the covariation model postulates that *moderate power asymmetries should be associated with a low kin bias in social interactions*. This means that first, the

relationship between degree of relatedness and differences in dominance rank should not be strong (see also Thierry 1990, 2007 on the relaxed rules of maternal rank inheritance in tolerant macaques). Second, *the degree of relatedness should have little influence on the strength of social bonds, on the frequency of coalitionary support and on levels of social tolerance*. Both models predict nevertheless that dominance relationships should be "tolerant". Consequently, differences in dominance rank should be a weak predictor of levels of social tolerance. Additionally, although these are indirect assumptions, social grooming and approaches should not be directed up the hierarchy as the result of more balanced social exchanges between high- and low-ranking females. Thus, higher-ranking females should not necessarily be more attractive social partners than lower-ranking ones.

4.3 Methods

4.3.1 Data collection

Crested macaques are endemic to the island of Sulawesi, Indonesia (Sugardjito et al. 1989). The study population inhabits the Tangkoko-Batuangus Nature Reserve (1˚33'N, 125˚10'E; e.g. Duboscq et al. 2008; Higham et al. 2012), broadly classified as a lowland rainforest with seasonal variation in rainfall and fruit abundance (O'Brien & Kinnaird 1997). The study was part of the Macaca Nigra Project, a long-term field project on the biology of crested macaques started in 2006. We studied two groups, "PB" and "R1", comprising about 60 and 80 individuals respectively. The monkeys were fully habituated to human observers. All adults could be individually identified based on physical characteristics. Observation conditions were excellent as the monkeys spend around 60% of their rime on the ground (O'Brien & Kinnaird 1997). This research adheres to all legal requirements and guidelines of the German and Indonesian governments and institutions, and to the ASAB/ASB guidelines for the treatment of animals in behavioural research and teaching.

We collected behavioural data between October 2008 and May 2010 on all adult females (15 – 18 in PB, 21 – 24 in R1) using focal animal sampling (Martin & Bateson 1993). We collected 30 activity-point-samples observation protocols in which we recorded the focal female's activity every minute: feeding (manipulating, ingesting or chewing food items), foraging (looking for food items), socialising (engaging in aggressive or affiliative interactions), traveling, resting, and self-grooming. Every second minute, we also wrote down the identity of neighbours in three proximity categories: in body contact, within 1 body-length, and within 5 body-lengths. We recorded focal social events continuously, including start and end time of interactions, sequence of all of the female's

behaviours, plus identity and behaviours of all social partners. In total, the study included 2480 hours of focal data from 36 females or 315 dyads (PB: median = 68 hours per female, range: 65 – 78, N = 15; R1: median = 66 hours per female, range: 59 – 71, N = 21). Inter-observer reliability was calculated with Cohen's kappa for categorical data and a set of Pearson's correlations for continuous data (Martin & Bateson 1993). Overall, reliability was good to excellent (κ = 0.69 – 0.90, correlation coefficients between behavioural variables = 0.79 – 0.98, all Ps < 0.05).

For genetic analyses, we collected at least three faecal samples from all females opportunistically, on different observation days (N = 140, median per female = 4, range = 3 - 4). We followed a two-step alcohol-silica storage (Nsubuga et al. 2004): we sampled 1 to 2 g of the surface of the faecal bolus, put it in a 50 ml plastic tube filled with 30 ml of alcohol (>95˚), tagged with the ID of the individual sampled, the group it belongs to, the time and date of collection together with the ID of the person collecting it. After 24 to 36h, the sample was taken out of alcohol, shortly dried on clean soft paper tissue and placed in another 50 ml plastic tube filled with 30 ml of silica beads, on top of a small square of toilet paper to avoid contact and to enhance drying. Tubes were tightly sealed with parafilm tape, tagged with a unique number and stored in airtight plastic boxes at room temperature.

4.3.2 Data processing and analyses

All behavioural interactions were expressed as duration or number per focal and per dyadic (sum of two focals) observation time. For dyadic variables, we summed up what was given to and received by each member of the dyad from/to the other member during their respective focal protocols.

4.3.2.1 Definition of social interactions and indices used

An instance of *feeding in proximity* was counted each time the focal female was engaged in feeding activity with other females in her vicinity, i.e. within five body-lengths. This is an indicator of the individuals' tolerance in proximity of each other in a competitive situation (e.g. Cooper & Bernstein 2008; de Waal & Luttrell 1989; Ventura et al. 2006).

We determined *reconciled conflicts* a posteriori by analysing the sequences of social interactions between the two previous opponents within 10 min after a conflict. We followed the procedure of Patzelt and colleagues (2009), who applied a derivative of the time-rule method (Aureli et al. 1989). The study females affiliated with each other on average 2.5 times per hour (Chapter 2 &

Chapter 3), meaning that an interaction occurring within 10 min was above the average probability of affiliating (24 min). Reconciled conflicts were thus those followed by a non-contact (e.g. lipsmacking) or contact (e.g. grooming) affiliation within 10 min after the occurrence of a conflict, providing the conflict did not start again within a minute after it had ended (Chapter 3). To control for the opportunity to reconcile, we divided the number of reconciled conflicts by the total number of conflicts the dyad had engaged in during the whole study period. To have a better estimation of the tendency of the dyad to reconcile, we selected only dyads that had at least three conflicts during the study period (N = 132 / 315).

We defined *support in aggressive interactions* as the focal female intervening aggressively or peacefully in support of another female or herself receiving such an intervention during an aggressive interaction with another individual (Petit & Thierry 1994a). We calculated the frequencies of support as the number of instances over the total number of aggressive interactions each member of the dyad was separately involved in (Chapter 3).

The *Composite Sociality Index* (CSI; Silk et al. 2006b) was used to quantify the strength of the social bond of a dyad compared to the average dyad in the group. It is built on matrices of correlated social behaviours, here grooming duration (duration of grooming given and received in minutes per hour of dyadic observation time), and frequency of proximity (number of instances females were in proximity of each other per hours of dyadic observation time). High values represent dyads that had stronger social bonds than the average dyad (see Appendix D, Tables D.2 & D.4). Following Micheletta and colleagues (2012), we considered that individuals had a strong bond when the dyad shared a CSI score greater than one standard-deviation above the mean of the group.

To account for differences in dominance between females, we used *Elo rating*, a recently developed dominance index, which reflects an individual's success in agonistic interactions and which is based on sequences of decided agonistic interactions (i.e. displacements or conflicts with a clear winner and loser, for instance the recipient leaves the proximity of the aggressor; Neumann et al. 2011; Chapter 2). Basically, at the beginning of the observation period, each individual in a group starts with a rating of 1000, which is updated after each agonistic interaction. The updating process increases or decreases the Elo rating of each individual according to the outcome of the interaction and a determined factor, k (here k = 100, following Neumann et al. 2011): the Elo of the winner increases and the one from the loser decreases. Expected outcomes (i.e. higher-rated individual wins) lead to smaller changes in individual Elo ratings than unexpected ones (i.e. lower-rated individual wins; Neumann et al. 2011). We calculated Elo ratings of all females at the end of the study period. We then subtracted the Elo rating of the 1st member of the dyad from the Elo rating of the 2nd member of the dyad and took the absolute difference (from here on called Elo difference).

An advantage of using Elo rating is that since it is a continuous measure, the magnitude of the rank differences can be taken into account: the rank difference between individual A (1st ranking) and individual C (3rd ranking) is not systematically doubled that of the difference between individual A and individual B (2nd ranking), for example. We ordered females according to their Elo ratings (higher Elo rating first) and we verified that this order was identical to the one obtained through the I&SI method which establishes the optimal rank order fitting a linear hierarchy (de Vries 1998). Since Elo rating is a rather new method in behavioural biology and ecology, we ran our analyses again with ordinal rank orders and differences. Results were identical.

4.3.2.2 Kinship

DNA was extracted from100-150 mg of faeces with the GEN-IAL® All-tissue DNA extraction kit following the manufacturer's instructions. We measured DNA purity of a subset of our samples by absorbance to verify that extraction has been successful and that samples were of good enough quality (Morin et al. 2001). Using a multi-tubes approach (Taberlet et al. 1996), we amplified 12 short-tandem repeats (or microsatellites), 10 tetranucleotide loci and 2 dinucleotide loci, proven to be informative in humans and other primates (* or $^{+}$ indicates primers that have been modified specifically for *M. fascicularis* or *M. nigra* respectively: D1s548, D3s1768*, D5s1457, D6s493^{+}, D6s501^{+}, D7s2204, D10s1432, D11s925, D12s67^{+}, D13s765*, D14s255^{+}, D18s536; Bayes et al. 2000; Douadi et al. 2007; Kanthaswamy et al. 2006; Zhang et al. 2001; Engelhardt & Perwitasari-Farajallah, unpublished data). We used a two-step multiplex chain polymerase reaction (PCR) approach (Arandjelovic et al. 2009). In a first step, all loci were amplified in a single reaction with 4 µL of DNA extract (diluted 1:25 – 1:50) for each 20 µL of reaction product (2 µL H_20, 2 µL QIAGEN® enzyme buffer (25 mM Tris-HCl pH 8.0, 35 mM KCl, 0.1 mM EDTA, 1 mM DTT, 50% glycerol, 0.5% Tween® 20, 0.5% Igepal® CA-630 and stabilizers) , 1 µL dNTPs 0.5 mM, 0.8 µL bovine serum albumine (BSA) 20 mg/mL, 0.4 µL MgCl 25 mM, 0.4 µL of each primer unlabelled forward and reverse, 0.2 µL QIAGEN® Hot Master Taq 5 U/µL) in an Eppendorf® Master Gradient machine. We started with 2 min of denaturation at 94˚C then ran 30 cycles of 20 sec. of denaturation at 94˚C, 30 sec. of annealing at 54˚C, 30 sec. of elongation at 70˚C and ended with 10 min of final elongation at 70˚C. We followed multiplex PCR by singleplex PCRs, following the same protocol but with each primer separated and different annealing temperatures specific to each primer. We included 1µL of multiplex PCR product and 19µL of reaction product (14 µL H_20, 2 µL QIAGEN® enzyme buffer (25 mM Tris-HCl pH 8.0, 35 mM KCl, 0.1 mM EDTA, 1 mM DTT, 50% glycerol, 0.5% Tween® 20, 0.5% Igepal® CA-630 and stabilizers), 1 µL dNTPs 0.5 mM, 0.8 µL BSA 20mg/mL, 0.5 µL of specific fluorescently labelled (HEX or FAM) primer forward and reverse, 0.2 µL QIAGEN® Hot Master Taq 5 U/µL). For primers D3s1768,

D6s501, and D12s67, we also added 0.4µL MgCl 25mM for better results, and consequently lowered the quantity of H_20 by the same amount. Singleplex PCR products were then prepared for sequencing by diluting PCR products between 1:25 and 1:100, and mixing 1.5µL of diluted product into 14µL of HiDye Formamide buffer mixed with a size standard (HD400 from Applied Biosystems®). Sequences were run on an ABI 3130xL sequencer. Allele sizes were finally read into PeakScanner (Applied Biosystems®). Given that we had several samples per individuals, allele sizes were considered definitive when at least two different extracts of the same individual produced the same results in at least four amplifications for heterozygotes, and six for homozygotes (Taberlet et al. 1996). Consensus genotypes were found for a median of 12 loci (range = 6 – 12). All adult males and females as well as all infants were being genotyped for on-going paternity analyses. We therefore calculated the degree of relatedness, *r*, between adult females based on the genotypes of all individuals (N = 156) so as to have a better estimates of the allele frequencies in the sampled population. To obtain the degree of relatedness between adult females, we processed the consensus genotypes of all individuals on all loci in COANCESTRY®, a software providing two likelihood methods and five moment estimators of relatedness (Wang 2011). Since we knew some mother-offspring relationships (N = 60), we compared the seven coefficients calculated in COANCESTRY with 0.5, the theoretical average *r* between mother and offspring. The dyadic maximum likelihood (DML) estimator of Milligan (2003) proved to be the most reliable estimator of those relationships (mean ± SD = 0.51 ± 0.12); we thus chose this coefficient for the relatedness value between adult females. DML between adult females ranged between 0 and 0.72 with a median of 0.05 (PB: median DML = 0.05, range = 0 – 0.53; R1: median DML = 0.05, range = 0 – 0.72; see Appendix D, Tables D.1 & D.3). Following Kapsalis and Berman (1996a), we took the threshold of DML < 0.125 to classify females as kin or non-kin when counting the number of close female kin per female in the group.

4.3.2.3 Age

We assessed the age category females belonged to based on their reproductive history since 2006 (the beginning of the Macaca Nigra Project), their body size, the shape of their nipples, and the presence of old physical injuries. Young females had less scars and wrinkles, smaller nipples than older ones and they had between none and maximum two infants since 2006. In addition, old females had sometimes a limp and/or they had stopped cycling (no dependent infant and no swelling observed over a period twice the gestation length (6 months); Engelhardt, unpublished data; Hadidian & Bernstein 1979), and/or they did not have an infant for at least 2 years (above the average birth interval; Engelhardt, unpublished data; Hadidian & Bernstein 1979). We categorised

females as young, middle-aged or old. Based on these categories, we then categorised dyads as belonging to the same age class or to different age classes.

4.3.3 Statistical analyses

To investigate biases in social interactions at the individual and dyadic levels, we made use of Generalised Linear Mixed Models (GLMMs) as it allows including a set of predictors together while accounting for repeated measurements (Bolker et al. 2008).

We first ran the analyses at the individual level to detect influences of individual attributes on frequencies of social interactions. We analysed the relationship between Elo rating, age, number of close kin (DML > 0.125, e.g. Kapsalis & Berman 1996a) and strong partners (mean CSI + 1SD, e.g. Micheletta et al. 2012) in the group, and frequencies of grooming, support, general proximity and feeding in proximity. We also tested whether grooming, approach and approach with a positive outcome were more often given up than down the hierarchy and whether this directionality was correlated with individual Elo ratings, i.e. whether lower-ranking females indeed gave more up than down the hierarchy compared to higher-ranking ones.

At the dyadic level, we first investigated the relationship between dyadic Elo rating difference, dyadic degree of relatedness (DML) and age difference (same age class / different age classes) in order to determine whether females close in rank were also genetically related or of the same age class. We then analysed the effect of difference in Elo ratings, degree of relatedness and age together on CSI, support, reconciled conflicts and feeding in proximity. In the model with support, reconciled conflicts and feeding in proximity, CSI scores were included as a main predictor as well. Dyadic frequencies of support were low and highly skewed towards zero, posing problems during modelling. We therefore transformed this variable into a binomial one: the behaviour occurred or did not occur within a dyad. We included the interaction between Elo difference and DML in all models as it could be that the effect of Elo difference on social relationships is more pronounced when a dyad is closely related than when it is not. We also tested a three-way interaction between Elo difference, DML and CSI score in the model for support and reconciled conflicts. We tested whether the interactions contributed significantly to the models with a likelihood ratio test (LRT; function “anova” with argument test “Chisq”) of the full versus a set of reduced models (i.e. without the three-way interaction and incrementally with and without the different two- way interactions and finally only with the two main effects independently). Interactions were removed whenever they did not significantly contribute to the models.

All analyses were done in R version 2.14.1 (R Development Core Team 2011). To calculate Elo ratings, we followed the R script provided with the article from Neumann and colleagues (2011). Wilcoxon exact signed rank tests were done using the "exactRankTests" package (Hothorn & Hornik 2011) and correlations using the "rcorr" function with type "spearman" from the package "Hmisc" (Harrel Jr 2012). We ran GLMMs with Gaussian (and Maximum Likelihood) or binomial error structure, and three random effects, member 1 and member 2 of a dyad, and group. We implemented GLMMs with the function "lmer" from the package "lme4" (Bates et al. 2011). We transformed variables whenever necessary (log, square-root or fourth root) and standardised all numeric variables to a mean of 0 and a standard deviation of 1 to make estimates comparable. For all models, we checked that the assumptions of normally distributed and/or homogeneous residuals were fulfilled by visually inspecting plots of the residuals and of the residuals against fitted values (Field et al. 2012). We also confirmed model stability by excluding data points one by one from the data and comparing the estimates derived in this way with those obtained from the full model (Field et al. 2012). Variance Inflation Factors were derived using the function "vif.mer" and we considered them acceptable below 4 (Field et al. 2012). Cooks distances and dfbetas were calculated and plotted with the function "influence" of the package "influence.ME" (Nieuwenhuis et al. 2012). Whenever potentially influential cases were identified (Cooks distance > 4 / N cases and dfbetas > 2 / square-rooted N cases), we ran the model without them and compared the results with the model including them. Results were identical, indicating that no case was influential. We finally tested the full or reduced model (including all fixed effects and random effects and interaction when relevant) against a null model (including only the intercept and random factors, control factors too when specified) using the likelihood ratio test. P values for models with Gaussian error structure were calculated based on Markov Chain Monte Carlo sampling, and derived using the function "pvals.fnc" of the package "languageR" (Baayen 2007). The significance threshold of all tests and the interpretation of all effects was set at 0.05.

4.4 Results

4.4.1 Relationship between individual attributes and frequency of interactions

Frequencies of interactions and number of female kin and strong partners for each group are summarised in Table 4.1.

Table 4.1 Median and range of number of female partners (kin and strong affiliates) and frequency of interactions between adult females in the two groups (PB = 15 females, R1 = 21 females). Approach frequency from Chapter 2.

	groups	
Variables	**PB**	**R1**
number female close kin	3 (1 - 6)	6 (2 - 12)
number female strong partners	1 (0 - 3)	2 (0 - 6)
grooming duration (min/hour)	1.92 (1.05 - 2.93)	2.07 (0.72 - 4.31)
approach (nb/hour)	4.95 (3.11 - 7.90)	5.00 (2.48 - 8.88)
positive approach (nb/hour)	1.62 (0.91 - 2.34)	1.70 (0.46 - 2.64)
feeding in proximity (nb/scan)	0.20 (0.09 - 0.29)	0.16 (0.05 - 0.27)
support (nb/agg/hour)	0.06 (0.02 - 0.15)	0.06 (0.04 - 0.23)

Females that had more numerous strong partners groomed and were in proximity of other females significantly more frequently than females with less numerous strong partners (Table 4.2, Models 2 & 4). Old females were involved in coalitionary support significantly more often than young or middle-aged females (Table 4.2, Model 3). Higher-ranking females had significantly fewer female kin in the group than lower-ranking ones (Table 4.2, Model 1). All other results were not statistically significant.

Females did not groom significantly more frequently up than down the hierarchy but they did approach significantly more often lower-ranking females than themselves compared to higher-ranking females (Wilcoxon signed-rank test, N = 32: grooming: up = 0.07 ± 0.06 min/h, down = 0.06 ± 0.04 min/h, V = 292, P = 0.612; approach: up = 0.12 ± 0.05 nb/h, down = 0.17 ± 0.05 nb/h, V = 471, P < 0.001). Positive outcome upon approach was also significantly more frequent down than up the hierarchy (Wilcoxon test, N = 32: up = 0.07 ± 0.04 nb/h, down = 0.08 ± 0.04 nb/h, V = 393, P = 0.015). Additionally, the occurrence of significant correlations between individual Elo ratings and frequencies of grooming, approaching and positive outcome upon approach given up and down the hierarchy revealed that higher-ranking females were more often responsible for approaching down the hierarchy, also with positive outcomes, than lower-ranking females (Spearman correlations, N = 32: approach: rho = 0.461, P = 0.007, positive approach: rho = 0.355, P = 0.050, all others: rho = -0.090 – 0.074, P = 0.615 – 0.862).

Table 4.2 Summary of results of GLMMs on the relationships between different individual attributes (model 1) and their influence on frequency of social interactions (models 2 – 5), N = 36.

1/ Elo rating					2/ grooming			
null vs full	χ^2 = 8.797, d.f. = 4, P = 0.066				null vs full	χ^2 = 23.329, d.f. = 5, P < 0.001		
main	β	SE	t value	$P_{(mcmc)}$	β	SE	t value	$P_{(mcmc)}$
intercept	-0.244	0.279	-0.873	0.625	-0.093	0.229	-0.405	0.815
age (mid)	0.527	0.357	1.475	0.167	0.238	0.299	0.797	0.481
age (old)	-0.136	0.433	-0.315	0.639	-0.149	0.353	-0.424	0.738
Elo rating					-0.158	0.137	-1.148	0.365
nb kin	-0.448	0.159	-2.809	0.006	0.069	0.143	0.479	0.608
nb partner	0.142	0.157	0.905	0.610	0.619	0.129	4.805	0.001
3/ support					4/ proximity			
null vs full	χ^2 = 13.429, d.f. = 5, P = 0.020				null vs full	χ^2 = 12.230, d.f. = 5, P = 0.032		
main	β	SE	t value	$P_{(mcmc)}$	β	SE	t value	$P_{(mcmc)}$
intercept	-0.483	0.264	-1.831	0.379	0.195	0.321	0.606	0.732
age (mid)	0.333	0.344	0.967	0.332	-0.387	0.34	-1.137	0.289
age (old)	1.560	0.406	3.840	0.002	0.233	0.404	0.577	0.547
Elo rating	0.059	0.158	0.373	0.991	-0.285	0.161	-1.776	0.147
nb kin	0.016	0.165	0.094	0.617	0.062	0.182	0.338	0.615
nb partner	0.077	0.148	0.520	0.797	0.471	0.148	3.171	0.006
5/ feeding in proximity								
null vs full	χ^2 = 2.219, d.f. = 5, P = 0.818							
main	β	SE	t value	$P_{(mcmc)}$				
intercept	-0.006	0.414	-0.014	0.980				
age (mid)	0.068	0.394	0.173	0.909				
age (old)	0.206	0.462	0.446	0.650				
Elo rating	0.249	0.191	1.304	0.245				
nb kin	0.303	0.214	1.418	0.195				
nb partner	-0.070	0.193	-0.362	0.843				
proximity	-0.004	0.194	-0.022	0.908				

4.4.2 Relationship between Elo difference, degree of relatedness and age difference

Degree of relatedness and age difference were not significantly related to Elo difference (full vs. null: χ^2 = 4.471, d.f. = 2, P = 0.107). Females closer in rank were not more genetically related or closer in age than females further in rank in the hierarchy or belonging to different age classes (kinship = β ± SE = -0.102 ± 0.059, $P_{(mcmc)}$ = 0.082; age difference = β ± SE = 0.130 ± 0.122, $P_{(mcmc)}$ = 0.277).

4.4.3 Influence of Elo difference, degree of relatedness and age on CSI, coalitionary support and tolerance

4.4.3.1 CSI

The full model with the interaction between Elo difference and degree of relatedness explained the variation in CSI scores significantly better than the reduced model without the interaction (full vs. red: $\chi^2 = 5.353$, d.f. = 1, P = 0.021. Appendix D, Table D.5). Dyads of females that were close in rank had significantly higher CSI scores than females distant in rank but the strength of the relationship was dependent of the degree of relatedness, the higher the degree of relatedness the higher the CSI score (Appendix D, Table D.5; Figure 4.1). Females belonging to the same age class tended to be stronger affiliates than those of different age classes (Appendix D, Table D.5; Figure 4.1).

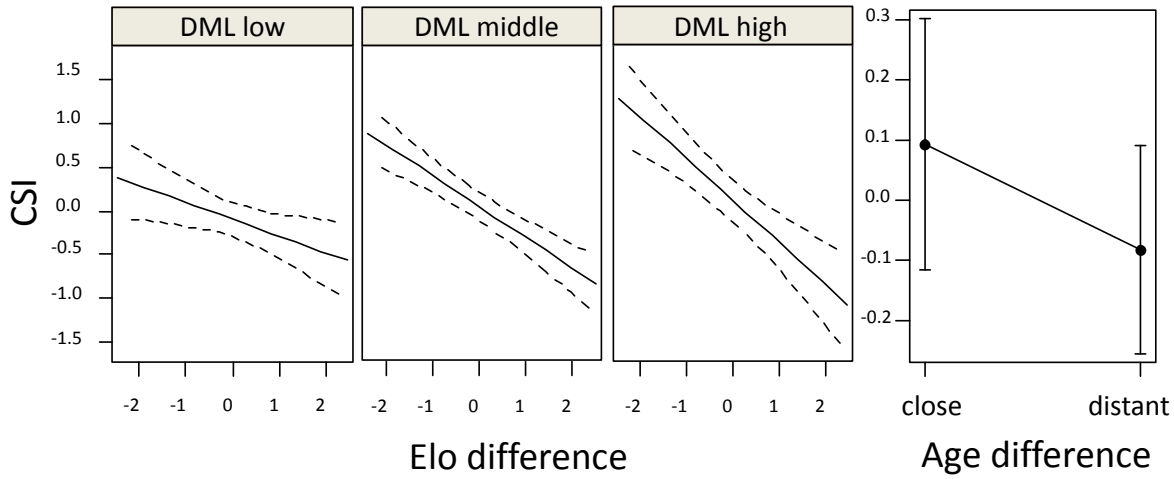

Figure 4.1 *Left side*: effects of the interaction between rank difference (Elo difference) and degree of relatedness (DML) on CSI scores. The continuous line represents the estimate as predicted by the GLMM, dashed lines are the associated standard errors. *Right side*: effect of the age difference (close vs. distant) on CSI scores. Dots and bars represent the estimates and standard errors of the GLMM, respectively (N = 315).

4.4.3.2 Coalitionary support

Models with the interactions between Elo difference, degree of relatedness and CSI scores were not significantly different from reduced models without (all LRTs; P > 0.05), allowing the interpretation of the single main predictors separately. Dyads of females closer in rank and belonging to different age classes were significantly more likely to support each other in aggression.

Neither degree of relatedness nor strength of the bond had an effect on the occurrence of support (Appendix D, Table D.5; Figure 4.2).

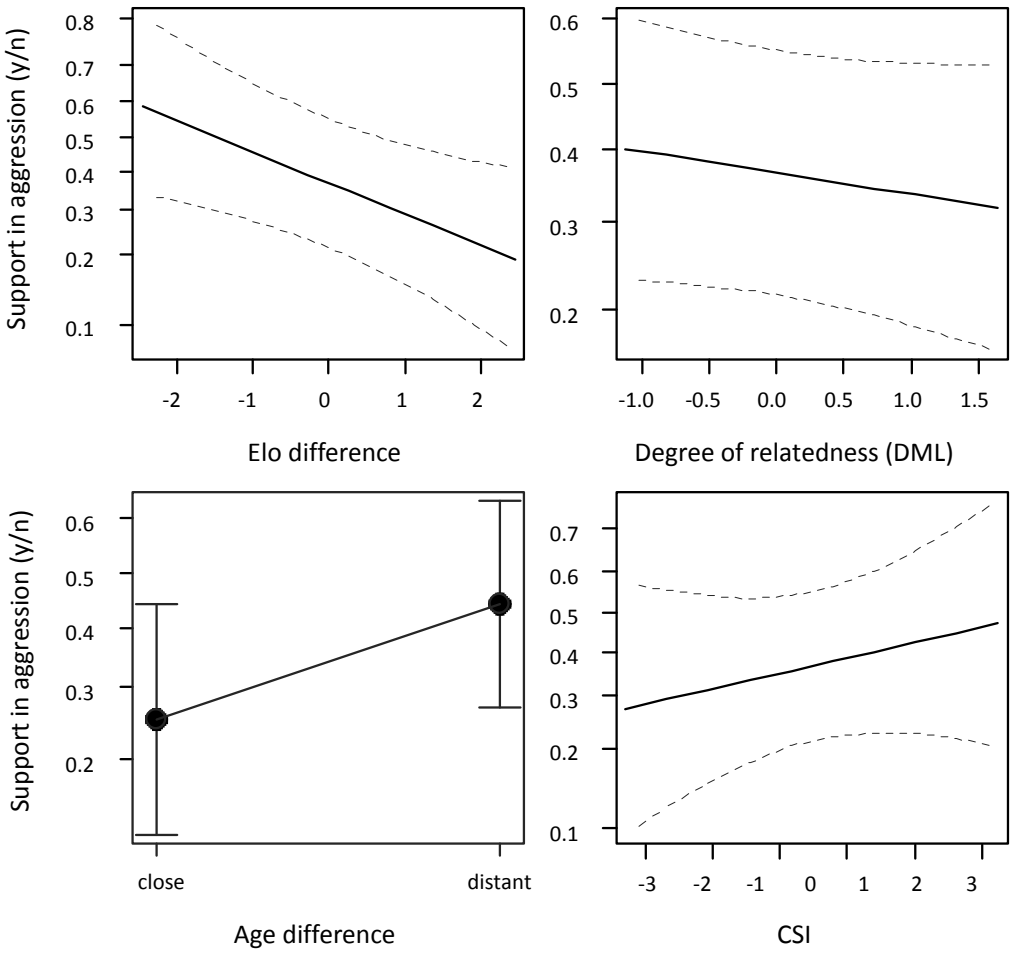

Figure 4.2 Effects of rank difference (Elo difference, upper left), of degree of relatedness (upper right), of age difference (close vs. distant, lower left) and CSI scores (lower right) on the occurrence of coalitionary support. The continuous line represents the estimate as predicted by the GLMM, the dashed lines are the associated standard errors. For age difference (lower left), dots and bars represent the estimates and standard errors of the GLMM, respectively (N = 315).

4.4.3.3 Tolerance

The frequency of feeding in proximity and of reconciled conflicts were not significantly influenced by any of the variables tested (feeding: full vs. null: χ^2 = 9.061, d.f. = 5, P = 0.107; reconciliation, N = 132: χ^2 = 3.455, d.f. = 5, P = 0.485; Appendix D, Table D.5).

4.5 Discussion

Our results show that dominance and kinship did not fully account for the variation found in the social relationships of wild female crested macaques. Hierarchical and nepotistic influences on the females' social life were limited, indicating that higher-ranking females or kin were not necessarily preferred cooperation partners. There were only weak biases in social interactions related to individual attributes. Degree of relatedness, rank difference and age were not related. Degree of relatedness was a weak predictor of social relationships, whereas rank difference and age similarity explained some of the variation in these bonds and in coalitionary support, but not in social tolerance. There have been divergent results on the effect of kinship and dominance in the different studies of tolerant Sulawesi macaques, potentially due to confounding factors such as the analysis of the effect of rank difference without controlling for kinship or the inclusion of mother-infant dyads (Baker & Estep 1985; Matsumura & Okamoto 1997; Thierry et al. 1990). In addition of confirming the variation in hierarchical and nepotistic influences in macaque societies, our study uncovers additional dimensions of social bonds in the more tolerant ones. Social relationships between the study female crested macaques only partly fit the predictions derived from the socioecological model. They generally match the tolerant profile of other Sulawesi macaques (Thierry 2007; Thierry et al. 1994; Thierry & Aureli 2006), and results are consistent with the scale of trait covariation recently outlined in Thierry (2013; p.3).

Higher-ranking females were not more attractive as social partners than lower-ranking ones, contrary to what is known in several cercopithecine species and also in other mammals characterised by female philopatry (Schino 2001; Silk 2007a; Smith et al. 2007). This result is however in accordance with an hypothesis derived from both the socioecological and the covariation models. In fact, approaches in close proximity, as well as positive outcomes upon approach, were directed down the hierarchy, and higher-ranking females seemed responsible for this pattern. The greater attractiveness of lower-ranking females as proximity partners compared to higher-ranking ones can be explained in several ways. Generally, lactating females with young infants, at least during the first few weeks of lactation, constitute a "social hub", attracting numerous individuals (macaques, baboons and vervets: Barrett & Henzi 2001; Berman 1982; Gumert 2007; Seyfarth 1976, 1980; Silk 1999). During the time of the study, however, births were relatively equally distributed across females of the different rank-classes, high, middle, and low. Alternatively, because both approach in close proximity and positive outcome upon approach were more often due to higher-ranking females, it could be argued that they "extorted" affiliations from lower-ranking ones (Clutton-Brock & Parker 1995; Silk 1982). The extortion hypothesis indeed predicts that high-ranking

females induce lower-ranking ones to groom them with the threat of aggression. However, this would work providing that first, aggressive females do not risk retaliation, and second, that aggression is costly enough for its avoidance to be actively sought out. These two conditions were not met in this population (Chapters 2 and 3). Furthermore, grooming was not directed up the hierarchy, suggesting that higher-ranking females do not extort it especially from lower-ranking ones. The fact that higher-ranking females were the main individuals seeking the proximity of other females may also reflect their greater centrality in the social network (Hemelrijk 2000; Krause & Ruxton 2002), or a higher social motivation (see below).

A surprising result was that higher-ranking females had less numerous female close kin in the group than lower-ranking ones. Since higher-ranking females seemed to reproduce better in this population (e.g. they experienced less foetus loss than others under certain conditions, Kerhoas et al., under review) and in other taxa in general (Silk 2007a), we would have expected them to have more female kin in the group, thus forming larger matrilines. Following the theories of adjustment of birth sex ratio (Hiraiwa-Hasegawa 1993; Silk 1983; Trivers & Willard 1973), and the apparent effect of ecological conditions on the study females' successful reproduction (Kerhoas et al., under review), we may speculate, based on the Trivers-Willars hypothesis, that in this population, higher-ranking females are in better conditions and that they can therefore afford to produce sons that will emigrate and successfully reproduce, whereas lower-ranking females, in worse conditions, rather produce daughters that will stay in the group and become useful allies in intra-group competition. The lesser number of close female kin of higher-ranking females has important implications for the structuring patterns of social relationships between the study females (see below) and it may explain their higher motivation to seek the proximity of other females.

Another peculiar result in the context of macaque societies was that dominance rank difference and degree of relatedness were not related, meaning that genetically related females did not necessarily rank close to each other in the hierarchy. This result goes in the direction of Thierry (2013)'s classification scheme and the covariation model rather than that of the socioecological model. It may be that the youngest daughter ascendency principle, whereby a mother supports her youngest daughter against her sisters - thus establishing an age-reversed dominance hierarchies within matrilines - does not hold in crested macaques as in several other tolerant macaque species (Barbary macaques *M. sylvanus*, Paul 2006; Tonkean macaques, Thierry unpublished data; Thierry 2007). It has been suggested that such a weakly nepotistic hierarchy stems from a low profitability of kin support under conditions of medium rank-related fitness differential that would arise under medium strength contest competition for food (Chapais 2004). This "strength of competition" model remains to be properly tested however. Alternatively, given the high male reproductive skew in this

population (Kerhoas & Engelhardt, unpublished data), it is possible that the proportion of paternal relatives is high. In matrilineal societies, paternal half-sibling share the same degree of relatedness than maternal ones but are less likely to rank close to each other than maternal half-sibling (Widdig in press), which could explain the independence of rank differences from the degree of relatedness. It raises questions about the matrilineal hierarchical organisation of the study crested macaques and the genetic and social structure of their groups (see below).

Partly infirming our hypotheses, stronger bonds were formed amongst females both closer in rank and relatedness, or of similar age than other dyads. The cumulative effect of rank difference and degree of relatedness on social bonds was not due to the relationship between the two variables, however, in contrast with other species of cercopithecines in which female kin also rank close to each other (Chapais 1992, 2004; Kapsalis & Berman 1996b; Silk 1982; Silk et al. 1999). Even at low degree of relatedness, females closer in rank had higher CSI scores than those more distant in rank. A further analysis showed that CSI scores between kin close in rank and non-kin close in rank, or kin distant in rank and non-kin distant in rank were not different from each other. Given that there was seemingly no competition to associate with higher-ranking females, attraction towards, or association between, females of adjacent ranks could stem from similar energetic needs or motivation (de Waal & Luttrell 1986), related to growth, reproductive state, or resource holding potential (Harcourt 1989). Concurrently, the combined effect of the degree of relatedness, rank and age similarity, an indicator of paternal relatedness in species with high male reproductive skew (Altmann 1979; Widdig in press), indicates that familiarity and preferential association amongst age peers could have persisted in adulthood. We are presently unable to distinguish between matrilines, and to separate clearly paternal and maternal relatives. Such discrimination might show that frequencies of social interactions, and thus the strength of social bonds, depend on the kin categories analysed (see Schülke et al. 2013; Smith et al. 2003; Wahaj et al. 2004; Widdig et al. 2002). This is a necessary undertaking for further analyses.

Contrary to what was predicted by the socioecological model, and in contrast with findings in other taxa (Silk et al. 2004; Smith et al. 2010; Widdig et al. 2006), but in partial accordance with the covariation model (but see Petit & Thierry 1994 for a different pattern), coalitionary support was not exchanged more between kin or “friends” or age mates than other dyads. Support was mainly exchanged amongst females close in rank or of different age classes. We studied only adult females for which the hierarchy was stable and power asymmetries moderately steep. The degree of relatedness was also not related to the age difference within a dyad, so it is unlikely that these alliances were formed between mothers and daughters. Altogether, these results indicate that these alliances amongst adjacent ranks were unlikely to function as rank-changing coalitions or as rank-

related benefit tactics. Although coalitionary support did not occur frequently and was a mix of peaceful and aggressive interventions, these alliances may serve instead to maintain the hierarchical status quo (Harcourt 1989). Given that higher-ranking females had less numerous close female kin, they may need to form alliances outside their kin network to outcompete others. Indeed, the frequency of coalitionary support between non-kin was higher, although not significantly, than between kin. This finding does not fit to the socioecological model. It also challenges Chapais's "strength of competition model" (2004) in that a tolerant social style with weakly nepotistic hierarchy should not be associated with extensive non-kin support. It may actually be that a tolerant social style fosters alliances both between kin and non-kin. It would help establishing and/or maintaining hierarchies, and it could be based on reciprocity or mutualism (Clutton-Brock 2009; Dugatkin 2002a, b).

Older females were more often involved in coalitionary support, although they were not necessarily higher-ranking than younger or middle-aged ones, nor did they have more numerous kin or female strong affiliates on average. This indicates that they were not necessarily more competent coalitionary partners, i.e. with more allies or more power. Older females may have been more available to support others because they did not have a small infant to take care of and/or where not pregnant at the time of the study; such circumstances have indeed been suggested to hinder females' availability and willingness to get involved in socially risky interactions such as aggression (Barrett & Henzi 2001). Alternatively, since older females are at risk of being outranked even by non-kin (e.g. Barbary macaques, Paul 2006), they could get more involved in support to cultivate their cooperative network and maintain their dominance rank. Older males of this population of crested macaques also steadily decrease in rank over time but they have been found to decrease less in rank if they participate in coalitions compared to when they are targets of coalitions (Neumann et al. unpublished manuscript).

Feeding in proximity of other females was not related to any of the variables tested, which suggests that the kinship, dominance or "friendship" status of females did not affect their tolerance during feeding. This indicates either that the level of feeding competition was low or that higher-ranking females showed "low competitive tendencies" as proposed by several authors (de Waal 1989; van Schaik 1989), and predicted both by the socioecological and covariation models. Similarly, reconciliation was also not influenced by kinship, rank or age similarity. The absence of kin bias in reconciliation was found in other tolerant macaques too (Barbary macaques, Aureli et al. 1997; Tonkean macaques, Demaria & Thierry 2001); it reflects the extent of cooperative relationships between kin and non-kin alike in these societies.

Much remains to be investigated in tolerant societies regarding how females structure their social relationships in relation to social (e.g., male influence) and environmental factors (e.g. competitive regimes). For instance, according to the socioecological model, strong between-group contest competition (BGC) generates tolerance between females, who would trade support in resource defence against access to these resources (van Schaik 1989). However, resources generating BGC are supposed to be large high-quality food patches, able to accommodate a whole group, precluding them of being monopolisable by a subset of individuals (O'Brien & Kinnaird 1997; van Schaik 1989). Under these conditions, it has been argued that lower-ranking females may still get access to these resources and thus, they may have enough incentive to participate in resource defence against other groups by themselves without trading support for access to these resources (Schülke & Ostner 2012). Although the frequency of intergroup encounters, an indicator of BGC and potentially of the group's home range quality, has a positive impact on foetus survival in this population for all females, under the same conditions of high home range quality, middle- and low-ranking females seem to suffer most of foetal loss due to within-group competition (WGC; Kerhoas et al. under review). Thus, it is unclear whether higher-ranking females really relinquish high quality food resources that are important for their fitness. This also indicates that the effects of WGC on females' fitness outweigh those of BGC (Kerhoas et al. under review) so the actual effect of BGC on female social relationships remains unsolved so far. Another line of future inquiry is to analyse male reproductive skew in relation to the males' dominance ranks and respective tenure length in the group, which can also influence the degree of relatedness between individuals from the paternal side (e.g. Schülke & Ostner 2008; Widdig in press). Both the socioecological and covariation models take into account only the effect of maternal kinship on female social relationships. However, it has been shown, mostly in "despotic" species such as rhesus macaques, chacma baboons *Papio cynocephalus*, and spotted hyenas *Crocuta crocuta*, that paternal relatives interact with each other substantially more often than with non-kin (Schülke et al. 2013; Smith et al. 2003; Wahaj et al. 2004; Widdig et al. 2002). Thus, the group genetic structure could affect the cooperation and competition strategies of females within their group.

To conclude, we found little evidence in crested macaques that strong bonds enhance females' fitness components on a short-term basis through support or tolerance while feeding, in contrast to findings in several other mammalian taxa (Silk 2007a). We do not have data yet allowing to measure the long-term effect of these bonds by relating it to ecological conditions and reproductive success or survival. In cercopithecine primates, the variation in social bond strength is liable to affect longevity (Silk et al. 2010), infant and adult survival (McFarland & Majolo 2013; Silk et al. 2003), and stress coping (Aureli 1997; Beehner et al. 2005; van Schaik & Aureli 2000).

Nevertheless, our study shows that tolerant female macaques do not rely only on kin and dominant individuals for cooperation; they form large affinitive networks, offsetting the influence of dominance and kinship. Our findings fit better to the covariation model (Thierry 2013) than to the socioecological model (Koenig 2002; Sterck et al. 1997; van Schaik 1989). They further indicate that the value and strength of social bonds are related to the social style of the species. Tolerant societies rely on diverse and complex social networks of individuals for cooperation whereas despotic ones are based on more focused and clustered ones (Sueur et al. 2011). This has important implications regarding the way females deal with the costs and benefits of sociality within their social structure. More general answers about the adaptive value of social bonds will await long-term data on the ecology and life-history of the populations under study.

CHAPTER 5

GENERAL DISCUSSION

Through the combination of behavioural and genetic data, my thesis constitutes the first exhaustive study on the social strategies of females in one of the less-known macaque species under natural conditions. My thesis brings novel insights on tolerant macaque societies, especially on the nature, structure and function of relationships between females. In addition, my results provide an empirical test of existent theories on the evolution of social diversity.

In Chapter 2, I confirmed that female crested macaques express a tolerant social style, that is, a species-specific set of interrelated social traits remarkably similar across species of grade-4 macaques, and contrasted in comparison with more despotic ones. In Chapter 3, I showed that the post-conflict interactions of female crested macaques and their function differ substantially from other species in that they more likely serve to signal peaceful intention or to reassert social status than to reduce anxiety or to repair relationships. In Chapter 4, I further demonstrated the weak influence of kinship and dominance on social bonds as well as their limited role on coalitions, reconciliation and proximity while feeding. The structure and function of female crested macaques' social relationships make sense in the light of their tolerant social style. These results confirm the occurrence of a tight interplay between interactions, relationships and structure, supporting the idea that social systems represent sets of traits that covary through the evolutionary process. The socioecological model proposed so far to explain primate societies should now integrate more fully the existence of such linkages between social traits.

5.1 Living in a tolerant society

5.1.1 Characteristics of a tolerant social style or the nature of social relationships

As the first comprehensive analysis of the social style of wild female crested macaques, Chapter 2 characterised the pattern of social tolerance typical of this group of Sulawesi macaques: behavioural patterns were similar in the two study groups and comparable to other groups of Sulawesi macaques living under different environmental conditions (e.g. Matsumura 1998; Petit et al. 1997; Thierry 1985). Furthermore, the comparison that I carried out across the macaque genus appears consistent with the conclusions of previous phylogenetic analyses and meta-analyses (e.g. Balasubramaniam et al. 2012a, b; Thierry et al. 2008). Behavioural patterns fitted the predicted

associations in the intensity and directionality of social interactions: a low intensity in conflicts was associated with high levels of counter-aggression, moderate power asymmetries, and a peaceful meaning of the silent bared-teeth display. High conciliatory tendencies were associated with high rates of body contact in affiliation, and diversified and balanced affinitive networks. Moreover, a low kin bias in affiliation and support in aggression, and a weak effect of dominance on social interactions, demonstrated in Chapter 4, confirmed the occurrence of a feedback loop between dominance and kinship. Altogether these results support the proposal that social styles represent robust sets of interrelated behaviours that occur only in some combinations (Thierry 1997, 2004, 2013; Figure 5.1).

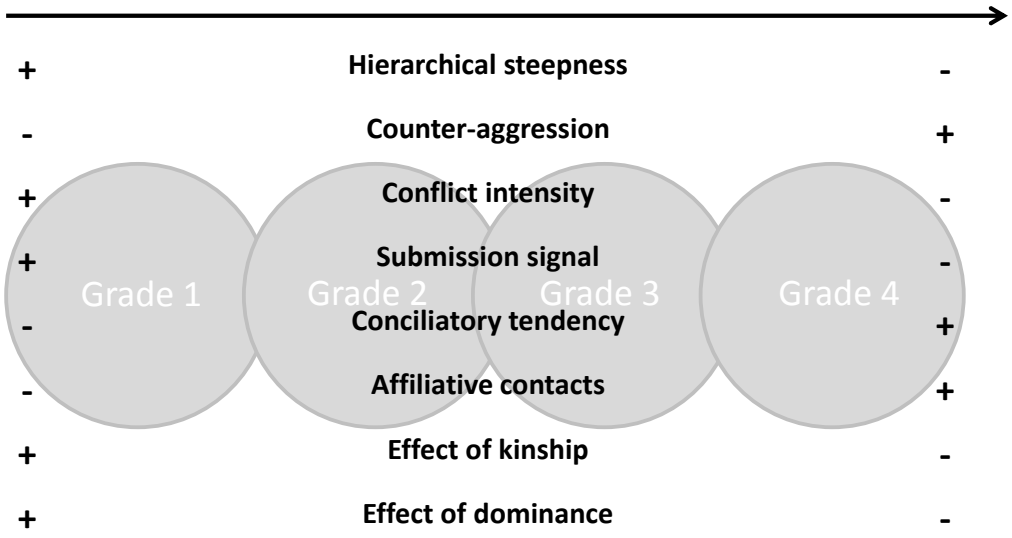

Figure 5.1 Results from this thesis confirm the link between social styles and variation in behavioural patterns (+: high or present, -: low or absent, arrow: gradient of variation from despotic (grade 1) to tolerant (grade 4); inspired from Thierry 2013)

A better understanding of the nature of social relationships gives insights about further interconnections. Tolerant relationships involve frequent contact and stimulate social negotiation between individuals, which can then develop open social networks. In turn, this favours communication, cohesion, and cooperation between individuals. For example, social tolerance promotes the evolution of multiple, and multimodal, signals of communication, which is suggested to have evolved concomitantly with more cooperative and conciliatory strategies, thus fostering the

negotiation of conflicts of interest (e.g. Dobson 2012; McComb & Semple 2005; Micheletta et al. 2013; Thierry et al. 2000a). More tolerant species display more shared consensus decision-making processes than despotic species during collective actions (Sueur & Petit 2008). Social tolerance also improves processes of mending of relationships after a fight, and thus promotes group cohesion (Aureli et al. 2012; de Waal 1989b; Thierry et al. 2008). Social tolerance generally enhances cooperation between partners, potentially by reducing competitive tendency and lowering the emotional reactivity associated with it (e.g. Hare et al. 2007; Petit et al. 1992). I will discuss the evolution of this social strategy and contrast it with other social strategies further along this chapter.

5.1.2 Structure and function of social relationships in a tolerant society: conflict management, cooperation, and dominance

The occurrence of conflicts amongst the study females, regardless of their characteristics or of those from the dyads involved, did not have a strong effect on behavioural indicators of anxiety, such as scratching or restlessness (Chapter 3). Although physiological measures of anxiety could give a different profile, I provisionally propose that the low reactivity of females to potentially stressful events, i.e. conflicts, is related to their high frequency, low intensity and high bidirectionality (Chapter 2). Such a mild nature of conflicts may indeed foster negotiation strategies instead of coercion ones, and it can thus be less stressful. Accordingly, reconciliation did not seem to have a stress-reduction function. The fact that more than half of the reconciliatory interactions involving body contact were preceded by a non-contact interaction, such as lipsmacking, suggests that conciliatory behaviours were used to signal peaceful intentions, which then can lead to the resumption of “normal” affiliative interactions (Silk 1996; Chapter 3).

Similarly, given that the strength of social bonds, the degree of relatedness and the frequency of support in aggression did not influence the likelihood of reconciliation, it does not appear that reconciliation serves to mend particularly “valuable” relationships (Chapter 3 and 4). Chapter 3 further shows that other characteristics of social relationships related to the symmetry or predictability of social exchanges may be more important to crested macaque females than the strength of bonds for example. On the one hand, preserving secure relationships, i.e. with less aggression and more consistent grooming exchanges, is considered beneficial. On the other hand, reconciling less secure, i.e. asymmetrical, relationships could underlie the high motivation of both partners, the one most responsible of maintaining the relationship, and the other getting the benefits of this relationship. To resolve this puzzle, it would be necessary in a next step to look

further at each social exchange or carry out experiments to manipulate the asymmetry of relationships. In Chapter 3, it was not possible to extract neatly the three components of social relationships, value, security and compatibility, so I cannot directly compare my results with those of other studies regarding this aspect. Nevertheless, my findings highlight the importance of taking into account the social style of species when analysing relationship qualities and their function in conflict management. My analyses also underscore the usefulness of considering all variables and post-conflict interactions together, as they can co-occur and thus influence each other. For instance, it seems that the occurrence of aggression created a localised "turmoil", increasing all kinds of social interactions with all kinds of partners as compared to baseline. Post-conflict interactions, between previous opponents or with third-parties not involved in the conflict, appeared mediated by emotions, and this may serve to preserve social cohesion with a large panel of partners in species of a tolerant nature, rather than with a smaller subset of group members as in more despotic species (Aureli 1997; Aureli et al. 2012). My results on conflict management reveal that tolerant species have evolved strategies involving the negotiation of conflicts of interest through elaborate social exchanges instead of the more coercive tactics displayed by more despotic species.

Female crested macaques form large affinitive networks (Chapter 2); they have few strong bonds and a majority of average social bonds (Chapter 4). In connection with the structure of these bonds, the strongest bonds are formed between females both adjacent in ranks and closely related, and of similar age. It is noteworthy that the degree of relatedness does not predict differences in rank relationships, so that females of adjacent ranks are not necessarily more related than others. This means that kin do not necessarily form the strongest bonds. In fact, social bonds are more influenced by rank and age difference, than by any other variables: females of adjacent ranks and belonging either to the same or to different age classes generally interact more often than others. This pattern could be related to individual attributes, needs and/or motivations (Chapter 4; Chapais 2006; de Waal 1986). Related to the function of these social bonds, not only kin do not necessarily form the strongest social bonds, but they also do not reconcile, support each other in aggression or tolerate each other while feeding more frequently than non-kin. Moreover, I did not find that dyads of females with stronger bonds reconcile, support or tolerate each other in proximity while feeding more frequently than others. These combined results indicate that in a tolerant society, females do not focus only on kin or dominant individuals for cooperation and they associate with multiple partners, perhaps opportunistically. Females established diverse and open social networks instead of focused and clustered ones (Chapter 2). I will develop further the consequences this may have on cooperation between females in this species.

Some more words on coalitionary support and the lack of a kinship effect are necessary. The function of coalitions in acquiring or maintaining rank is still little documented in females of the more tolerant species of macaques. Further analyses will be needed regarding the identity and goals of participants and targets. It will also be necessary to determine how young females integrate the adult hierarchy. Tonkean macaques, another grade-4 species, indeed show a high proportion of peaceful interventions mainly performed by higher-ranking individuals (Petit & Thierry 1994a). These patterns are somewhat different from more despotic species (e.g. Chapais 1983, 1992). They reflect an ability to negotiate conflicts of interest between multiple partners, enhanced by the tolerant and mild nature of the Sulawesi macaques' social style.

In addition, a seemingly recurrent feature of the grade-4 macaques, at least concerning females, is that dominance rank *per se* does not seem influential for partner choice and frequency of social interactions (Chapters 3 and 4; Bernstein & Baker 1988; Paul 2006; Thierry & Aureli 2006). Actually, the emerging pattern from my study is that lower-ranking females retain some social leverage over higher-ranking ones. Conflicts are indeed more likely to be reconciled when a lower-ranking female starts the conflict, and higher-ranking females initiate reconciliation more often than lower-ranking ones (Chapter 3). Given that counter-aggression is frequent in the study population (Chapter 2), I argue that higher-ranking females should be most motivated to display peaceful behaviours, and to restore tolerance with their partners indiscriminately (Chapter 3). Another explanation for this pattern is that higher-ranking females just exploit the situation and extort affiliation out of lower-ranking ones (Clutton-Brock & Parker 1995), but this was disproved in Chapter 4 as social grooming and approach were not skewed up the hierarchy. In fact, lower-ranking females seemed to be more attractive as proximity partners than higher-ranking ones. This leads me to suggest that higher-ranking females are more conciliatory in the largest sense because moderate power asymmetries prevent them to coerce lower-ranking ones into submission or avoidance. As far as I know, this species lacks proper submission signals, unlike most other macaques (Chapter 2; Petit & Thierry 1992; Thierry et al. 1989); thus, higher-ranking females could be the ones in need to reassert or to advertise their status (Preuschoft & van Schaik 2000). This can also explain why higher-ranking females do initiate more secondary aggression than lower-ranking ones after being involved in a conflict; I propose that it could serve to reinforce a "winner effect" and to reassert their higher social status (Aureli et al. 2012; Chapter 3). How higher-ranking females do so on a daily basis is still unclear however. Since rank differences are not related to the degree of relatedness between dyads of females in this population (Chapter 4), it may also be that the hierarchy has some individualistic elements, and that dominance rank could also be based on the personality or "social power" of a female in addition to her "birth right" (Flack & de Waal 2004). A related explanation is that kin are

not the only useful allies, especially in this species; thus maintaining a well-connected network could help establishing and maintaining the hierarchical order (Chapais et al. 1991; Chapais & St-Pierre 1997).

Although I could not distinguish matrilines, or between maternal and paternal relatives, higher-ranking females of this population seem to have less numerous female close kin than lower-ranking ones (Chapter 4). Regardless of the mechanisms behind this finding, it is likely that higher-ranking females need to build relationships outside their kin network for cooperation and for competition. This is actually the case in male crested macaques, where more connected - and less anxious - males achieve a higher rank than others (Neumann et al. unpublished manuscript). Cooperation amongst non-kin is often explained on the basis of several mechanisms, such as reciprocal altruism, by-product mutualism, coercion or biological market (Clutton-Brock 2009; Dugatkin 1997, 2002; Noë & Hammerstein 1995; Trivers 1971). An important endeavour in the future will be to analyse patterns of exchanges of "goods" and "services" between females. For example, an interesting point of the biological market is related to power asymmetries between individuals: in societies with shallow hierarchies, reciprocal exchanges should predominate over the interchange of rank-related benefits (e.g. support in aggression) for other "services" (e.g. grooming) because it is more likely that individuals exchange services for their intrinsic properties than to get access to other, rank-related, benefits (Barrett et al. 1999; Noë et al. 1991; Noë & Hammerstein 1995).

The apparent lack of influence of kinship and of bond strength on various social interactions between female crested macaques raises questions about the adaptive value of the strength of bonds compared to their diversity. Long-term data on the ecology and life-history of these females as well as more information in related species will be necessary to tackle this question. Indeed, although more data is accumulating in diverse taxa (e.g feral horses, *Equus caballus*, Cameron et al. 2009; bottlenose dolphins, *Tursiops sp.*, Frère et al. 2010), the majority of research on the adaptive value of the strong social bonds in females has been done in baboons, who live in a harsh environment with great seasonal variation and high predation pressure, and show a comparatively despotic behavioural profile (Silk 2007b). This may be an additional and meaningful difference between tolerant and despotic social strategies, which could have arisen throughout the evolutionary history of species.

I will now critically review the different theories that have been proposed to explain the evolution of different social styles, and I will suggest a tentative general scenario that has the potential to encompass them all (Figure 5.2).

5.2 Evolution of different social styles: the potential link between external and internal factors

5.2.1 External factors

The first part of the primate socioecological model, the effect of ecological conditions on females' grouping and competitive regimes, is well supported by available empirical information, including data from macaques (reviewed in Schülke & Ostner 2012). Indeed macaque species live in multi-male multi-female groups where females stay their whole life in the group they were born in (Cords 2012; Schülke & Ostner 2012). They are mainly frugivores, meaning that they feed on a rich and monopolisable resource for which females contest, giving rise to linear hierarchies and possibly, rank-related fitness benefits (Koenig 2002; Koenig et al. 2013; Schülke & Ostner 2012). Macaque species grouped in the RNT category live on isolated oceanic islands with no felid predator and no catarrhine competitor, thus in a potentially lower competitive environment (Riley 2010, van Schaik 1989). Crested macaques of the study population furthermore live in an environment phenologically diverse in fruit trees, capable of supporting a highly frugivorous species throughout the year without dietary shifts (O'Brien & Kinnaird 1997).

However, the second part of the model, i.e. the influence of these competitive regimes on females' social relationships, hence social structures, still has major loopholes (Koenig 2002; Koenig et al. 2013). According to Schülke and Ostner (2012), "*social structure is still perhaps the aspect of the social system in which the action of different social and ecological factors is least understood*" (p. 210). For instance, according to the model, the conditions giving rise to between-group contest competition are high population density - because of a predator-free environment - and large high quality food patches able to accommodate a whole group. Under these conditions, the model predicts that females trade participation in resource defence against other groups for access to this resource, and lower-ranking females have leverage over higher-ranking ones through the threat of defection. This would relax power asymmetries and promote social tolerance (Koenig 2002; Sterck et al. 1997). I would make two critical points here. First, high quality food patches large enough to accommodate a whole group preclude these resources to be monopolisable or worth being monopolised. Under these conditions, lower-ranking females may still get access to these resources and thus, they may have enough incentive to participate in resource defence against other groups by themselves without trading support for access to these resources (Schülke & Ostner 2012). Second,

since high between-group competition (BGC) systematically means high within-group competition (WGC; Koenig 2002; Sterck et al. 1997; van Schaik 1989), the relative weight of BGC compared to WGC on female-female relationship is unclear. For example, under strong WGC, there is no reason why higher-ranking females would relinquish a resource important for their fitness (Schülke & Ostner 2012). A study on the same population of crested macaques suggests that such a balance in level and degree of competition has an effect on females' fitness (Kerhoas et al. under review). There was indeed a positive link between the frequency of intergroup encounter (a proxie of BGC) and foetus survival in all females, potentially linked to high quality home ranges. However, under these same conditions of high food availability and heightened feeding competition, middle- and low-ranking females suffered the most from foetus loss compared to high-ranking females (Kerhoas et al. under review). These findings hint at the possibility that females adjust their competitive strategies to local ecological conditions, but it nevertheless tells little on how the balance between BGC and WGC shape female-female social relationships in general. In line with the view that strong BGC and strong WGC have incompatible effects on female social relationships (van Schaik 1989), WGC may thus override any residual effects of BGC on female relationships.

A related model on the "strength of competition" suggests that a weakly nepotistic hierarchy and an egalitarian dominance style stem from a low profitability of kin support under conditions of medium rank-related fitness differential that would arise under medium strength contest competition for food (Chapais 2004). However, in the study females, the frequency of coalitionary support between non-kin was actually higher, although not significantly, than between kin. This finding contradicts the socioecological model and challenges the "strength of competition model" (Chapais 2004) in that a tolerant social style with weakly nepotistic hierarchy should not be associated with extensive non-kin support. Both models remain to be properly tested however and to do so requires long-term data on the ecology and life-history of females. An important issue to address is also the question of trading favours, i.e. resource defence against social tolerance. It is a difficult one to tackle as one has to contend, amongst other factors, with book-keeping of favours exchanged, partner choice and control, leverage, competence, or punishment of cheaters and defectors (Clutton-Brock & Parker 1995; Noë & Hammerstein 1994, 1995).

Another line of explanation for social tolerance in macaques relates male reproductive skew to the degree of relatedness between females: the higher the skew, the higher the overall degree of relatedness in the group (Schülke & Ostner 2008; Widdig et al. 2004). Male reproductive skew is not thought of being related to the degree of social tolerance between females, because it is influenced by female cycle synchrony and environmental seasonality. Incidentally, however, a recent study

suggests that more tolerant species show higher male reproductive skew (Schülke & Ostner 2008). Generally, since the degree of relatedness should structure social relationships between individuals (kin selection theory, Hamilton 1964), the higher overall degree of relatedness in species with high male reproductive skew should result in a diversification of affiliative and proximity interactions amongst more numerous related partners. Regardless of kin recognition mechanisms, a consequence could be that the dilution effect of numerous close kin on social relationships produces many average social bonds and no or very few strong bonds. Traditionally however, models of social evolution mainly account for maternal kin. An important issue to be addressed in the future is the differential in social interaction frequencies according to the degree of relatedness and the number of different kin present in the groups, paternal, maternal or both (Altmann et al. 1996; Widdig in press; Widdig et al. 2004). The genetic structure of a group is thus likely to have great influence on the patterning of cooperative and competitive relationships and their associated benefits but this question remains as yet to be fully investigated in other populations and species.

5.2.2 Internal factors

The socioecological model has been the main explanatory framework accounting for behavioural contrasts between macaque societies until it was realised that differences and consistencies persist regardless of ecological variations (Ménard 2004; Thierry 2007; Thierry et al. 2000b), and that some traits vary according to the phylogenetic relatedness of species (Thierry et al. 2008; Thierry et al. 2000b). This has prompted the emergence of an alternative model of social evolution which emphasises the occurrence of constraints acting within social systems, without excluding the action of ecological factors (Thierry 2013).

The study of links between behavioural traits is already part of life history, personality, neuroscience and genetic research, and it can give useful insights into the correlations of traits. In personality research for example, variation in coping styles or in temperaments has been shown to be important for evolutionary processes (Bergmüller 2010; Sih et al. 2004a). Aggressive and affiliative behavioural tendencies are also related to various hormones and neurotransmitters (Adkins-Regan 2005). For example, variation in the serotonin system, associated with anxiety- and aggression-related traits, explains inter-individual and inter-species variation in aggression-related behaviour (Wendland et al. 2006; Westergaard et al. 2003; Westergaard et al. 1999). In human and non-human primates, a low serotonin activity is associated with more aggressive, impulsive and risk-

taking behaviour in females and males alike, as well as with low levels of sociability (Anestis 2011; Higley et al. 1996; Higley et al. 2011; Suomi et al. 2011). Despotic rhesus macaques systematically show lower serotonin level and more polymorphism of serotonin gene variants than more tolerant Tonkean, stumptail and Barbary macaques, which match the differences in their behavioural tendencies (Anestis 2010; Higley et al. 2011; Suomi et al. 2011; Wendland et al. 2006). More despotic macaques also often score higher in fear or hostility than more tolerant macaques, who are more curious and explorative of their environment (Clarke & Boinski 1995; Clarke & Mason 1988). An additional but connected level of constraint is developmental. Maternal effects and characteristics of the social environment during development shape offspring behavioural phenotypes (Sachser & Kaiser 2010; Sachser et al. 2013). For example, it has been shown that tolerant bonnet macaque infants initiate interactions with their mother more often than despotic rhesus macaque infants. Bonnet macaque mothers also often accept these interaction attempts more often than rhesus macaque mothers. These differences have been attributed to the species respective temperament and contribute greatly to the "inheritance" of behavioural tendencies (Mason et al. 1993). These different behavioural phenotypes thus appear underpinned by complex genetic-neuro-physiological regulatory systems.

Since behavioural traits are linked at different levels, they have the potential to covary such as a change in one trait would result in a chain of changes in other traits. As already mentioned, this could however happen with significant costs, and some resistance, from the system, due to the coupling of traits: for example a change in a correlated trait that is not the target of selection would be deleterious (Bergmüller 2010; Price & Langen 1992; Sih et al. 2004a). Specific clusters of behaviour can actually emerge through self-organisation in the sense that individuals do not behave in isolation but interact with each other and influence each other's behavioural responses (Hemelrijk 1999, 2004; Hemelrijk & Puga-Gonzales 2012; Puga-Gonzales et al. 2009). Moreover, phylogenetically related species tend to share similar profiles or strategies, adding an additional layer of constraint to the system. Taken together, all these limiting factors may explain the patterning of traits that seem little responsive to environmental pressures or ancestral traits that seem no longer adaptive (Fuentes 2011; Sih et al. 2004a).

5.2.3 An integrative view on the evolution of different social styles

Altogether, the influence of diverse factors on different but connected aspects of social behaviour has prompted a debate on an alternative model of social evolution taking into account an external component, the ecological environment, and an internal component, including both the organism and the social system (Clutton-Brock & Janson 2012; Kappeler 2013; Thierry 2013).

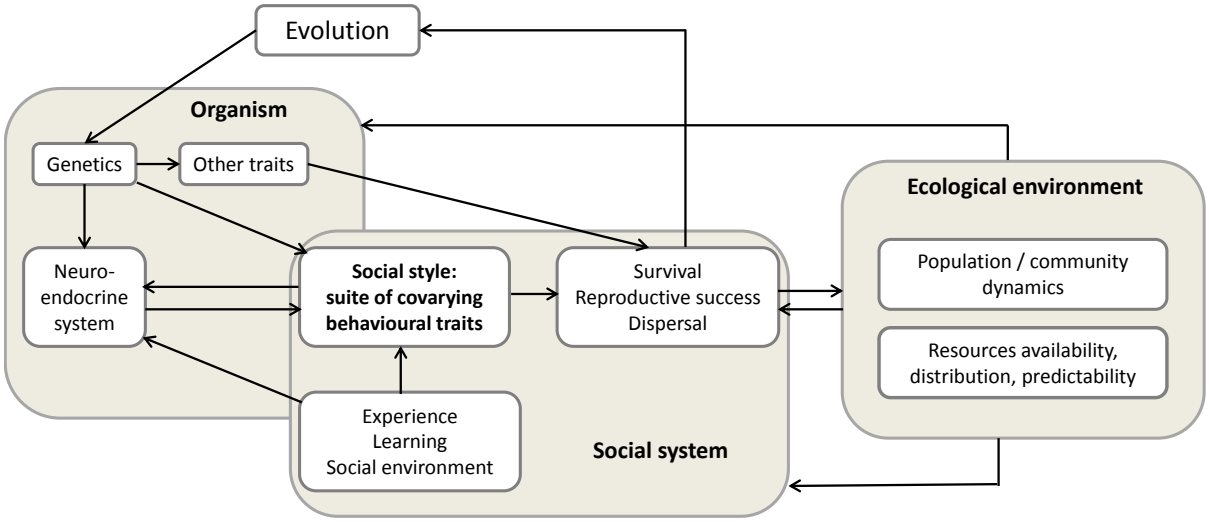

Figure 5.2 An integrative overview of interactions between social styles (as behavioural-syndrome-like clusters of traits) and social and ecological environment (small boxes and connections are redrawn and adapted from Sih et al. 2004b, except for the "social style" box, which replaces a "behavioural syndrome" box; big boxes and their connections are inspired from Thierry 2013)

Social styles are clusters of covarying behavioural patterns ranging around certain modes (Figure 5.1). They are stable across time and contexts, and consistent within but different between species or groups of species. This description is similar to the one given for behavioural syndromes as "*suite of correlated behaviours reflecting between-individual consistency in behaviour across multiple situations*" (Sih et al. 2004a, p. 372). As previously argued, variation in social style has probably part of its roots in the variation of individual and species temperaments (Capitanio 2004; Mendoza & Manson 1989; Thierry 2004). As such, social styles can be considered as the analogues at the social level of behavioural syndromes envisioned at the individual level. At the individual level, behavioural syndromes can explain trade-offs between behavioural strategies and the evolution of different but equally adaptive "coping styles". These syndromes are shaped by genetic, social and

environmental factors, and have been shown to have evolutionary relevance (Bergmüller 2010; Sih et al. 2004b). In this section, I will summarise the ideas presented above into an evolutionary scenario showing that behavioural syndrome research provides a framework allowing to account for the consistency and flexibility of behaviours and to link external and internal factors in the evolution of different social styles (Figure 5.2).

If we consider macaques' social styles as different coping strategies that evolved to solve the same social and ecological problems, i.e. how to benefit from living in groups, a scenario of social evolution can be drawn as follows (see Figure 5.2). Some species may have evolved in a milieu requiring caution and high reactivity - e.g. an environment with high predation risk - which in combination with a certain resource distribution and abundance, may have selected for emotionally reactive, aggressive and intolerant individuals. These behavioural tendencies, because they share regulatory systems, would have spilled out onto other social characters such as conciliatory tendency, mother's permissiveness, or male migration patterns. Under these conditions, it may have been advantageous and/or within the reaction-norm of individuals to focus more on kin and few reliable social partners for cooperation. Altogether, this may have generated strict linear matrilineal hierarchies and clustered social networks. In contrast, other species might have evolved in a safer environment with limited predation and/or no sympatric competitors, allowing for a more relaxed coping style. Given a certain resource distribution, this would have favoured cooperative, sociable and curious individuals, who can afford to, or are in need of, building open social networks. This in turn would have lessened power asymmetries and relaxed social rules in cooperation. Again, this may have spilled over to other characteristics. Evolutionary processes in the end would make adjustments, link and stabilise these sets of traits (Figure 5.2). Similarly, fluctuations in the environment across evolutionary times may maintain several strategies in a population, and correlations between behaviours can vary if different correlations are favoured under different environments (Sih et al. 2004a).

Ultimately, which strategy is more beneficial first, is probably impossible to determine, so many are the factors involved, and second, it is probably dependent of the conditions under which it has evolved. Thierry (2013) indeed speculated that *"(i) a reactive temperament allows better resistance to stressful conditions, whereas a more tractable one is physiologically less costly, (ii) a higher rate of male dispersal favours gene flow, but a lower rate decreases mortality in bachelors, (iii) clear-cut contests reduce the number of potential conflicts and shorten their duration, but elaborated negotiation skills favour the resolution of conflicts and diminish the occurrence of wounds, (iv) higher maternal restrictiveness protects an infant against short-term dangers, but*

allowing alloparental care increases the number of potential protectors, (v) a lower level of tolerance corresponds to an appropriate cautiousness when facing the unknown, but a higher level enhances social contacts and information transmission between group-mates." (p. 6).

The promising avenue of looking at this variation and interrelation through the glass of behavioural syndromes not only provide a full account of different behavioural strategies under different contexts and of different individuals from both sexes, but it also allows for the examination of proximate mechanisms, ultimate functions and developmental pathways altogether (Bergmüller 2010; Sih et al. 2004a; Sih et al. 2004b; Figure 5.3).

5.4 Outlook and conclusion

My thesis constitutes both an empirical contribution to our knowledge of macaque societies, and a starting point to go further in the understanding of diverse societies. I show that within a tolerant society, social rules and dynamics are likely to be relaxed, open and diversified and that interpreting the function of social behaviour in this context provides fruitful avenues of thinking.

A major endeavour is to relate the social style of females with the one of males. It has indeed often been argued that macaque social styles represent only the female story, and that males' behavioural strategies are necessarily different because they are shaped by different selection pressures. However, there are hints that variation amongst males of different species occurs in the same direction as in females: for example, males of despotic societies have less numerous and complex affiliative interactions with each other than males of tolerant ones (e.g. Hill 1994; Preuschoft et al. 1998; Riley 2010; Silk 1994). To confirm this point, we need a comprehensive investigation of the males' social style on the same scale that the one used for females. By case, it has been shown recently that male crested macaques show a personality factor, connectedness, that seems to be absent from other macaques' profile studied so far (Neumann et al. 2013). In addition, this personality trait is related to the males' social success in the group (Neumann et al. unpublished manuscript). This personality trait seems to be present in females too, who build extended affinitive networks, and it could be typical of the tolerant style of social relationships.

What remains to be done is to relate the behavioural patterns I uncovered with the ecology of females. An important study to carry out in the future is on the level and dynamic of between-group competition, as this is a central hypothesis of the primate socioecological model for the evolution of tolerant societies. It will not be enough to analyse patterns and frequencies of inter-

group encounters related to local ecological conditions. The crucial point will be to investigate whether females do exchange participation in resource defence against access to these resources or other commodities, for example grooming (Cheney 1992). In this respect, biological market theory is a promising framework. Moreover, given the high sexual dimorphism and the combination of several sexual secondary characteristics in males, indicator of harsh competition between males, it is possible that males play a proactive role in intergroup encounters too. Whether male participation has such an influence that it may cancel out any effect of BGC on female-female relationships is an important question to answer in this respect.

Related to the previous topic, another point of interest is the dynamic of social relationships between females related to the costs and benefits of sociality. Barrett and Henzi (2001) have repeatedly stressed that female social relationships are influenced by contingent events, and they have outlined the need of taking into account these dynamics, for example in relation to the female reproductive state or to social constraints such as demographic ones. With the advancement of social network analyses, one can now tackle social dynamics beyond the dyadic level. However, social network analyses rely on matrices of interactions, which represent a snapshot of the social relationships only, difficult to use to study dynamic processes. This has been acknowledged as an issue as well in the analysis of dominance hierarchies (Neumann et al. 2011), and Neumann and colleagues have developed an already existing index to account for interaction dynamics: this Elo rating updates dominance rating continuously after each agonistic interaction. By combining what is currently developed in social network research (Blonder et al. 2012; Croft et al. 2008; Sih et al. 2009) and the process of Elo rating, it would be possible to elaborate a kind of "social Elo rating", able to track the social trajectory of the individuals alongside those of other group members.

My thesis uncovers patterns on the nature, structure and function of social relationships in wild female tolerant crested macaques. It shows that the picture drawn from the study population differs substantially from the typical cercopithecine primate model. It emphasises the usefulness of considering differences in social style while addressing the adaptive function of behaviours. Finally, it stresses the need to take into account the interrelation of all levels of a social system for a better understanding of the evolution of diversity in animal societies.

Bibliography

Abegg, C. & Thierry, B. 2002. Macaque evolution and dispersal in insular south-east Asia. *Biological Journal of the Linnean Society*, 75, 555-576.

Adkins-Regan, E. 2005. *Hormones and animal social behavior*. Princeton: Princeton University Press.

Albers, P. C. H. & de Vries, H. 2001. Elo-rating as a tool in the sequential estimation of dominance strengths. *Animal Behaviour*, 61, 489-495.

Alberts, S. C. 2012. Magnitude and sources of variation in male reproductive performance. In: *The evolution of primate societies* (Ed. by J. C. Mitani, J. Call, P. M. Kappeler, R. A. Palombit & J. B. Silk), pp. 412-431. Chicago: The University of Chicago Press.

Alexander, R. D. 1974. The evolution of social behavior. *Annual Review of Ecology and Systematics*, 5, 325-383.

Altizer, S., Nunn, C. L., Thrall, P. H., Gittleman, J. L., Antonovics, J., Cunningham, A. A., Cunnningham, A. A., Dobson, A. P., Ezenwa, V., Jones, K. E., Pedersen, A. B., Poss, M. & Pulliam, J. R. C. 2003. Social organization and parasite risk in mammals: integrating theory and empirical studies. *Annual Review of Ecology, Evolution, and Systematics*, 34, 517-547.

Altmann, J. 1979. Age cohorts as paternal sibships. *Behavioral Ecology and Sociobiology*, 6, 161-164.

Altmann, J., Alberts, S. C., Haines, S. A., Dubach, J., Muruthi, P., Coote, T., Geffen, E., Cheesman, D. J., Mututua, R. S., Saiyalel, S. N., Wayne, R. K., Lacy, R. C. & Bruford, M. W. 1996. Behavior predicts genetic structure in a wild primate group. *Proceedings of the National Academy of Sciences, USA*, 93, 5797-5801.

Anestis, S. F. 2010. Hormones and social behavior in primates. *Evolutionary Anthropology: Issues, News, and Reviews*, 19, 66-78.

Anestis, S. F. 2011. Primate personality and behavioral endocrinology. In: *Personality and temperament in nonhuman primates* (Ed. by A. Weiss, J. E. King & L. Murray), pp. 169-192. New York: Springer Science + Business Media.

Arandjelovic, M., Guschanski, K., Schubert, T., Harris, R., Thalmann, O., Siedel, H. & Vigilant, L. 2009. Two-step multiplex polymerase chain reaction improves the speed and accuracy of genotyping using DNA from noninvasive and museum samples. *Molecular Ecology Resources*, 9, 28-36.

Archie, E. A., Morrison, T. A., Foley, C. A. H., Moss, C. J. & Alberts, S. C. 2006. Dominance rank relationships among wild female African elephants, *Loxodonta africana*. *Animal Behaviour*, 71, 117-127.

Arnold, K. & Aureli, F. 2006. Postconflict reconciliation. In: *Primates in Perspective* (Ed. by C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger & S. K. Bearder), pp. 592-608. Oxford: Oxford University Press.

Arnold, K. & Whiten, A. 2001. Post-conflict behaviour of wild chimpanzees (*Pan troglodytes schweinfurthii*) in the Budongo Forest, Uganda. *Behaviour*, 138, 649-690.

Asquith, P. J. 1989. Provisioning and the study of free-ranging primates: history, effects and prospects. *Yearbook of Physical Anthropology*, 32, 129-158.

Aureli, F. 1992. Post-conflict behaviour among wild long-tailed macaques (*Macaca fascicularis*). *Behavioral Ecology and Sociobiology*, 31, 329-337.

Aureli, F. 1997. Post-conflict anxiety in nonhuman primates: the mediating role of emotion in conflict resolution. *Aggressive Behavior*, 23, 315-328.

Aureli, F., Cords, M. & van Schaik, C. P. 2002. Conflict resolution following aggression in gregarious animals: a predictive framework. *Animal Behaviour*, 64, 325-343.

Aureli, F., Das, M. & Veenema, H. C. 1997. Differential kinship effect on reconciliation in three species of macaques (*Macaca fascicularis*, *M. fuscata*, *M. sylvanus*). *Journal of Comparative Psychology*, 111, 91-99.

Aureli, F., Das, M., Verleur, D. & van Hooff, J. A. R. A. M. 1994. Postconflict social interactions among Barbary macaques (*Macaca sylvanus*). *International Journal of Primatology*, 15, 471-485.

Aureli, F. & de Waal, F. B. M. 2000. *Natural Conflict Resolution*. Berkeley: University of California Press.

Aureli, F., Fraser, O. N., Schaffner, C. M. & Schino, G. 2012. The regulation of social relationships. In: *The evolution of primate societies* (Ed. by J. C. Mitani, J. Call, P. M. Kappeler, R. A. Palombit & J. B. Silk), pp. 531-551. Chicago: The University of Chicago Press.

Aureli, F. & Schaffner, C. A. 2006. Causes, consequences and mechanisms of reconciliation: the role of cooperation. In: *Cooperation in Primates and Humans: Mechanisms and Evolution* (Ed. by P. M. Kappeler & C. P. van Schaik), pp. 121-136. Berlin: Springer.

Aureli, F. & Schaffner, C. M. 2013. Why so complex? Emotional mediation of revenge, forgiveness and reconciliation. *Behavioral and Brain Sciences*, 36, 15-16.

Aureli, F. & Schino, G. 2004. The role of emotions in social relationships. In: *Macaque Societies* (Ed. by B. Thierry, M. Singh & W. Kaumanns), pp. 38-60. Cambridge: Cambridge University Press.

Aureli, F., van Schaik, C. P. & van Hooff, J. A. R. A. M. 1989. Functional aspects of reconciliation among captive long-tailed macaques (*Macaca fascicularis*). *American Journal of Primatology*, 19, 39-51.

Aureli, F., Veenema, H. C., van Panthaleon van Eck, C. J. & van Hooff, J. A. R. A. M. 1993. Reconciliation, consolation, and redirection in Japanese macaques (*Macaca fuscata*). *Behaviour*, 124, 1-21.

Aureli, F. & Yates, K. 2010. Distress prevention by grooming others in crested black macaques. *Biology Letters*, 6, 27-29.

Axelrod, R. & Hamilton, W. D. 1981. The evolution of cooperation. *Science*, 211, 1390-1396.

Baayen, R. H. 2007. *Analyzing Linguistic Data: A practical introduction to statistics using R.* Cambridge: Cambridge University Press.

Baker, S. C. & Estep, D. Q. 1985. Kinship and affiliative behavior patterns in a captive group of Celebes black apes (*Macaca nigra*). *Journal of Comparative Psychology*, 99, 356-360.

Balasubramaniam, K. N., Dittmar, K., Berman, C. M., Butovskaya, M. L., Cooper, M. A., Majolo, B., Ogawa, H., Schino, G., Thierry, B. & de Waal, F. B. M. 2012a. Hierarchical steepness and phylogenetic models: phylogenetic signals in *Macaca*. *Animal Behaviour*, 83, 1207-1218.

Balasubramaniam, K. N., Dittmar, K., Berman, C. M., Butovskaya, M. L., Cooper, M. A., Majolo, B., Ogawa, H., Schino, G., Thierry, B. & de Waal, F. B. M. 2012b. Hierarchical steepness, counter-aggression, and macaque social style scale. *American Journal of Primatology*, 74, 915-925.

Barrett, L., Gaynor, D. & Henzi, S. P. 2002. A dynamic interaction between aggression and grooming reprocity among female chacma baboons. *Animal Behaviour*, 63, 1047-1053.

Barrett, L. & Henzi, S. P. 2001. Constraints on relationship formation among female primates. *Behaviour*, 139, 263-289.

Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E. & Hill, R. A. 1999. Market forces predict grooming reciprocity in female baboons. *Proceedings of the Royal Society B: Biological Sciences*, 266, 665-670.

Bates, D. M., Maechler, M. & Bolker, B. 2011. lme4: Linear mixed-effects models using S4 classes. In: *http://CRAN.R-project.org/package=lme4*: R package version 0.999375-42.

Bayes, M. K., Smith, K. L., Alberts, S. C., Altmann, J. & Bruford, M. W. 2000. Testing the reliability of microsatellite typing from faecal DNA in the savannah baboon. *Conservation Genetics*, 1, 173-176.

Beehner, J. C., Bergman, T. J., Cheney, D. L., Seyfarth, R. M. & Whitten, P. L. 2005. The effect of new alpha males on female stress in free-ranging baboons. *Animal Behaviour*, 69, 1211-1221.

Bergmüller, R. 2010. Animal personality and behavioural syndromes. In: *Animal Behaviour: Evolution and Mechanisms* (Ed. by P. M. Kappeler), pp. 587-621. Berlin: Springer.

Berman, C. M. 1982. The ontogeny of social relationships with group companions among free-ranging infant rhesus monkeys II. Differentiation and attractiveness. *Animal Behaviour*, 30, 163-170.

Berman, C. M., Ionica, C. S. & Li, J. 2004. Dominance style among *Macaca thibetana* on Mt. Huangshan, China. *International Journal of Primatology*, 25, 1283-1312.

Berman, C. M., Ogawa, H., Ionica, C., Yin, H. & Li, J. 2008. Variation in kin bias over time in a group of Tibetan macaques at Huangshan, China: contest competition, time constraints or risk response? *Behaviour*, 145, 863-896.

Berman, C. M. & Thierry, B. 2010. Variation in kin bias: species differences and time constraints in macaques. *Behaviour*, 147, 1863-1887.

Bernstein, I. S. & Baker, S. C. 1988. Activity patterns in a captive group of Celebes black apes (*Macaca nigra*). *Folia Primatologica*, 51, 61-75.

Blonder, B., Wey, T. W., Dornhaus, A., James, R. & Sih, A. 2012. Temporal dynamics and network analysis. *Methods in Ecology and Evolution*, 3, 958-972.

Bolker, B., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H. & White, J.-S. S. 2008. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, 24, 127-135.

Bshary, R. & Bergmüller, R. 2008. Distinguishing four fundamental approaches to the evolution of helping. *Journal of Evolutionary Biology*, 21, 405-420.

Call, J., Aureli, F. & de Waal, F. B. M. 1999. Reconciliation patterns among stumptailed macaques: a multivariate approach. *Animal Behaviour*, 58, 165-172.

Cameron, E. Z., Setsaas, T. H. & Linklater, W. L. 2009. Social bonds between unrelated females increase reproductive success in feral horses. *Proceedings of the National Academy of Sciences*, 106, 13850-13853.

Capitanio, J. P. 2011. Individual differences in emotionality: social temperament and health. *American Journal of Primatology*, 73, 507-515.

Castles, D. L., Aureli, F. & de Waal, F. B. M. 1996. Variation in conciliatory tendency and relationship quality across groups of pigtail macaques. *Animal Behaviour*, 52, 389-403.

Chaffin, C. L., Friedlen, K. & de Waal, F. B. M. 1995. Dominance style of Japanese macaques compared with rhesus and stumptail macaques. *American Journal of Primatology*, 35, 103-116.

Chapais, B. 1983. Dominance, relatedness and the structure of female relationships in rhesus monkeys. In: *Primate Social Relationships: An Integrated Approach* (Ed. by R. A. Hinde), pp. 208-219. Oxford: Blackwell.

Chapais, B. 1992. The role of alliances in social inheritance of rank among female primates. In: *Coalitions and Alliances in Humans and Other Animals* (Ed. by A. H. Harcourt & F. B. M. de Waal), pp. 29-59. Oxford: Oxford University Press.

Chapais, B. 2004. How kinship generates dominance structures: a comparative perspective. In: *Macaque Societies* (Ed. by B. Thierry, M. Singh & W. Kaumanns), pp. 186-204. Cambridge: Cambridge University Press.

Chapais, B. 2006. Kinship, competence and cooperation in primates. In: *Cooperation in primates and humans: mechanisms and evolution* (Ed. by P. M. Kappeler & C. P. van Schaik). Berlin: Springer.

Chapais, B. & Berman, C. M. 2004. *Kinship and behavior in primates*. New York: Oxford University Press.

Chapais, B., Girard, M. & Primi, G. 1991. Non-kin alliances, and the stability of matrilineal dominance relations in Japanese macaques. *Animal Behaviour*, 41, 481-491.

Chapais, B. & St-Pierre, C.-E. G. 1997. Kinship bonds are not necessary for maintaining matrilineal rank in captive Japanese macaques. *International Journal of Primatology*, 18, 375-385.

Cheney, D. L. 1992. Intragroup cohesion and intergroup hostility: the relation between grooming distributions and intergroup competition among female primates. *Behavioral Ecology*, 3, 334-345.

Cheney, D. L. & Seyfarth, R. M. 2009. Stress and coping mechanisms in female primates. *Advances in the Study of Behavior*, 39, 1-44.

Cheney, D. L., Seyfarth, R. M. & Silk, J. B. 1995. The role of grunts in reconciling opponents and facilitating interactions among adult female baboons. *Animal Behaviour*, 50, 249-257.

Clarke, A. S. & Boinski, S. 1995. Temperament in nonhuman primates. *American Journal of Primatology*, 37, 103-125.

Clarke, A. S. & Mason, W. A. 1988. Differences among three macaque species in responsiveness to an observer. *International Journal of Primatology*, 9, 347-364.

Clutton-Brock, T. H. 2002. Breeding together: kin selection and mutualism in cooperative vertebrates. *Science*, 296, 69-72.

Clutton-Brock, T. H. 2009. Cooperation between non-kin in animal societies. *Nature*, 462, 51-57.

Clutton-Brock, T. H. & Janson, C. H. 2012. Primate socioecology at the crossroads: past, present, and future. *Evolutionary Anthropology*, 21, 136-150.

Clutton-Brock, T. H. & Lukas, D. 2012. The evolution of social philopatry and dispersal in female mammals. *Molecular Ecology*, 21, 472-492.

Clutton-Brock, T. H. & Parker, G. A. 1995. Punishment in animal societies. *Nature*, 373, 209-215.

Clutton-Brock, T. H., West, S. A., Ratnieks, F. L. W. & Foley, R. A. 2009. The evolution of society. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364, 3127-3133.

Cohen, S. & Wills, T. A. 1985. Stress, social support, and the buffering hypothesis. *Psychological Bulletin*, 98, 310-357.

Cools, A. K. A., van Hout, A. J.-M. & Nelissen, M. H. J. 2008. Canine reconciliation and third-party-initiated postconflict affiliation: do peacemaking social mechanisms in dogs rival those of higher primates? *Ethology*, 114, 53-63.

Cooper, M. A. 2004. Inter-group relationships. In: *Macaque societies* (Ed. by B. Thierry, M. Singh & W. Kaumanns), pp. 204-208. Cambridge: Cambridge University Press.

Cooper, M. A., Aureli, F. & Singh, M. 2007. Sex differences in reconciliation and post-conflict anxiety in bonnet macaques. *Ethology*, 113, 26-38.

Cooper, M. A. & Bernstein, I. S. 2008. Evaluating dominance styles in Assamese and rhesus macaques. *International Journal of Primatology*, 29, 225-243.

Cordoni, G. & Palagi, E. 2008. Reconciliation in wolves (*Canis lupus*): new evidence for a comparative perspective. *Ethology*, 114, 298-308.

Cords, M. 2012. The behavior, ecology and social evolution of cercopithecine monkeys. In: *The evolution of primate societies* (Ed. by J. C. Mitani, J. Call, P. M. Kappeler, R. A. Palombit & J. B. Silk), pp. 91-112. Chicago: The University of Chicago Press.

Cords, M. & Aureli, F. 1996. Reasons for reconciling. *Evolutionary Anthropology*, 5, 42-45.

Cords, M. & Aureli, F. 2000. Reconciliation and relationship qualities. In: *Natural Conflict Resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 177-198. Berkeley: University of California Press.

Crockford, C., Wittig, R. M., Whitten, P. L., Seyfarth, R. M. & Cheney, D. L. 2008. Social stressors and coping mechanisms in wild female baboons (*Papio hamadryas ursinus*). *Hormones and Behavior*, 53, 254-265.

Croft, D. P., James, R. & Krause, J. 2008. *Exploring animal social networks*. Princeton: Princeton University Press.

Darwin, C. 1859. *On the origin of species*. London: John Murray.

Das, M. 2000. Conflict management via third parties: post-conflict affiliation. In: *Natural Conflict Resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 263-280. Berkeley: University of California Press.

De Marco, A., Cozzolino, R., Dessi-Fulgheri, F. & Thierry, B. 2010. Conflicts induce affiliative interactions among bystanders in a tolerant species of macaque (*Macaca tonkeana*). *Animal Behaviour*, 80, 197-203.

De Marco, A., Cozzolino, R., Dessi-Fulgheri, F. & Thierry, B. 2011. Interactions between third parties and consortship partners in Tonkean macaques (*Macaca tonkeana*). *International Journal of Primatology*, 32, 708-720.

de Vries, H. 1995. An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Animal Behaviour*, 50, 1375-1389.

de Vries, H. 1998. Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. *Animal Behaviour*, 55, 827-843.

de Vries, H., Netto, W. J. & Hanegraaf, P. L. H. 1993. Matman: a program for the analysis of sociometric matrices and behavioural transition matrices. *Behaviour*, 125, 157-175.

de Vries, H., Stevens, J. M. G. & Vervaecke, H. 2006. Measuring and testing the steepness of dominance hierarchies. *Animal Behaviour*, 71, 585-592.

de Waal, F. B. M. 1986. The integration of dominance and social bonding in primates. *The Quarterly Review of Biology*, 61, 459-479.

de Waal, F. B. M. 1989a. Dominance 'style' and primate social organization. In: *Comparative Socioecology: The Behavioural Ecology of Humans and other Mammals* (Ed. by V. Standen & R. A. Foley), pp. 243-263. Oxford: Blackwell.

de Waal, F. B. M. 1989b. *Peacemaking Among Primates*. Cambridge: Harvard University Press.

de Waal, F. B. M. 1996. Conflict as negotiation. In: *Great Ape Societies* (Ed. by W. C. McGrew, L. F. Marchant & T. Nishida), pp. 159-172. Cambridge: Cambridge University Press.

de Waal, F. B. M. 2000. The first kiss: foundations of conflict resolution research in animals. In: *Natural Conflict Resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 15-33. Berkeley: University of California Press.

de Waal, F. B. M. & Aureli, F. 1996. Consolation, reconciliation, and a possible cognitive difference between macaques and chimpanzees. In: *Reaching in Thought: The Minds of the Great Apes* (Ed. by A. E. Russon, K. A. Bard & S. T. Parker), pp. 80-110. Cambridge: Cambridge University Press.

de Waal, F. B. M. & Aureli, F. 1997. Conflict resolution and distress alleviation in monkeys and apes. In: *The Integrative Neurobiology of Affiliation* (Ed. by S. C. Carter, I. I. Lederhendler & B. Kirkpatrick), pp. 317-328. New York: New York Academy of Sciences.

de Waal, F. B. M. & Luttrell, L. M. 1985. The formal hierarchy of rhesus macaques: an investigation of the bared-teeth display. *American Journal of Primatology*, 9, 73-85.

de Waal, F. B. M. & Luttrell, L. M. 1986. The similarity principle underlying social bonding among female rhesus monkeys. *Folia Primatologica*, 46, 215-234.

de Waal, F. B. M. & Luttrell, L. M. 1989. Toward a comparative socioecology of the genus *Macaca*: different dominance styles in rhesus and stumptail monkeys. *American Journal of Primatology*, 19, 83-109.

de Waal, F. B. M. & van Roosmalen, A. 1979. Reconciliation and consolation among chimpanzees. *Behavioral Ecology and Sociobiology*, 5, 55-66.

de Waal, F. B. M. & Yoshihara, D. 1983. Reconciliation and redirected affection in rhesus monkeys. *Behaviour*, 85, 224-241.

Delson, E. 1980. Fossil macaques, phyletic relationships and a scenario of deployment. In: *The Macaques: Studies in Ecology, Behavior, and Evolution* (Ed. by D. G. Lindburg), pp. 10-30. Amsterdam: Van Nostrand Rheinhold.

Demaria, C. & Thierry, B. 2001. A comparative study of reconciliation in rhesus and Tonkean macaques. *Behaviour*, 138, 397-410.

Dingemanse, N. J., Kazem, A. J. N., Réale, D. & Wright, J. 2010. Behavioural reaction norms: animal personality meets individual plasticity. *Trends in Ecology & Evolution*, 25, 81-89.

Dingemanse, N. J. & Réale, D. 2005. Natural selection and animal personality. *Behaviour*, 142, 1159-1184.

Dobson, S. D. 2012. Coevolution of facial expression and social tolerance in macaques. *American Journal of Primatology*, 74, 229-235.

Douadi, M. I., Gatti, S., Levrero, F., Duhamel, G., Bermejo, M., Vallet, D., Menard, N. & Petit, E. J. 2007. Sex-biased dispersal in western lowland gorillas (Gorilla gorilla gorilla). *Molecular Ecology*, 16, 2247-2259.

Duboscq, J., Neumann, C., Perwitasari-Farajallah, D. & Engelhardt, A. 2008. Daytime birth of a baby crested black macaque (*Macaca nigra*) in the wild. *Behavioural Processes*, 79, 81-84.

Dugatkin, L. A. 1997. *Cooperation Among Animals*. Oxford: Oxford University Press.

Dugatkin, L. A. 2002a. Animal cooperation among unrelated individuals. *Naturwissenschaften*, 89, 533-541.

Dugatkin, L. A. 2002b. Cooperation in animals: an evolutionary overview. *Biology and Philosophy*, 17, 459-476.

Dugatkin, L. A., Mesterton-Gibbons, M. & Houston, A. I. 1992. Beyond the prisoner's dilemma: toward models to discriminate among mechanisms of cooperation in nature. *Trends in Ecology & Evolution*, 7, 202-205.

Dunbar, R. I. M. 1989. Social systems as optimal strategy sets: the cost and benefits of sociality. In: *Comparative Socioecology: The Behavioural Ecology of Humans and other Mammals* (Ed. by V. Stanen & R. A. Foley), pp. 131-149. Oxford: Blackwell.

East, M. L. & Hofer, H. 2010. Social environments, social tactics and their fitness consequences in complex mammalian societies. In: *Social Behaviour: Genes, Ecology and Evolution* (Ed. by T. Székely, A. J. Moore & J. Komdeur). Cambridge: Cambridge University Press.

Ellis, L. 1995. Dominance and reproductive success among nonhuman animals: a cross-species comparison. *Ethology and Sociobiology*, 16, 257-333.

Emlen, S. T. 1995. An evolutionary theory of the family. *Proceedings of the National Academy of Sciences*, 92, 8092-8099.

Emlen, S. T. 1997. Predicting family dynamics in social vertebrates. In: *Behavioural Ecology: An Evolutionary Approach, 4th ed* (Ed. by J. R. Krebs & N. B. Davies), pp. 228-253. Oxford: Blackwell.

Estrada, A., Estrada, R. & Ervin, F. 1977. Establishment of a free-ranging colony of stumptail macaques (*Macaca arctoides*): social relations I. *Primates*, 18, 647-676.

Fa, J. E. 1985. *Use of Time and Resources by Provisioned Troops of Monkeys: Social Behaviour, Time and Energy in the Barbary Macaque (Macaca sylvanus L.) at Gibraltar*. Basel: Karger.

Feh, C. 1999. Alliances and reproductive success in Camargue stallions. *Animal Behaviour*, 57, 705-713.

Field, A., Miles, J. & Field, Z. 2012. *Discovering statistics using R*. London: SAGE Publications Ltd.

Flack, J. C. & de Waal, F. B. M. 2004. Dominance style, social power, and conflict management in macaque societies: a conceptual framework. In: *Macaque Societies* (Ed. by B. Thierry, M. Singh & W. Kaumanns), pp. 157-182. Cambridge: Cambridge University Press.

Fooden, J. 1969. *Taxonomy and Evolution of the Monkeys of Celebes (Primates: Cercopithecidae)*. Basel: Karger.

Fooden, J. 1980. Classification and distribution of the living macaques. In: *The Macaques: Studies in Ecology, Behavior, and Evolution* (Ed. by D. G. Lindburg), pp. 1-9. New York: Van Nostrand Reinhold.

Fooden, J. 1982. Ecogeographic segregation of macaque species. *Primates*, 23, 574-579.

Fraser, O. N. & Bugnyar, T. 2010. The quality of social relationships in ravens. *Animal Behaviour*, 79, 927-933.

Fraser, O. N. & Bugnyar, T. 2011. Ravens reconcile after aggressive conflicts with valuable partners. *PLoS ONE*, 6, e18118.

Fraser, O. N. & Bugnyar, T. 2012. Reciprocity of agonistic support in ravens. *Animal Behaviour*, 83, 171-177.

Fraser, O. N., Schino, G. & Aureli, F. 2008. Components of relationship quality in chimpanzees. *Ethology*, 114, 834-843.

Frère, C. H., Krützen, M., Mann, J., Connor, R. C., Bejder, L. & Sherwin, W. B. 2010. Social and genetic interactions drive fitness variation in a free-living dolphin population. *Proceedings of the National Academy of Sciences*, 107, 19949-19954.

Fry, D. P. 2000. Conflict management in cross-cultural perspective. In: *Natural conflict resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 334-351. Berkeley: University of California Press.

Fuentes, A. 2011. Social systems and socioecology. In: *Primates in perspective* (Ed. by C. J. Campbell, A. Fuentes, K. C. MacKinnon, S. K. Bearder & R. M. Stumpf), pp. 500-512. New York: Oxford University Press, Inc.

Furuichi, T. 1983. Interindividual distance and influence of dominance on feeding in a natural Japanese macaque troop. *Primates*, 24, 445-455.

Gammell, M. P., de Vries, H., Jennings, D. J., Carlin, C. M. & Hayden, T. J. 2003. David's score: a more appropriate dominance ranking method than Clutton-Brock et al.'s index. *Animal Behaviour*, 66, 601-605.

Giraudoux, P. 2012. pgirmess: Data analysis in ecology. (Ed. by R. p. v. 1.5.4). R package version 1.5.4: http://CRAN.R-project.org/package=pgirmess.

Gumert, M. D. 2000. Reciprocity in an wild group of long tailed macaques (*Macaca fascicularis*) at Tanjung Puting National Park, Kalimantan Tengah, Indonesia: an analysis of social currency exchange. MSc, Bucknell University.

Gumert, M. D. 2007. Grooming and infant handling interchange in *Macaca fascicularis*: the relationship between infant supply and grooming payment. *International Journal of Primatology*, 28, 1059-1074.

Hadidian, J. & Bernstein, I. S. 1979. Female reproductive cycles and birth data from an Old World monkey colony. *Primates*, 20, 429-442.

Hamilton, W. D. 1964a. The genetical evolution of social behaviour I. *Journal of Theoretical Biology*, 7, 1-16.

Hamilton, W. D. 1964b. The genetical evolution of social behaviour II. *Journal of Theoretical Biology*, 7, 17-52.

Hand, J. L. 1986. Resolution of social conflicts: dominance, egalitarianism, spheres of dominance, and game theory. *The Quarterly Review of Biology*, 61, 201-220.

Hanya, G., Matsubara, M., Hayaishi, S., Zamma, K., Yoshihiro, S., Kanaoka, M. M., Sugaya, S., Kiyono, M., Nagai, M., Tsuriya, Y., Hayakawa, S., Suzuki, M., Yokota, T., Kondo, D. & Takahata, Y. 2008. Food conditions, competitive regime, and female social relationships in Japanese macaques: within-population variation on Yakushima. *Primates*, 49, 116-125.

Harcourt, A. H. 1989. Social influences on competitive ability: alliances and their consequences. In: *Comparative Socioecology: The Behavioural Ecology of Humans and other Mammals* (Ed. by V. Stanen & R. A. Foley), pp. 223-242. Oxford: Blackwell.

Harcourt, A. H. & de Waal, F. B. M. 1992. *Coalitions and Alliances in Humans and other Animals*. New York: Oxford Univ Press.

Hare, B., Melis, A. P., Woods, V., Hastings, S. & Wrangham, R. W. 2007. Tolerance allows bonobos to outperform chimpanzees on a cooperative task. *Current Biology*, 17, 619-623.

Hare, B., Wobber, V. & Wrangham, R. W. 2012. The self-domestication hypothesis: evolution of bonobo psychology is due to selection against agression. *Animal Behaviour*, 83, 573-584.

Harrel Jr, F. E. 2012. Hmisc: Harrel Miscellaneous. *R package version 3.9-3*, http://CRAN.R-project.org/package=Hmisc.

Heesen, M., Rogahn, S., Ostner, J. & Schülke, O. 2013. Food abundance affects energy intake and reproduction in frugivorous female Assamese macaques. *Behavioral Ecology and Sociobiology*, 67, 1053-1066.

Hemelrijk, C. K. 1999. An individual-orientated model of the emergence of despotic and egalitarian societies. *Proceedings of the Royal Society B: Biological Sciences*, 266, 361-369.

Hemelrijk, C. K. 2000. Towards the integration of social dominance and spatial structure. *Animal Behaviour*, 59, 1035-1048.

Hemelrijk, C. K. 2004. The use of artificial-life models for the study of social organization. In: *Macaque Societies* (Ed. by B. Thierry, M. Singh & W. Kaumanns), pp. 295-313. Cambridge: Cambridge University Press.

Hemelrijk, C. K. & Puga-Gonzales, I. 2012. An individual-oriented model on the emergence of support in fights, its reciprocation and exchange. *PLoS ONE*, 7.

Henzi, S. P. & Barrett, L. 2007. Coexistence in female-bonded primate groups. *Advances in the Study of Behavior*, 37, 43-81.

Henzi, S. P., Lusseau, D., Weingrill, T., van Schaik, C. P. & Barrett, L. 2009. Cyclicity in the structure of female baboon social networks. *Behavioral Ecology and Sociobiology*, 63, 1015-1021.

Higham, J. P., Heistermann, M. & Maestripieri, D. 2011. The energetics of male-male endurance rivalry in free-ranging rhesus macaques, *Macaca mulatta*. *Animal Behaviour*, 81, 1001-1007.

Higham, J. P., Heistermann, M., Saggau, C., Agil, M., Perwitasari-Farajallah, D. & Engelhardt, A. 2012. Sexual signalling in female crested macaques and the evolution of primate fertility signals. *BMC Evolutionary Biology*, 12, 22.

Higley, J. D., Mehlman, P. T., Poland, R. E., Taub, D. M., Vickers, J., Suomi, S. J. & Linnoila, M. 1996. CSF testosterone and 5-HIAA correlate with different types of aggressive behaviors. *Biological Psychiatry*, 40, 1067-1082.

Higley, J. D., Suomi, S. J. & Chaffin, A. C. 2011. Impulsivity and aggression as personality traits in nonhuman primates. In: *Personality and temperament in nonhuman primates* (Ed. by A. Weiss, J. E. King & L. Murray), pp. 257-284. New York: Springer Science+Business Media.

Hill, D. A. 1994. Affiliative behaviour between adult males of the genus *Macaca*. *Behaviour*, 130, 293-308.

Hill, D. A. 2004. Intraspecific variation: implications for interspecific comparisons. In: *Macaque Societies* (Ed. by B. Thierry, M. Singh & W. Kaumanns). Cambridge: Cambridge University Press.

Hill, D. A. & Okayasu, N. 1995. Absence of "youngest ascendancy" in the dominance relations of sisters in wild Japanese macaques (*Macaca fuscata yakaui*). *Behaviour*, 132, 367-379.

Hinde, R. A. 1976. Interactions, relationships and social structure. *Man*, 11, 1-17.

Hiraiwa-Hasegawa, M. 1993. Skewed birth sex ratios in primates: Should high-ranking mothers have daughters or sons? *Trends in Ecology & Evolution*, 8, 395-400.

Hirsch, B. T., Stanton, M. A. & Maldonado, J. E. 2012. Kinship shapes affiliative social networks but not aggression in ring-tailed coatis. *PLoS ONE*, 7.

Hofer, H. & East, M. L. 2000. Conflict management in female-dominated spotted hyenas. In: *Natural Conflict Resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 232-234. Berkeley: University of California Press.

Holekamp, K. E., Sakai, S. T. & Lundrigan, B. L. 2007. Social intelligence in the spotted hyena (*Crocuta crocuta*). *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362, 523-538.

Holekamp, K. E., Smith, J. E., Strelioff, C. C., Van Horn, R. C. & Watts, H. E. 2012. Society, demography and genetic structure in the spotted hyenas. *Molecular Ecology*, 21, 613-632.

Holekamp, K. E., Swanson, E. M. & Van Meter, P. E. 2013. Developmental constraints on behavioural flexibility. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368.

Hothorn, T. & Hornik, K. 2011. exactRankTests: Exact distributions for rank and permutation tests. In: *http://CRAN.R-project.org/package=exactRankTests*: R package version 0.8-22.

House, J. S., Landis, K. R. & Umberson, D. 1988. Social relationships and health. *Science*, 241, 540-545.

Janson, C. H. 2000. Primate socio-ecology: the end of a golden age. *Evolutionary Anthropology*, 9, 73-86.

Judge, P. G. 1991. Dyadic and triadic reconciliation in pigtail macaques (*Macaca nemestrina*). *American Journal of Primatology*, 23, 225-237.

Judge, P. G. 2000. Coping with crowded conditions. In: *Natural Conflict Resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 129-154. Berkeley: University of California Press.

Judge, P. G. & Mullen, S. H. 2005. Quadratic postconflict affiliation among bystanders in hamadryas baboon group. *Animal Behaviour*, 69, 1345-1355.

Kamilar, J. M. & Cooper, N. 2013. Phylogenetic signal in primate behaviour, ecology and life history. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368.

Kanthaswamy, S., von Dollen, A., Kurushima, J. D., Alminas, O., Rogers, J., Ferguson, B., Lerche, N. W., Allen, P. C. & Smith, D. G. 2006. Microsatellite markers for standardized genetic management of captive colonies of rhesus macaques (Macaca mulatta). *American Journal of Primatology*, 68, 73-95.

Kappeler, P. M., Barrett, L., Blumstein, D. T. & Clutton-Brock, T. H. 2013. Constraints and flexibility in mammalian social behaviour: introduction and synthesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368.

Kappeler, P. M. & van Schaik, C. P. 2002. Evolution of primate social systems. *International Journal of Primatology*, 23, 707-740.

Kappeler, P. M. & van Schaik, C. P. 2006. *Cooperation in Primates and Humans*. Berlin: Springer.

Kapsalis, E. 2004. Matrilineal kinship and primate behavior. In: *Kinship and behavior in primates* (Ed. by B. Chapais & C. M. Berman), pp. 153-176. New York: Oxford University Press.

Kapsalis, E. & Berman, C. M. 1996a. Models of affiliative relationships among free-ranging rhesus monkeys (*Macaca mulatta*) I. Criteria for kinship. *Behaviour*, 133, 1209-1234.

Kapsalis, E. & Berman, C. M. 1996b. Models of affiliative relationships among free-ranging rhesus monkeys (*Macaca mulatta*) II. Testing predictions for three hypothesized organizing principles. *Behaviour*, 133, 1235-1263.

Kavan, M. G., Elsasser, G. & Barone, E. J. 2009. Generalized anxiety disorder: practical assessment and management. *American family physician*, 79, 785-791.

Kazem, A. J. N. & Aureli, F. 2005. Redirection of aggression: multiparty signalling within a network? In: *Animal Communication Networks* (Ed. by P. K. McGregor), pp. 191-218. Cambridge: Cambridge University Press.

Kerhoas, D., Mundry, R., Perwitasari-Farajallah, D., Agil, M., Widdig, A. & Engelhardt, A. under review. The interaction of social and ecological parameters on foetus and infant survival in wild crested macaques.

Klass, K. & Cords, M. 2011. Effect of unknown relationships on linearity, steepness and rank ordering of dominance hierarchies: simulation studies based on data from wild monkeys. *Behavioural Processes*, 88, 168-176.

Koenig, A. 2002. Competition for resources and its behavioral consequences among female primates. *International Journal of Primatology*, 23, 759-784.

Koenig, A. & Borries, C. 2009. The lost dream of ecological determinism: time to say goodbye? ... Or a White Queen's proposal? *Evolutionary Anthropology*, 18, 166-174.

Koenig, A., Scarry, C. J., Wheeler, B. C. & Borries, C. 2013. Variation in grouping patterns, mating systems and social structure: what socio-ecological models attempt to explain. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368.

Koolhaas, J. M., Korte, S. M., de Boer, S. F., van der Vegt, B. J., van Reenen, C. G., Hopster, H., de Jong, I. C., Ruis, M. A. W. & Blokhuis, H. J. 1999. Coping styles in animals: current status in behavior and stress-physiology. *Neuroscience & Biobehavioral Reviews*, 23, 925-935.

Koski, S. E., de Vries, H., van den Tweel, S. W. & Sterck, E. H. M. 2007a. What to do after a fight? The determinants and inter-dependency of post-conflict interactions in chimpanzees. *Behaviour*, 144, 529-555.

Koski, S. E., Koops, K. & Sterck, E. H. M. 2007b. Reconciliation, relationship quality, and postconflict anxiety: testing the integrated hypothesis in captive chimpanzees. *American Journal of Primatology*, 69, 158-172.

Kotrschal, K., Scheiber, I. B. R. & Hirschenhauser, K. 2010. Individual performance in complex social systems: the greylag goose example. In: *Animal behaviour: Evolution and mechanisms* (Ed. by P. M. Kappeler), pp. 121-148. Berlin: Springer.

Koyama, N. F. 2001. The long-term effects of reconciliation in Japanese macaques *Macaca fuscata*. *Ethology*, 107, 975-987.

Koyama, N. F. 2003. Matrilineal cohesion and social networks in *Macaca fuscata*. *International Journal of Primatology*, 24, 797-811.

Krause, J. & Ruxton, G. D. 2002. *Living in groups*. Oxford: Oxford University Press.

Krebs, J. R. & Davies, N. B. 1997. *Behavioural ecology: an evolutionary approach*. Oxford: Blackwell.

Kuester, J. & Paul, A. 1996. Female-female competition and male mate choice in Barbary macaques (*Macaca sylvanus*). *Behaviour*, 133, 763-790.

Kummer, H. 1978. On the value of social relationships to nonhuman primates: a heuristic scheme. *Social Science Information*, 17, 687-705.

Kutsukake, N. 2000. Matrilineal rank inheritance varies with absolute rank in Japanese macaques. *Primates*, 41, 321-335.

Kutsukake, N. & Clutton-Brock, T. H. 2008. Do meerkats engage in conflict management following aggression? Reconciliation, submission and avoidance. *Animal Behaviour*, 75, 1441-1453.

Leca, J.-B., Fornasieri, I. & Petit, O. 2002. Aggression and reconciliation in *Cebus capucinus*. *International Journal of Primatology*, 23, 979-998.

Leiva, D. & de Vries, H. 2011. steepness: Testing steepeness of dominance hierarchies. (Ed. by R. p. v. 0.2). R package version 0.2: http://CRAN.R-project.org/package=steepness.

Lindenfors, P., Fröberg, L. & Nunn, C. L. 2004. Females drive primate social evolution. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 271, S101-S103.

Lingon, D. 1991. Cooperation and reciprocity in birds and mammals. In: *Kin recognition* (Ed. by P. G. Hepper), pp. 30-59. Cambridge: Cambridge University Press.

Logan, C., Emery, N. J. & Clayton, N. S. 2012. Alternative behavioral measures of postconflict affiliation. *Behavioral Ecology*, 24, 98-112.

Lott, D. F. 1991. *Intraspecific variation in the social systems of wild vertebrates*. Cambridge: Cambridge University Press.

Maestripieri, D., Schino, G., Aureli, F. & Troisi, A. 1992. A modest proposal: displacement activities as an indicator of emotions in primates. *Animal Behaviour*, 44, 967-979.

Majolo, B., Ventura, R. & Koyama, N. F. 2009a. Anxiety level predicts post-conflict behaviour in wild Japanese macaques (*Macaca fuscata yakui*). *Ethology*, 115, 986-995.

Majolo, B., Ventura, R. & Koyama, N. F. 2009b. A statistical modelling approach to the occurrence and timing of reconciliation in wild Japanese macaques. *Ethology*, 115, 152-166.

Majolo, B., Ventura, R., Koyama, N. F., Hardie, S. M., Jones, B. M., Knapp, L. A. & Schino, G. 2009c. Analysing the effects of group size and food competition on Japanese macaque social relationships. *Behaviour*, 146, 113-137.

Majolo, B., Ventura, R. & Schino, G. 2010. Asymmetry and dimensions of relationships quality in the Japanese macaque (*Macaca fuscata yakui*). *International Journal of Primatology*, 31, 736-750.

Martin, P. & Bateson, P. 1993. *Measuring Behaviour - An Introductory Guide*, 2nd edn. Cambridge: Cambridge University Press.

Mason, W. A., Long, D. D. & Mendoza, S. P. 1993. Temperament and mother-infant conflict in macaques: a transactional analysis. In: *Primate Social Conflict*, pp. 205-227. Albany: State University of New York Press.

Matsumura, S. 1996. Postconflict affiliative contacts between former opponents among wild moor macaques (*Macaca maurus*). *American Journal of Primatology*, 38, 211-219.

Matsumura, S. 1998. Relaxed dominance relations among female moor macaques (*Macaca maurus*) in their natural habitat, south Sulawesi, Indonesia. *Folia Primatologica*, 69, 346-356.

Matsumura, S. & Okamoto, K. 1997. Factors affecting proximity among members of a wild group of moor macaques during feeding, moving, and resting. *International Journal of Primatology*, 18, 929-940.

Maynard Smith, J. 1974. The theory of games and the evolution of animal conflicts. *Journal of Theoretical Biology*, 47, 209-221.

Maynard Smith, J. 1976. Evolution and the theory of games. *American Scientist*, 64, 41-45.

McComb, K. & Semple, S. 2005. Coevolution of vocal communication and sociality in primates. *Biology Letters*, 1, 381-385.

McFarland, R. & Majolo, B. 2011. Exploring the components, asymmetry and distribution of relationship quality in wild Barbary macaques (*Macaca sylvanus*). *PLoS ONE*, 6, e28826.

McFarland, R. & Majolo, B. 2012. Reconciliation and the costs of aggression in wild Barbary macaques (*Macaca sylvanus*): a test of the integrated hypothesis. *Ethology*, 117, 928-937.

McFarland, R. & Majolo, B. 2013. Coping with the cold: predictors of survival in wild Barbary macaques, Macaca sylvanus. *Biology Letters*, 9.

Ménard, N. 2004. Do ecological factors explain variation in social organization? In: *Macaque Societies* (Ed. by B. Thierry, M. Singh & W. Kaumanns), pp. 237-262. Cambridge: Cambridge University Press.

Mendoza, S. P. & Mason, W. A. 1989. Primate relationships: social dispositions and physiological responses. In: *Perspectives in Primate Biology* (Ed. by P. K. Seth & S. Seth), pp. 129-143. New Delhi: Today & Tomorrow's Printers and Publishers.

Mendoza, S. P., Reeder, D. M. & Mason, W. A. 2002. Nature of proximate mechanism underlying primate social systems: simplicity and redundancy. *Evolutionary Anthropology*, Suppl. 1, 112-116.

Micheletta, J., Engelhardt, A., Matthews, L. E. E., Agil, M. & Waller, B. M. 2013. Multicomponent and multimodal lipsmacking in crested macaques (*Macaca nigra*). *American Journal of Primatology*, 75, 763-773.

Micheletta, J. & Waller, B. 2012. Friendship affects gaze following in a tolerant species of macaques (*Macaca nigra*). *Animal Behaviour*, 83, 459-467.

Micheletta, J., Waller, B., Panggur, M. R., Neumann, C., Duboscq, J., Agil, M. & Engelhardt, A. 2012. Social bonds affect anti-predator behaviour in a tolerant species of macaques, *Macaca nigra*. *Proceedings of the Royal Society B: Biological Sciences*, 279, 4042-4050.

Milligan, B. 2003. Maximum-likelihood estimation of relatedness. *Genetics*, 163, 1153-1167.

Mori, A., Watanabe, K. & Yamaguchi, N. 1989. Longitudinal changes of dominance rank among the females of the Koshima group of Japanese monkeys. *Primates*, 30, 147-173.

Morin, P. A., Chambers, K. E., Boesch, C. & Vigilant, L. 2001. Quantitative polymerase chain reaction analysis of DNA from non-invasive samples for accurate microsatellite genotyping of wild chimpanzees (*Pan troglodytes verus*). *Molecular Ecology*, 10, 1835-1844.

Nakamichi, M. 2003. Age-related differences in social grooming among adult female Japanese monkeys (*Macaca fuscata*). *Primates*, 44, 239-246.

Nakamichi, M. & Shizawa, Y. 2003. Distribution of grooming among adult females in a large, free-ranging group of Japanese macaques. *International Journal of Primatology*, 24, 607-625.

Neumann, C., Agil, M., Engelhardt, A. & Widdig, A. Unpublished manuscript. Coalitions and dominance rank in wild male crested macaques, *Macaca nigra*.

Neumann, C., Agil, M., Widdig, A. & Engelhardt, A. Unpublished manuscript. Personality factors predict future male dominance rank in a social mammal.

Neumann, C., Agil, M., Widdig, A. & Engelhardt, A. In press. Personality of wild male crested macaques (*Macaca nigra*). *PLoS ONE*.

Neumann, C., Assahad, G., Hammerschmidt, K., Perwitasari-Farajallah, D. & Engelhardt, A. 2010. Loud calls in male crested macaques, *Macaca nigra*: a signal of dominance in a tolerant species. *Animal Behaviour*, 79, 187-193.

Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., Widdig, A. & Engelhardt, A. 2011. Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. *Animal Behaviour*, 82, 911-921.

Nieuwenhuis, R., Pelzer, B. & te Grotenhuis, M. 2012. influence.ME: Tools for detecting influential data in mixed effects models. *R package version 0.9*.

Noë, R. 2006. Cooperation experiments: coordination through communication versus acting apart together. *Animal Behaviour*, 71, 1-18.

Noë, R. & Hammerstein, P. 1994. Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioral Ecology and Sociobiology*, 35, 1-11.

Noë, R. & Hammerstein, P. 1995. Biological Markets. *Trends in Ecology & Evolution*, 10, 336-339.

Noë, R., van Schaik, C. P. & van Hooff, J. A. R. A. M. 1991. The market effect: an explanation for pay-off asymmetries among collaborating animals. *Ethology*, 87, 97-118.

Nsubuga, A. M., Robbins, M. M., Roeder, A. D., Morin, P. A., Boesch, C. & Vigilant, L. 2004. Factors affecting the amount of genomic DNA extracted from ape faeces and the identification of an improved sample storage method. *Molecular Ecology*, 13, 2089-2094.

Nunn, C. L. & Altizer, S. 2006. *Infectious diseases in primates: Behavior, Ecology and Evolution*. New York: Oxford University Press.

O'Brien, T. G. & Kinnaird, M. F. 1997. Behavior, diet, and movements of the Sulawesi crested black macaque (*Macaca nigra*). *International Journal of Primatology*, 18, 321-351.

Oi, T. 1988. Sociological study on the troop fission of wild Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island. *Primates*, 29, 1-19.

Oi, T. 1990. Patterns of dominance and affiliation in wild pig-tailed macaques (*Macaca nemestrina nemestrina*) in west Sumatra. *International Journal of Primatology*, 11, 339-356.

Okamoto, K. & Matsumura, S. 2002. Intergroup encounters in wild moor macaques (*Macaca maurus*). *Primates*, 43, 119-125.

Packer, C., Pusey, A. E. & Eberly, L. E. 2001. Egalitarianism in female African lions. *Science*, 293, 690-693.

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

Paul, A. 2006. Kinship and behaviour in Barbary macaques. In: *The Barbary macaques: Biology, Management and Conservation* (Ed. by J. K. Hodges & J. Cortes). Nottingham: Nottingham University Press.

Petit, O., Abegg, C. & Thierry, B. 1997. A comparative study of aggression and conciliation in three cercopithecine monkeys (*Macaca fuscata, Macaca nigra, Papio papio*). *Behaviour*, 134, 415-432.

Petit, O., Desportes, C. & Thierry, B. 1992. Differential probability of "coproduction" in two species of macaques (*Macaca tonkeana*, *M. mulatta*). *Ethology*, 90, 107-120.

Petit, O. & Thierry, B. 1992. Affiliative function of the silent bared-teeth display in moor macaques (*Macaca maurus*): further evidence for the particular status of Sulawesi macaques. *International Journal of Primatology*, 13, 97-105.

Petit, O. & Thierry, B. 1994a. Aggressive and peaceful interventions in conflicts in Tonkean macaques. *Animal Behaviour*, 48, 1427-1436.

Petit, O. & Thierry, B. 1994b. Reconciliation in a group of black macaques, *Macaca nigra*. *Dodo*, 30, 89-95.

Popp, J. L. & deVore, I. 1979. Aggressive competition and social dominance theory: synopsis. In: *The Great Apes* (Ed. by D. A. Hamburg & E. R. McCown), pp. 317-338. Menlo Park: Benjamin/Cummings.

Preuschoft, S., Paul, A. & Kuester, J. 1998. Dominance styles of female and male Barbary macaques (*Macaca sylvanus*). *Behaviour*, 135, 731-755.

Preuschoft, S. & van Schaik, C. P. 2000. Dominance and communication - conflict management in various social settings. In: *Natural Conflict Resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 77-105. Berkeley: University of California Press.

Price, T. & Langen, T. 1992. Evolution of correlated characters. *Trends in Ecology & Evolution*, 7, 307-310.

Puga-Gonzales, I., Hildenbrandt, H. & Hemelrijk, C. K. 2009. Emergent patterns of social affiliation in primates, a model. *PLoS Computational Biology*, 5, 1-17.

Pulliam, H. R. & Caraco, T. 1984. Living in groups: is there an optimal group size? In: *Behavioural Ecology: an evolutionary approach* (Ed. by J. R. Krebs & N. B. Davis), pp. 122-147. London: Blackwell.

Pusey, A. E. 2012. Magnitude and sources of variation in female reproductive performance. In: *The evolution of primate societies* (Ed. by J. C. Mitani, J. Call, P. M. Kappeler, R. A. Palombit & J. B. Silk), pp. 343-366. Chicago: The University of Chicago Press.

Pusey, A. E. & Packer, C. 1987. Dispersal and philopatry. In: *Primate Societies* (Ed. by B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker), pp. 250-266. Chicago: Chicago University Press.

R Development Core Team. 2011. R: A language and environment for statistical computing. *R Foundation for Statistical Computing*, Vienna, Austria, version 2.14.11.

Richter, C., Mevis, L., Malaivijitnond, S., Schülke, O. & Ostner, J. 2009. Social relationships in free-ranging male *Macaca arctoides*. *International Journal of Primatology*, 30, 625-642.

Riley, E. P. 2010. Male–male affiliation in Sulawesi Tonkean macaques. In: *Indonesian Primates* (Ed. by S. L. Gursky-Doyen & J. Supriatna), pp. 257-268. New York: Springer.

Sachser, N. & Kaiser, S. 2010. The social modulation of behavioural development. In: *Animal behaviour: Evolution and mechanisms* (Ed. by P. M. Kappeler). Berlin: Springer.

Sachser, N., Kaiser, S. & Hennessy, M. B. 2013. Behavioural profiles are shaped by social experience: when, how and why. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368.

Sade, D. S. 1972. Sociometrics of *Macaca mulatta* I. Linkages and cliques in grooming matrices. *Folia Primatologica*, 18, 196-223.

Samuels, A. & Flaherty, C. 2000. Peaceful conflict resolution in the sea? In: *Natural Conflict Resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 229-231. Berkeley: University of California Press.

Schino, G. 1998. Reconciliation in domestic goats. *Behaviour*, 135, 343-356.

Schino, G. 2000. Beyond the primates: expanding the reconciliation horizon. In: *Natural Conflict Resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 225-242. Berkeley: University of California Press.

Schino, G. 2001. Grooming, competition and social rank among female primates: a meta analysis. *Animal Behaviour*, 62, 265-271.

Schino, G. 2007. Grooming and agonistic support: a meta-analysis of primate reciprocal altruism. *Behavioral Ecology*, 18, 115-120.

Schino, G. & Aureli, F. 2008a. Grooming reciprocation among female primates: a meta-analysis. *Biology Letters*, 4, 9-11.

Schino, G. & Aureli, F. 2008b. Trade-offs in primate grooming reciprocation: testing behavioural flexibility and correlated evolution. *Biological Journal of the Linnean Society*, 95, 439-446.

Schino, G., Perretta, G., Taglioni, A. M., Monaco, V. & Troisi, A. 1996. Primate displacement activities as an ethopharmacological model of anxiety. *Anxiety*, 2, 186-191.

Schradin, C. 2013. Intraspecific variation in social organization by genetic variation, developmental plasticity, social flexibility or entirely extrinsic factors. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368.

Schülke, O., Bhagavatula, J., Vigilant, L. & Ostner, J. 2010. Social bonds enhance reproductive success in male macaques. *Current Biology*, 20, 1-4.

Schülke, O. & Ostner, J. 2008. Male reproductive skew, paternal relatedness, and female social relationships. *American Journal of Primatology*, 70, 695-698.

Schülke, O. & Ostner, J. 2012. Ecological and social influences of sociality. In: *The evolution of primate societies* (Ed. by J. C. Mitani, J. Call, P. M. Kappeler, R. A. Palombit & J. B. Silk), pp. 195-219. Chicago: The University of Chicago Press.

Schülke, O., Wenzel, S. & Ostner, J. 2013. Paternal relatedness predicts the strength of social bonds among female rhesus macaques. *PLoS ONE*, 8, e59789.

Seyfarth, R. M. 1976. Social relationships among adult female baboons. *Animal Behaviour*, 24, 917-938.

Seyfarth, R. M. 1977. A model of social grooming among adult female monkeys. *Journal of Theoretical Biology*, 65, 671-698.

Seyfarth, R. M. 1980. The distribution of grooming and related behaviours among adult female vervet monkeys. *Animal Behaviour*, 28, 798-813.

Seyfarth, R. M., Silk, J. B. & Cheney, D. L. 2012. Variation in personality and fitness in wild female baboons. *Proceedings of the National Academy of Sciences*, 109, 16980-16985.

Shannon, C. E. & Weaver, W. 1949. *The mathematical theory of communication*. Urbana: University of Illinois Press.

Siegel, S. & Castellan, N. J. 1988. *Nonparametric Statistics for the Behavioral Sciences*, 2nd edn. New York: McGraw-Hill.

Sih, A., Bell, A. & Johnson, J. C. 2004a. Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*, 19, 372-378.

Sih, A., Bell, A. M., Johnson, J. C. & Ziemba, R. E. 2004b. Behavioral syndromes: an integrative overview. *The Quarterly Review of Biology*, 79, 241-277.

Sih, A., Hanser, S. F. & McHugh, K. A. 2009. Social network theory: new insights and issues for behavioral ecologists. *Behavioral Ecology and Sociobiology*, 63, 975-988.

Sih, A. 2011. Behavioral syndromes: a behavioral ecologist's view on the evolutionary and ecological implications of animal personalities. In: *Personality and temperament in nonhuman primates* (Ed. by A. Weiss, J. E. King & L. Murray), pp. 313-336. New York: Springer Science+Business Media.

Silk, J. B. 1982. Altruism among female *Macaca radiata*: explanations and analysis of patterns of grooming and coalition formation. *Behaviour*, 79, 162-188.

Silk, J. B. 1983. Local resource competition and facultative adjustment of sex ratios in relation to competitive abilities. *The American Naturalist*, 121, 56-66.

Silk, J. B. 1994. Social relationships of male bonnet macaques: male bonding in a matrilineal society. *Behaviour*, 130, 271-291.

Silk, J. B. 1996. Why do primates reconcile? *Evolutionary Anthropology*, 5, 39-42.

Silk, J. B. 1999. Why are infant so attractive to others? The form and function of infant handling in bonnet macaques. *Animal Behaviour*, 57, 1021-1032.

Silk, J. B. 2002. Using the 'F'-word in primatology. *Behaviour*, 139, 421-446.

Silk, J. B. 2003. Cooperation without counting: the puzzle of friendship. In: *Genetic and Cultural Evolution of Cooperation* (Ed. by P. Hammerstein), pp. 37-54. Cambridge: MIT Press.

Silk, J. B. 2006. Practising Hamilton's rule: kin selection in primate groups. In: *Cooperation in primates and humans* (Ed. by P. Kappeler & C. P. van Schaik), pp. 25-46. Berlin: Springer.

Silk, J. B. 2007a. The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362, 539-559.

Silk, J. B. 2007b. Social components of fitness in primate groups. *Science*, 317, 1347-1351.

Silk, J. B. 2012. The adaptive value of sociality. In: *The evolution of primate societies* (Ed. by J. C. Mitani, J. Call, P. M. Kappeler, R. A. Palombit & J. B. Silk), pp. 552-564. Chicago: The University of Chicago Press.

Silk, J. B., Alberts, S. C. & Altmann, J. 2003. Social bonds of female baboons enhance infant survival. *Science*, 302, 1231-1234.

Silk, J. B., Alberts, S. C. & Altmann, J. 2004. Patterns of coalition formation by adult female baboons in Amboseli, Kenya. *Animal Behaviour*, 67, 573-582.

Silk, J. B., Alberts, S. C. & Altmann, J. 2006a. Social relationships among adult female baboons (*Papio cynocephalus*) II. Variation in the quality and stability of social bonds. *Behavioral Ecology and Sociobiology*, 61, 197-204.

Silk, J. B., Altmann, J. & Alberts, S. C. 2006b. Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behavioral Ecology and Sociobiology*, 61, 183-195.

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Witt, R. M., Seyfarth, R. M. & Cheney, D. L. 2010. Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology*, 20, 1359-1361.

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M. & Cheney, D. L. 2009. The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proceedings of the Royal Society B: Biological Sciences*, 276, 3099-3104.

Silk, J. B., Cheney, D. L. & Seyfarth, R. M. 1996. The form and function of post-conflict interactions between female baboons. *Animal Behaviour*, 52, 259-268.

Silk, J. B., Seyfarth, R. M. & Cheney, D. L. 1999. The structure of social relationships among female savanna baboons in Moremi Reserve, Botswana. *Behaviour*, 136, 679-703.

Smith, J. E., Kolowski, J. M., Graham, K. E., Dawes, S. E. & Holekamp, K. E. 2008. Social and ecological determinants of fission–fusion dynamics in the spotted hyena. *Animal Behaviour*, 76, 619-636.

Smith, J. E., Memenis, S. K. & Holekamp, K. E. 2007. Rank-related partner choice in the fission-fusion society of the spotted hyena (*Crocuta crocuta*). *Behavioral Ecology and Sociobiology*, 61, 753-765.

Smith, J. E., Powning, K. S., Dawes, S. E., Estrada, J. R., Hopper, A. L., Piotrowski, S. L. & Holekamp, K. E. 2011. Greetings promote cooperation and reinforce social bonds among spotted hyenas. *Animal Behaviour*, 81, 401-415.

Smith, J. E., van Horn, R. C., Powning, K. S., Cole, A. R., Graham, K. E., Memenis, S. K. & Holekamp, K. E. 2010. Evolutionary forces favoring intragroup coalitions among spotted hyenas and other animals. *Behavioral Ecology*, 21, 284-303.

Smith, K., Alberts, S. C. & Altmann, J. 2003. Wild female baboons bias their social behaviour towards paternal half-sisters. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 270, 503-510.

Southwick, C. H., Siddiqi, M. F., Farrooqui, M. Y. & Chandra Pal, B. 1976. Effects of artificial feeding on aggressive behaviour of rhesus monkeys in India. *Animal Behaviour*, 24, 11-15.

Standen, V. & Foley, R. A. 1989. *Comparative socioecology: the behavioural ecology of humans and other mammals*. Oxford: Blackwell.

Sterck, E. H. M., Watts, D. P. & van Schaik, C. P. 1997. The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, 41, 291-309.

Sueur, C. & Petit, O. 2008. Shared or unshared consensus decision in macaques? *Behavioural Processes*, 78, 84-92.

Sueur, C., Petit, O., De Marco, A., Jacobs, A., Watanabe, K. & Thierry, B. 2011. A comparative network analysis of social style in macaques. *Animal Behaviour*, 82, 845-852.

Sugardjito, J., Southwick, C. H., Supriatna, J., Kohlhaas, A., Baker, S. C., Erwin, J., Froehlich, J. & Lerche, N. 1989. Population survey of macaques in northern Sulawesi. *American Journal of Primatology*, 18, 285-301.

Suomi, S. J., Chaffin, A. C. & Higley, J. D. 2011. Reactivity and behavioral inhibition as personality traits in nonhuman primates. In: *Personality and temperament in nonhuman primates* (Ed. by A. Weiss, J. E. King & L. Murray), pp. 285-312. New York: Springer Science+Business Media, LCC.

Sussman, R. W. & Garber, P. A. 2011. Cooperation, collective action and competition in primate social interactions. In: *Primates in perspective* (Ed. by C. J. Campbell, A. Fuentes, K. C. MacKinnon, S. K. Bearder & R. M. Stumpf), pp. 587-598. New-York: Oxford University Press, Inc.

Taberlet, P., Griffin, S., Goossens, B., Questiau, S., Manceau, V., Escaravage, N., Waits, L. P. & Bouvet, J. 1996. Reliable genotyping of samples with very low DNA quantities using PCR. *Nucleic Acids Research*, 24, 3189-3194.

Taylor, S. E., Klein, L. C., Lewis, B. P., Gruenewald, T. L., Gurung, R. A. R. & Updegraff, J. A. 2000. Biobehavioral responses to stress in females: Tend-and-befriend, not fight-or-flight. *Psychological Review*, 107, 411-429.

Thierry, B. 1985. Patterns of agonistic interactions in three species of macaque (*Macaca mulatta, M. fascicularis, M. tonkeana*). *Aggressive Behavior*, 11, 223-233.

Thierry, B. 1990. Feedback loop between kinship and dominance: the macaque model. *Journal of Theoretical Biology*, 145, 511-522.

Thierry, B. 1997. Adaptation and self-organization in primate societies. *Diogenes*, 45, 39.

Thierry, B. 2000. Covariation of conflict management patterns across macaque species. In: *Natural Conflict Resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 106-128. Berkeley: University of California Press.

Thierry, B. 2004. Social epigenesis. In: *Macaque Societies* (Ed. by B. Thierry, M. Singh & W. Kaumanns), pp. 267-290. Cambridge: Cambridge University Press.

Thierry, B. 2006. The macaques: a double-layered social organization. In: *Primates in Perspective* (Ed. by C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. A. Panger & S. K. Bearder), pp. 224-239. Oxford: Oxford University Press.

Thierry, B. 2007. Unity in diversity: lessons from macaque societies. *Evolutionary Anthropology*, 16, 224-238.

Thierry, B. 2008. Primate socioecology, the lost dream of ecological determinism. *Evolutionary Anthropology*, 17, 93-96.

Thierry, B. 2011. The macaques: a double-layered social organization. In: *Primates in perspective* (Ed. by C. J. Campbell, A. Fuentes, K. C. MacKinnon, S. K. Bearder & R. M. Stumpf), pp. 229-240. New York: Oxford University Press, Inc.

Thierry, B. 2013. Identifying constraints in the evolution of primate societies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368.

Thierry, B., Anderson, J. R., Demaria, C., Desportes, C. & Petit, O. 1994. Tonkean macaque behaviour from the perspective of the evolution of Sulawesi macaques. In: *Current Primatology: Social Development, Learning and Behaviour* (Ed. by J. J. Roeder, B. Thierry, J. R. Anderson & N. Herrenschmidt), pp. 103-117. Strasbourg: Université Louis Pasteur.

Thierry, B. & Aureli, F. 2006. Barbary but not barbarian: social relations in a tolerant macaque. In: *The Barbary Macaque* (Ed. by J. K. Hodges & J. Cortes), pp. 29-45. Nottingham: Nottingham University Press.

Thierry, B., Aureli, F., Nunn, C. L., Petit, O., Abegg, C. & de Waal, F. B. M. 2008. A comparative study of conflict resolution in macaques: insights into the nature of trait covariation. *Animal Behaviour*, 75, 847-860.

Thierry, B., Bynum, E. L., Baker, S. C., Kinnaird, M. F., Matsumura, S., Muroyama, Y., O'Brien, T. G., Petit, O. & Watanabe, K. 2000a. The social repertoire of Sulawesi macaques. *Primate Research*, 16, 203-226.

Thierry, B., Demaria, C., Preuschoft, S. & Desportes, C. 1989. Structural convergence between silent bared-teeth display and relaxed open-mouth display in the Tonkean macaque (*Macaca tonkeana*). *Folia Primatologica*, 52, 178-184.

Thierry, B., Gauthier, C. & Peignot, P. 1990. Social grooming in Tonkean macaques (*Macaca tonkeana*). *International Journal of Primatology*, 11, 357-373.

Thierry, B., Iwaniuk, A. N. & Pellis, S. M. 2000b. The influence of phylogeny on the social behaviour of macaques (Primates: Cercopithecidae, genus *Macaca*). *Ethology*, 106, 713-728.

Tinbergen, N. 1963. On aims and methods of Ethology. *Zeitschrift für Tierpsychologie*, 20, 410-433.

Trivers, R. L. 1971. The evolution of reciprocal altruism. *The Quarterly Review of Biology*, 46, 35-57.

Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual selection and the descent of man 1871-1971* (Ed. by B. Campbell), pp. 136-179. Chicago: Aldine Publishing Company.

Trivers, R. L. 2006. Reciprocal altruism: 30 years later. In: *Cooperation in Primates and Humans* (Ed. by P. M. Kappeler & C. P. van Schaik). New York: Springer.

Trivers, R. L. & Willard, D. E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science*, 179, 90-92.

Uchino, B. 2006. Social Support and Health: A Review of Physiological Processes Potentially Underlying Links to Disease Outcomes. *Journal of Behavioral Medicine*, 29, 377-387.

van Hooff, J. A. R. A. M. & van Wensing, J. A. B. 1987. Dominance and its behavioural measures in a captive wolf pack. In: *Man and Wolf* (Ed. by H. Frank), pp. 219-252. Dordrecht: Dr. W. Junk Publisher.

van Noordwijk, M. A. & van Schaik, C. P. 1987. Competition among female long-tailed macaques, *Macaca fascicularis*. *Animal Behaviour*, 35, 577-589.

van Schaik, C. P. 1983. Why are diurnal primates living in groups ? *Behaviour*, 87, 120-144.

van Schaik, C. P. 1989. The ecology of social relationships amongst female primates. In: *Comparative Socioecology: The Behavioural Ecology of Humans and other Mammals* (Ed. by V. Standen & R. A. Foley), pp. 195-218. Oxford: Blackwell.

van Schaik, C. P. & Aureli, F. 2000. The natural history of valuable relationships in primates. In: *Natural Conflict Resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 307-333. Berkeley: University of California Press.

van Schaik, C. P. & Kappeler, P. 2006. Cooperation in primates and humans: closing the gap. In: *Cooperation in primates and humans* (Ed. by P. Kappeler & C. P. van Schaik), pp. 3-21. Berlin: Springer.

van Schaik, C. P. & van Hooff, J. A. R. A. M. 1983. On the ultimate causes of primate social systems. *Behaviour*, 85, 91-117.

van Schaik, C. P. & van Noordwijk, M. A. 1988. Scramble and contest in feeding competition among female long-tailed macaques (*Macaca fascicularis*). *Behaviour*, 105, 77-98.

Veenema, H. C., Das, M. & Aureli, F. 1994. Methodological improvements for the study of reconciliation. *Behavioural Processes*, 31, 29-38.

Vehrencamp, S. L. 1983. A model for the evolution of despotic versus egalitarian societies. *Animal Behaviour*, 31, 667-682.

Ventura, R., Majolo, B., Koyama, N. F., Hardie, S. M. & Schino, G. 2006. Reciprocation and interchange in wild Japanese macaques: grooming, cofeeding, and agonistic support. *American Journal of Primatology*, 68, 1138-1149.

Viblanc, V. A., Valette, V., Kauffmann, M., Malosse, N. & Groscolas, R. 2012. Coping with social stress: heart rate responses to agonistic interactions in king penguins. *Behavioral Ecology*, 23, 1178-1185.

Wahaj, S. A., Van Horn, R. C., Van Horn, T. L., Dreyer, R., Hilgris, R., Schwarz, J. & Holekamp, K. E. 2004. Kin discrimination in the spotted hyena (*Crocuta crocuta*): nepotism among siblings. *Behavioral Ecology and Sociobiology*, 56, 237-247.

Wang, J. 2011. COANCESTRY: a program for simulating, estimating and analysing relatedness and inbreeding coefficients. *Molecular Ecology Resources*, 11, 141-145.

Wascher, C. A. F., Scheiber, I. B. R. & Kotrschal, K. 2008. Heart rate modulation in bystanding geese watching social and non-social events. *Proceedings of the Royal Society B: Biological Sciences*, 275, 1653-1659.

Watts, D. P., Colmenares, F. & Arnold, K. 2000. Redirection, consolation, and male policing: how targets of aggression interact with bystanders. In: *Natural Conflict Resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 281-304. Berkeley: University of California Press.

Wendland, J. R., Lesch, K.-P., Newman, T. K., Timme, A., Gachot-Neveu, H., Thierry, B. & Suomi, S. J. 2006. Differential functional variability of serotonin transporter and monoamine oxidase A genes in macaque species displaying contrasting levels of aggression-related behavior. *Behavior Genetics*, 36, 163-172.

Westergaard, G. C., Suomi, S. J., Chavanne, T. J., Houser, L., Hurley, A., Cleveland, A., Snoy, P. J. & Higley, J. D. 2003. Physiological correlates of aggression and impulsivity in free-ranging female primates. *Neuropsychopharmacology*, 28, 1045-1055.

Westergaard, G. C., Suomi, S. J., Higley, J. D. & Mehlman, P. T. 1999. CSF 5-HIAA and aggression in female macaque monkeys: species and interindividual differences. *Psychopharmacology*, 146, 440-446.

Whitehead, H. 2008. *Analyzing Animal Societies: Quantitative Methods for Vertebrate Social Analysis*. Chicago: University of Chicago Press.

Widdig, A. in press. The impact of male reproductive skew on kin structure and sociality in multi-male groups: Altmann (1979) revisited. *Evolutionary Anthropology*.

Widdig, A., Bercovitch, F. B., Streich, W. J., Sauermann, U., Nürnberg, P. & Krawczak, M. 2004. A longitudinal analysis of reproductive skew in male rhesus macaques. *Proceedings of the Royal Society B: Biological Sciences*, 271, 819-826.

Widdig, A., Nürnberg, P., Krawczak, M., Streich, W. J. & Bercovitch, F. 2002. Affiliation and aggression among adult female rhesus macaques: a genetic analysis of paternal cohorts. *Behaviour*, 139, 371-391.

Widdig, A., Streich, W. J., Nürnberg, P., Croucher, P., Bercovitch, F. B. & Krawczak, M. 2006. Paternal kin bias in the agonistic interventions of adult female rhesus macaques (*Macaca mulatta*). *Behavioral Ecology and Sociobiology*, 61, 205-214.

Wilkinson, G. S. 1984a. Food sharing in vampire bats. *Scientific American*, 262, 76-82.

Wilkinson, G. S. 1984b. Reciprocal food sharing in the vampire bat. *Nature*, 308, 181-184.

Wilson, E. O. 1975. *Sociobiology - The New Synthesis*. Cambridge: Harvard University Press.

Wittig, R. M. & Boesch, C. 2003. The choice of post-conflict interactions in wild chimpanzees (*Pan troglodytes*). *Behaviour*, 140, 1527-1559.

Worthington Jr, E. L. 2006. *Forgiveness and reconciliation: theory and application*. New York: Brunner-Routledge.

Worthington Jr, E. L. S. M. 2004. Forgiveness is an emotion-focused coping strategy that can reduce health risks and promote health resilience: theory, review, and hypotheses. *Psychology & Health*, 19, 385-405.

Wrangham, R. W. 1974. Artificial feeding of chimpanzees and baboons in their natural habitat. *Animal Behaviour*, 22, 83-93.

Wrangham, R. W. 1980. An ecological model of female-bonded primate groups. *Behaviour*, 75, 262-300.

Wrangham, R. W. 1987. Evolution of social structure. In: *Primate Societies* (Ed. by B. B. Smuts, D. Cheney, R. Seyfarth, R. W. Wrangham & T. T. Struhsaker). Chicago: The University of Chicago Press.

Wrangham, R. W. & Rubenstein, D. I. 1986. Social evolution in birds and mammals. In: *Ecological Aspects of Social Evolution - Birds and Mammals* (Ed. by D. I. Rubenstein & R. W. Wrangham), pp. 452-470. Princeton: Princeton University Press.

Yarn, D. H. 2000. Law, love and reconciliation: Searching for natural conflict resolution in *Homo sapiens*. In: *Natural Conflict Resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 54-70. Berkeley: University of California Press.

Zhang, Y.-w., Morin, P., Ryder, O. & Zhang, Y.-p. 2001. A set of human tri- and tetra-nucleotide microsatellite loci useful for population analyses in gorillas (*Gorilla gorilla gorilla*) and orangutans (*Pongo pygmaeus*). *Conservation Genetics*, 2, 391-395.

List of figures

Figure 1.1 Representation of the current socioecological model on the ecology of social relationships amongst female primates (adapted from Schülke & Ostner 2012; see also Sterck et al. 1997; van Schaik 1989). 8

Figure 2.1 Detailed characteristics of agonistic interactions (see definition in text): intensity of aggression as a proportion of all agonistic interactions (a) and response to aggression as a proportion of all aggressive acts (b) across the two groups combined (median, interquartiles and 1.5 interquartile range, N = 36 females). 31

Figure 2.2 Two of the behavioural parameters indicators of social tolerance in macaques: outcome of approach (a – b) as a proportion of non-agonistic approaches and context of occurrence of silent bared-teeth display (c – d) as a proportion of all occurrences in PB (a and c panels) (N = 15) and R1 (b and d panels) (N = 21) groups (median, interquartiles and 1.5 interquartile range; post-hoc tests after Friedman, * = observed difference > critical difference, ns = observed difference < critical difference). 33

Figure 2.3 Variation of four social parameters according to social style grades, summarized across studies conducted on females under natural conditions. Means of corrected conciliatory tendency (upper left), percentage of agonistic interactions involving bites (upper right) or counter-aggression (lower left) and steepness values (lower right) are represented. The four variables were extracted from published studies or calculated from (un)published data. The dataset includes only studies of adult females, followed as focal individuals, under natural conditions, with or without provisioning. Data points within one grade represent means in different studies and/or different groups of the same or different species, abbreviated next to the data point. Different species have different symbols. Several data points may overlap when means are similar. (References: *M. fuscata* (M.fus, empty square): Furuichi 1983; Hanya et al. 2008; Hill & Okayasu 1995; Koyama 2003; Kutsukake 2000; Majolo et al. 2009c; Mori et al. 1989; Nakamichi 2003; Nakamichi & Shizawa 2003; Oi 1988; Schino & Aureli 2008b; *M. mulatta* (M.mul, full square): Cooper & Bernstein 2008; Sade 1972; *M. assamensis* (M. ass, full circle): Cooper & Bernstein 2008; *M. fascicularis* (M.fas, empty hexagone): Gumert 2000; *M. thibetana* (M.thi, empty circle): Berman et al. 2004; Berman et al. 2008; *M. arctoides* (M.arc, full cross): Estrada et al. 1977; *M. nemestrina* (M.nem, empty triangle): Oi 1990; *M. radiata* (M.rad, full triangle): Cooper et al. 2007;; *M. sylvanus* (M.syl, full diamond): Fa 1985; Kuester & Paul 1996; Patzelt et al. 2009; Thierry & Aureli 2006; Thierry et al. 2008; *M. maurus* (M.mau, empty cross): Matsumura 1996, 1998; *M. nigra* (M.nig, empty diamond): this study, PB and R1 groups separately) 36

Figure 3.1 Restlessness, scratching frequency (number per minute) and secondary aggression frequency (number per hour) a) according to role of focal female in initial aggression, aggressor or recipient, and b) in post-conflict periods (pc) and baseline (median and inter-quartiles, N = 36, see text for test results). 60

Figure 4.1 *Left side*: effects of the interaction between rank difference (Elo difference) and degree of relatedness (DML) on CSI scores. The continuous line represents the estimate as predicted by the GLMM, dashed lines are the associated standard errors. *Right side*: effect of the age difference (close vs. distant) on CSI scores. Dots and bars represent the estimates and standard errors of the GLMM, respectively (N = 315). 83

Figure 4.2 Effects of rank difference (Elo difference, upper left), of degree of relatedness (upper right), of age difference (close vs. distant, lower left) and CSI scores (lower right) on the occurrence of coalitionary support. The continuous line represents the estimate as predicted by the GLMM, the dashed lines are the associated standard errors. For age difference (lower left), dots and bars represent the estimates and standard errors of the GLMM, respectively (N = 315). 84

Figure 5.1 Results from this thesis confirm the link between social styles and variation in behavioural patterns (+: high or present, -: low or absent, arrow: gradient of variation from despotic (grade 1) to tolerant (grade 4); inspired from Thierry 2013) 95

Figure 5.2 An integrative overview of interactions between social styles (as behavioural-syndrome-like clusters of traits) and social and ecological environment (small boxes and connections are redrawn and adapted from Sih et al. 2004b, except for the “social style” box, which replaces a “behavioural syndrome” box; big boxes and their connections are inspired from Thierry 2013) 104

Figure A.1 Diversity and distribution of Sulawesi macaques (from Riley 2010). 141

Figure A.2 Map of the Tangkoko-Batuangus-DuaSaudara Nature Reserves where the Macaca Nigra project is implemented in North Sulawesi, Indonesia, and exemplar picture of two female crested macaques with an newborn infant (credit map: Marcel Quiten). 142

List of tables

Table 1.1 Tentative scaling of macaque social styles (grade 1: despotic, grade 4: tolerant; from Thierry 2007). 15

Table 2.1 Summary of behavioural data in the two study groups 30

Table 2.2 Parameters of hierarchies considering two types of dominance-related interactions: *winner – loser* interactions and *displacement* interactions, as well as *all initiated* aggressive acts (see text for definitions). Number of interactions recorded (N interactions), percentage of unknown relationships (% unknown) and of two-way relationships in the matrices (% two-ways) (see text for definition), steepness values with Dij and Pij indices (all significant) and Directional Consistency Indices (DCI) are also given. 34

Table 2.3 Summary of social variables within grade 4 social style: mean percentages of bite, contact attack, counter-aggression, mean corrected conciliatory tendency (CCT) with contact affiliation and steepness (with D_{ij} indices) in females of different grade 4 macaque species: captive *M. nigra*, captive *M. tonkeana* and captive and provisioned *M. maurus*, as compared to the studied crested macaques (*M. nigra*, wild). Whether data have been published for non-related individuals only (non-kin) or all individuals (all) is indicated in the first line. Steepness was computed regardless of kin relationships (all) 35

Table 3.1 Details of predictions and summary of results on the four potential functions of three post-conflict interactions. 50

Table 3.2 Summary of behavioural variables, their definitions, units and scales 55

Table 4.1 Median and range of number of female partners (kin and strong affiliates) and frequency of interactions between adult females in the two groups (PB = 15 females, R1 = 21 females). Approach frequency from Chapter 2. 81

Table 4.2 Summary of results of GLMMs on the relationships between different individual attributes (model 1) and their influence on frequency of social interactions (models 2 – 5), N = 36. 82

Table B.1 Matrix of displacement interactions in PB group (N = 15 – row = giver, column = receiver) 145

Table B.2 Matrix of winner-loser interactions in PB group (N = 15 – row = giver, column = receiver) 145

Table B.3 Matrix of all initiated aggressions in PB group (N = 15 – row = giver, column = receiver) . 146

Table B.4 Matrix of displacement interactions in R1 group (N = 21 – row = giver, column = receiver) 146

Table B.5 Matrix of winner-loser interactions in R1 group (N = 21 – row = giver, column = receiver) 147

Table B.6 Matrix of all initiated aggressions in R1 group (N = 21 – row = giver, column = receiver) . 148

Table C.1 Lists of Generalised Linear Mixed Models, with number of cases (N), response variable, its state (cat.) and transformation (transf., only given once per variables), main and control fixed effect factors and their levels if categorical, and random effect factors (for abbreviations, see notes). 149

Table C.2 a) Influence of affiliation between opponents, of affiliation with 3rd-parties, of conflict and dyad characteristics on the occurrence of scratching (Model 1a), on restlessness index (Model 1b) and on the occurrence of secondary aggression (Model 1c); b) Differences between PC and baseline levels of opponent affiliation per proximity scans (aff.opp, Model 2a), of opponent presence in proximity (prox.opp, Model 2b), and of frequency of opponent/3rd-party affiliation (aff.3rd, Model 2c). When the full model is not different from the null model, only the estimates and standard errors are given. See Methods for details. 151

Table C.3 a) Influence of conflict and dyadic characteristics on the occurrence of affiliation between opponents (aff.opp., Model 3a) and the occurrence of affiliation with 3rd-party (aff.3rd., Model 3b); b) Influence of dyad characteristics on the dyadic number of reconciled conflicts (Model 4). When the full model is not different from the null model, only the estimates and standard errors are given. See Methods for details.....152

Table D.1 Dyad Maximum Likelihood coefficient between female dyads in PB (N = 105). 153

Table D.2 CSI scores of female dyads in PB (N = 105).....153

Table D.3 Dyad Maximum Likelihood coefficient between female dyads in R1 (N = 210). 154

Table D.4 CSI scores of female dyads in R1 (N = 210).....154

Table D.5 Summary of results of GLMMs on the influence of Elo difference (Elo #), degree of relatedness (DML), age difference (age #) on CSI scores (Model 1) and on the influence of all previous factors plus CSI on support, feeding in proximity and reconciliation (Models 2-4), N = 315. 155

Appendices

Appendix A –
Additional details on the study area and study species

Sulawesi macaques live on the island of Sulawesi in Indonesia (Fooden 1969; Groves 1980). The island is part of the Wallacea region, a hotspot of diversity and endemism (Bynum 1999; Whitten et al. 1987). Seven distinct sympatric species have been recognised (Riley 2010). Sulawesi macaques differ from others in several ways. There is no felid predator on the island and no catarrhine competitors (Riley 2010). Characteristically, males have loud call vocalisations, the function of which is still quite unclear, from intragroup spacing (Riley 2005) to signal of dominance (Neumann et al. 2010).

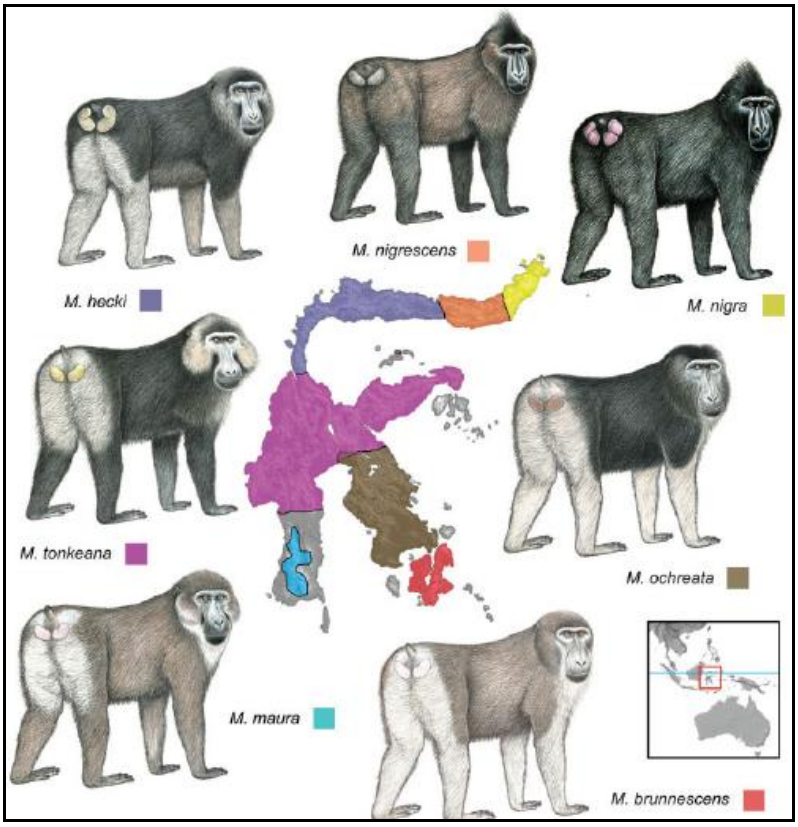

Figure A.1 Diversity and distribution of Sulawesi macaques (from Riley 2010).

Crested macaques, *Macaca nigra*, inhabit the most northern tip of the island of Sulawesi (Fooden 1969; Groves 1980). The study population lives in the Tangkoko-Batuangus Reserve and has been studied intermittently by several research teams in the last 20 years (e.g. Engelhardt &

Perwitasari-Farajallah 2008; Neumann et al. 2010; O'Brien & Kinnaird 1997). This study is part of the Macaca Nigra Project, a long-term field project on the biology and conservation of crested macaques started in 2006.

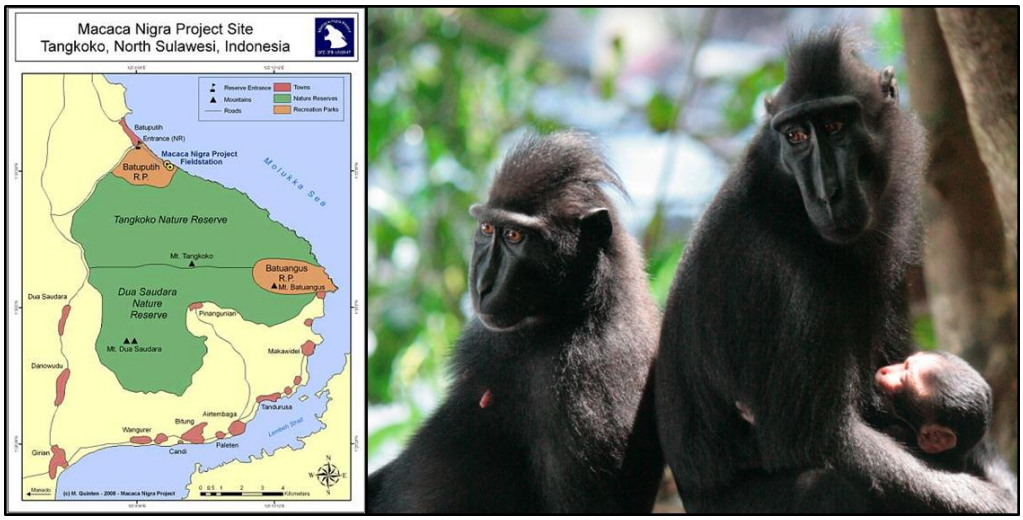

Figure A.2 Map of the Tangkoko-Batuangus-DuaSaudara Nature Reserves where the Macaca Nigra project is implemented in North Sulawesi, Indonesia, and exemplar picture of two female crested macaques with an newborn infant (credit map: Marcel Quiten).

The research area is part of an 8 867-ha nature reserve ranging in elevation from sea level to 1351m. It is a mix of primary and secondary forests, typically classified as lowland rain forest, and old regenerating gardens. Seasonal variation in rainfall is pronounced but temperatures are rather constant throughout the year, ranging between 22 and 34˚C (O'Brien & Kinnaird 1997).

The fur of the crested macaques is entirely black to dark grey, except for the ano-genital region where the skin and the reniform ischial callosities are red to pale beige (Ashmore DeClue 1992; Fooden 1969). They typically bear a crest and prominent cheek bones. Sexual dimorphism is pronounced: males are bigger and heavier than females (Ashmore DeClue 1992; Fooden 1969; Plavcan & van Schaik 1997). Interestingly, males display several secondary sexual characters that make them unique amongst the Sulawesi macaques: in addition of uttering loud calls, they have long and sharp canines and a flashy red scrotum (Ashmore DeClue 1992; Neumann et al. 2010; Plavcan 2001). Females have sexual swellings, i.e. a tumescence of the ano-genital skin around the ischial callosities, and utter copulation calls during mating (Higham et al. 2012). Reproduction occurs all year round, although in the study population, 80% of all births are concentrated within a few months (Engelhardt & Perwitasari-Farajallah 2008). Although both sexes mate promiscuously, the alpha male gets more than half of all mating (study population: 63%, Engelhardt et al. in preparation) and

possibly, sires a good share of all infants. In the study population, the male cohort composition in the group appears dynamic with frequent changes (Neumann et al. 2011) and an average alpha tenure of 10 months (Marty, unpublished data), whereas the female one is stable with changes only due to death or maturation of individuals (Neumann et al. 2011).

Crested macaques are mainly frugivorous but also eat seeds, vegetal parts (leaves, flowers) and invertebrates, and have been observed to predate on small vertebrates opportunistically (O'Brien & Kinnaird 1997; Macaca Nigra Project, unpublished data). *Anacardiacea* (especially *Dracontomelum dao*) and *Moracea* (especially *Ficus sp.*) genera are an especially important part of their fruit diet (Kinnaird et al. 1999; O'Brien & Kinnaird 1997). *Ficus* and *Dracontomelum* trees are often large enough to accommodate a whole group (O'Brien & Kinnaird 1997). Crested macaques' only natural predator is the reticulated python, *Python reticulatus*, which have been seen occasionally eating juveniles and attacking adults (Micheletta et al. 2012; Duboscq & Micheletta, unpublished data; Macaca Nigra Project, personal observation). Population density is quite high in the Tangkoko-Batuangus-DuaSaudara Nature Reserves (Kyes et al. 2013; Palacios et al. 2012); thus the groups' home ranges overlap considerably (e.g. O'Brien & Kinnaird 1997). Intergroup encounters occur throughout the year, with a higher frequency between October and May, corresponding to the wet season (but see Kinnaird & O'Brien 2000 for a different distribution), and can be peaceful as much as aggressive (Duboscq, unpublished data).

Ashmore DeClue, P. C. 1992. Macaques: An adaptive array (a summary and synthesis of the literature on the genus *Macaca* from an ecological perspective). PhD thesis, Washington University.
Bynum, E. L. 1999. Biogeography and evolution of Sulawesi macaques. *Tropical Biodiversity*, 6, 19-36.
Engelhardt, A. & Perwitasari-Farajallah, D. 2008. Reproductive biology of Sulawesi crested black macaques (*Macaca nigra*). *Folia Primatologica*, 79, 326.
Fooden, J. 1969. *Taxonomy and Evolution of the Monkeys of Celebes (Primates: Cercopithecidae)*. Basel: Karger.
Groves, C. P. 1980. Speciation in *Macaca*: the view from Sulawesi. In: *The Macaques: Studies in Ecology, Behavior, and Evolution* (Ed. by D. G. Lindburg). New York: Van Nostrand Reinhold.
Higham, J. P., Heistermann, M., Saggau, C., Agil, M., Perwitasari-Farajallah, D. & Engelhardt, A. 2012. Sexual signalling in female crested macaques and the evolution of primate fertility signals. *BMC Evolutionary Biology*, 12, 22.
Kinnaird, M. F. & O'Brien, T. G. 2000. Comparative movement patterns of two semi-terrestrial cercopithecine primates: the Tana river crested mangabey and the Sulawesi crested black macaque. In: *On the Move: How and why Animals travel in Groups* (Ed. by S. Boinski & P. A. Garber). Chicago: University of Chicago Press.
Kinnaird, M. F., O'Brien, T. G. & Suryadi, S. 1999. The importance of figs to Sulawesi's imperiled wildlife. *Tropical Biodiversity*, 6, 5-18.
Kyes, R. C., Iskandar, E., Onibala, J., Paputungan, U., Laatung, S. & Huettmann, F. 2013. Long-Term Population Survey of the Sulawesi Black Macaques (Macaca nigra) at Tangkoko Nature Reserve, North Sulawesi, Indonesia. *American Journal of Primatology*, 75, 88-94.
Micheletta, J., Waller, B., Panggur, M. R., Neumann, C., Duboscq, J., Agil, M. & Engelhardt, A. 2012. Social bonds affect anti-predator behaviour in a tolerant species of macaques, *Macaca nigra*. *Proceedings of the Royal Society B: Biological Sciences*, 279, 4042-4050.

Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., Widdig, A. & Engelhardt, A. 2011. Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. *Animal Behaviour*, 82, 911-921.

Neumann, C., Assahad, G., Hammerschmidt, K., Perwitasari-Farajallah, D. & Engelhardt, A. 2010. Loud calls in male crested macaques, *Macaca nigra*: a signal of dominance in a tolerant species. *Animal Behaviour*, 79, 187-193.

O'Brien, T. G. & Kinnaird, M. F. 1997. Behavior, diet, and movements of the Sulawesi crested black macaque (*Macaca nigra*). *International Journal of Primatology*, 18, 321-351.

Palacios, J. F. G., Engelhardt, A., Agil, M., Hodges, J. K., Bogia, R. & Walter, M. 2012. Status of, and conservation recommendations for, the critically endangered crested black macaque *Macaca nigra* in Tangkoko, Indonesia. *ORYX*.

Plavcan, J. M. 2001. Sexual dimorphism in primate evolution. *Yearbook of Physical Anthropology*, 44, 25-53.

Plavcan, J. M. & van Schaik, C. P. 1997. Intrasexual competition and body weight dimorphism in anthropoid primates. *American Journal of Physical Anthropology*, 103, 37-68.

Riley, E. P. 2005. The loud call of the Sulawesi Tonkean macaque, *Macaca tonkeana*. *Tropical Biodiversity*, 8, 199-209.

Riley, E. P. 2010. The endemic seven: four decades of research on the Sulawesi macaques. *Evolutionary Anthropology*, 19, 22-36.

Whitten, A. J., Mustafa, M. & Henderson, G. S. 1987. *The Ecology of Sulawesi*: Gadjah Mada University Press.

Appendix B –
Supplementary material to Chapter 2

Table B.1 Matrix of displacement interactions in PB group (N = 15 – row = giver, column = receiver)

g/r	ap	bp	cp	dp	ep	fp	gp	hp	ip	jp	lp	np	rp	sp	yp
ap	0	0	1	0	0	1	0	0	0	0	0	1	3	0	3
bp	6	0	8	7	5	4	0	2	0	10	3	3	1	4	1
cp	2	0	0	4	1	2	0	0	0	0	0	3	6	0	4
dp	0	0	0	0	0	0	0	0	1	0	0	8	2	0	4
ep	4	1	1	4	0	1	0	0	0	1	0	5	4	0	0
fp	4	0	5	8	2	0	0	0	0	0	0	8	4	0	2
gp	2	1	1	1	4	0	0	1	4	4	0	2	2	3	1
hp	5	2	4	5	4	3	0	0	8	6	2	7	6	8	7
ip	2	10	0	5	10	9	0	2	0	12	0	8	5	15	3
jp	7	1	6	8	9	5	1	0	0	0	2	4	5	1	3
lp	3	10	9	7	2	6	3	7	11	7	0	17	5	20	5
np	1	0	0	0	0	0	0	0	0	0	0	0	4	0	5
rp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
sp	3	6	8	6	7	5	0	0	0	5	3	4	2	0	4
yp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table B.2 Matrix of winner-loser interactions in PB group (N = 15 – row = giver, column = receiver)

g/r	ap	bp	cp	dp	ep	fp	gp	hp	ip	jp	lp	np	rp	sp	yp
ap	0	0	0	1	0	0	0	0	1	0	0	1	1	0	1
bp	3	0	1	0	0	1	0	0	0	3	0	2	0	0	0
cp	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
dp	0	0	0	0	0	0	0	0	0	0	0	3	2	0	1
ep	1	0	1	2	0	0	0	0	0	0	0	0	1	0	1
fp	1	0	0	1	0	0	0	0	0	0	0	3	2	0	0
gp	0	0	3	3	3	3	0	1	3	3	0	0	0	0	1
hp	1	2	4	2	4	0	0	0	2	3	0	2	2	4	3
ip	2	1	2	4	0	0	0	0	0	3	0	5	0	5	3
jp	1	0	3	1	3	1	0	0	0	0	0	1	2	0	3
lp	1	3	1	3	0	5	2	3	12	6	0	2	3	6	0
np	0	0	0	0	0	0	0	0	0	0	0	0	3	0	3
rp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7
sp	0	5	1	1	1	3	0	0	0	5	1	4	0	0	1
yp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table B.3 Matrix of all initiated aggressions in PB group (N = 15 – row = giver, column = receiver)

g/r	ap	bp	cp	dp	ep	fp	gp	hp	ip	jp	lp	np	rp	sp	yp
ap	0	0	0	1	2	2	0	1	0	0	0	1	3	1	3
bp	3	0	2	0	0	1	0	3	4	2	2	2	0	0	0
cp	0	1	0	1	0	1	0	2	0	0	0	0	0	1	3
dp	0	2	4	0	1	0	0	3	2	2	2	4	2	2	1
ep	1	2	2	3	0	0	2	5	7	1	10	0	1	1	1
fp	1	2	1	3	0	0	0	1	1	0	1	6	2	0	1
gp	0	1	3	4	4	2	0	1	3	8	0	0	2	0	1
hp	1	1	4	2	4	0	0	0	4	6	0	2	2	6	2
ip	5	2	2	3	1	2	0	1	0	2	1	5	0	6	3
jp	1	7	3	2	5	1	1	1	12	0	6	3	2	4	4
lp	1	5	2	3	1	6	2	5	13	7	0	2	4	7	0
np	0	1	1	0	0	0	0	2	2	0	0	0	7	1	4
rp	0	0	0	0	0	0	0	0	0	0	0	0	0	1	8
sp	2	6	4	5	1	5	1	4	7	7	3	4	1	0	1
yp	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0

Table B.4 Matrix of displacement interactions in R1 group (N = 21 – row = giver, column = receiver)

g/r	as	bs	cs	ds	es	gs	hs	is	js	ks	ms	ns	os	ps	qs	rs	ss	ts	us	xs	ys
as	0	0	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
bs	5	0	0	2	3	1	0	0	1	3	0	0	0	7	0	0	2	0	3	0	7
cs	1	5	0	4	0	2	1	7	0	2	22	0	1	1	2	0	0	2	4	2	3
ds	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
es	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1
gs	1	3	0	3	1	0	2	0	0	3	0	0	0	4	0	0	0	0	3	0	2
hs	2	5	0	2	3	5	0	0	3	2	4	0	0	1	0	0	1	1	4	1	5
is	1	1	1	3	2	0	3	0	1	3	5	0	0	1	0	0	0	0	4	5	3
js	2	2	0	4	2	4	0	0	0	2	0	0	0	3	0	0	1	0	3	0	3
ks	3	0	0	5	4	0	0	0	0	0	0	0	0	6	0	0	0	1	2	1	0
ms	1	5	1	5	3	1	0	0	5	3	0	0	0	3	0	0	0	7	2	1	2
ns	5	7	17	11	0	13	17	11	7	6	32	0	3	2	13	9	2	9	9	5	10
os	0	2	4	2	3	1	2	3	2	2	2	0	0	5	2	0	0	4	0	1	1
ps	4	0	1	5	3	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
qs	3	9	4	8	0	4	4	4	4	1	13	0	0	1	0	0	3	5	7	4	7
rs	1	1	7	3	0	1	1	0	1	0	2	0	1	2	2	0	0	1	5	1	1
ss	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
ts	2	1	1	5	1	0	0	0	3	3	0	0	0	0	0	0	1	0	4	0	2
us	5	0	0	5	1	0	0	0	0	4	0	0	0	3	0	0	0	0	0	0	5
xs	2	2	0	2	1	2	1	0	1	3	0	0	0	1	0	0	3	1	7	0	6
ys	1	1	0	2	3	0	0	0	1	0	1	0	0	2	0	0	1	0	0	0	0

Table B.5 Matrix of winner-loser interactions in R1 group (N = 21 – row = giver, column = receiver)

g/r	as	bs	cs	ds	es	gs	hs	is	js	ks	ms	ns	os	ps	qs	rs	ss	ts	us	xs	ys
as	0	0	0	2	3	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
bs	2	0	0	1	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	1
cs	1	0	0	0	0	1	1	1	0	0	1	0	0	0	2	1	0	2	1	0	1
ds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
es	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
gs	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	5	0	3
hs	1	1	0	5	1	2	0	0	0	0	9	0	0	1	0	0	1	2	3	2	2
is	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	3	0
js	5	0	0	0	3	3	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0
ks	2	0	0	4	1	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	1
ms	5	0	0	5	0	0	2	0	0	2	0	0	0	1	0	0	1	4	2	2	0
ns	2	0	2	0	0	0	1	0	1	4	0	0	2	1	3	2	0	4	1	1	1
os	1	2	2	2	0	2	3	4	0	1	2	0	0	2	0	0	0	2	2	2	1
ps	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0
qs	9	1	0	4	0	1	2	3	0	4	2	0	0	2	0	0	0	1	2	0	2
rs	2	3	0	2	0	0	1	1	3	0	1	0	0	0	1	0	1	1	0	0	0
ss	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ts	3	0	0	1	1	0	0	0	1	2	0	0	1	2	0	0	1	0	0	0	0
us	2	0	0	5	0	0	1	0	0	4	0	0	0	3	0	0	1	0	0	0	3
xs	1	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	0	1	0	1
ys	2	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0

Table B.6 Matrix of all initiated aggressions in R1 group (N = 21 – row = giver, column = receiver)

g/r	as	bs	cs	ds	es	gs	hs	is	js	ks	ms	ns	os	ps	qs	rs	ss	ts	us	xs	ys
as	0	0	1	2	4	0	2	2	0	0	1	0	0	0	2	0	0	0	0	0	0
bs	6	0	0	1	3	0	0	0	0	2	0	0	0	5	0	0	0	1	1	0	3
cs	3	1	0	1	0	2	3	1	1	0	7	2	0	1	1	1	0	2	1	0	1
ds	0	0	2	0	1	1	4	2	0	0	7	0	0	1	1	0	0	1	0	1	0
es	0	0	0	0	0	0	1	0	0	1	0	0	1	1	1	0	1	0	0	0	1
gs	1	0	1	0	1	0	2	1	0	8	0	0	0	3	0	0	0	0	7	2	2
hs	4	3	7	4	0	3	0	2	1	1	9	7	1	1	5	1	1	1	2	1	2
is	2	0	0	0	1	1	2	0	3	0	0	2	0	2	0	3	0	1	0	5	0
js	6	0	13	2	4	2	8	8	0	5	14	5	4	1	9	1	0	1	1	0	1
ks	4	0	6	6	3	2	0	0	0	0	3	1	1	2	3	0	1	2	2	0	2
ms	18	0	20	7	1	0	7	0	4	3	0	4	2	2	3	1	1	8	6	2	0
ns	2	1	3	2	0	0	0	1	2	4	3	0	3	2	3	3	0	4	3	3	1
os	1	2	3	1	1	2	5	4	0	1	4	0	0	2	4	0	0	2	3	3	1
ps	2	0	1	3	1	0	0	0	0	0	3	0	0	0	0	0	4	0	0	0	0
qs	10	1	1	5	1	1	2	3	1	3	3	1	1	2	0	0	1	3	2	1	3
rs	2	2	1	1	1	0	4	0	3	2	3	1	1	0	1	0	2	1	0	0	1
ss	1	0	0	3	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
ts	4	0	0	1	0	0	1	0	2	1	0	0	2	5	0	1	1	0	0	0	1
us	6	0	4	9	3	0	8	1	2	4	5	0	0	3	1	1	1	0	0	1	2
xs	3	0	0	2	4	2	0	0	2	3	0	0	0	3	0	0	1	0	2	0	2
ys	4	0	1	5	2	0	1	3	0	0	12	1	0	3	1	0	1	2	0	0	0

Appendix C –
Supplementary material to Chapter 3

C.1 Methods: model presentation

Table C.1 Lists of Generalised Linear Mixed Models, with number of cases (N), response variable, its state (cat.) and transformation (transf., only given once per variables), main and control fixed effect factors and their levels if categorical, and random effect factors (for abbreviations, see notes).

	N	responses	cat. (transf.)	main fixed factors (transf.)	control fixed factors	random factors
Model 1:						
1a	450	occurrence scratching	bin.	affiliation opponents: yes/no	focal recipient: y/n	aggressor recipient group
1b	424	restlessness	cont.	affiliation 3rd party: yes/no		
1c	450	occurrence aggression	bin.	CSI (4^{th} root) |Elo difference| (sqrt) sign Elo difference: +/- affiliation symmetry CV (4^{th} root) aggression (4^{th} root) counter-aggression (4^{th} root) support (4^{th} root) aggression duration (log) intensity: display/contact decided: yes/no polyadic: yes/no context: social/food redirection: yes/no [a,b] renewed: yes/no		
Model 2:						
2a	210	affiliation opponent	cont./ sqrt			
2b	210	proximity opponent	cont./ log	session: PC / baseline	focal recipient: yes/no	focal group
2c	283	affiliation opponent/3rd-party	cont./ log			
Model 3:						
3a	450	occurrence affiliation opponent	bin.	[a,b] affiliation 3rd party: yes/no [c] affiliation opponent : yes/no	focal recipient: yes/no	aggressor recipient group
3b	450	occurrence affiliation opponent / 3rd-party	bin.	CSI		

			|Elo difference| sign Elo difference: +/- affiliation symmetry CV aggression counter-aggression support aggression duration intensity: display/contact decided: yes/no polyadic: yes/no context: social/food redirection: yes/no [c] renewed: yes/no		
Model 4					
270	number conflicts with affiliation opponent	count	|Elo difference| CSI affiliation symmetry CV aggression counter-aggression support	offset term: nb aggression per dyad	member 1 member 2 group

notes: cat. = category (cont. = continuous, bin. = binomial, count = count), tranf. = transformation (sqrt = square root, log = log), aff. opp. = affiliation between opponent, aff. 3rd = affiliation between opponent and 3rd-party, CSI, ASI & CV = see Methods, agg. = aggressor, rec. = recipient, mb = member, nb = number, letters in superscript refer to model in the same category in which the superscripted variable is included (for example, Model 3a, 3b or 3c).

C.2 Tables of results

Table C.2 a) Influence of affiliation between opponents, of affiliation with 3rd-parties, of conflict and dyad characteristics on the occurrence of scratching (Model 1a), on restlessness index (Model 1b) and on the occurrence of secondary aggression (Model 1c); b) Differences between PC and baseline levels of opponent affiliation per proximity scans (aff.opp, Model 2a), of opponent presence in proximity (prox.opp, Model 2b), and of frequency of opponent/3rd-party affiliation (aff.3rd, Model 2c). When the full model is not different from the null model, only the estimates and standard errors are given. See Methods for details.

a)		Model 1a: scratching			Model 1b: restlessness			Model 1c: secondary aggression	
	LRT test full vs null	χ^2 = 29, d.f. = 17, P = 0.034			χ^2 = 382, d.f. = 17, P < 0.001			χ^2 = 13, d.f. = 16, P = 0.685	
factors	variables	β	SE	p	β	SE	p_{MCMC}	β	SE
fixed	intercept	-0.943	0.569	0.098	0.013	0.265	0.943	-1.104	0.565
	aff. opp (y)	-0.384	0.289	0.183	0.079	0.136	0.606	-0.241	0.301
	aff. 3rd (y)	-0.530	0.268	0.048	-0.195	0.127	0.127	0.531	0.283
	CSI	-0.059	0.163	0.717	0.159	0.084	0.116	0.097	0.168
	|Elo difference|	0.119	0.144	0.407	0.078	0.067	0.278	-0.056	0.147
	sign Elo (+)	0.381	0.351	0.278	0.287	0.165	0.096	0.154	0.354
	ASI	-0.006	0.136	0.963	-0.047	0.066	0.569	0.058	0.137
	CV	-0.027	0.144	0.851	-0.078	0.071	0.220	0.087	0.146
	aggression	-0.014	0.135	0.917	-0.076	0.067	0.395	-0.012	0.140
	counter-aggression	-0.061	0.136	0.656	0.012	0.062	0.773	0.001	0.135
	support	0.010	0.151	0.948	-0.053	0.068	0.357	-0.113	0.156
	context (social)	0.216	0.352	0.506	-0.157	0.148	0.269	0.534	0.337
	intensity (n)	1.044	0.395	0.008	0.172	0.169	0.376	-0.266	0.369
	decided (y)	0.169	0.252	0.603	-0.315	0.151	0.047	0.139	0.330
	polyadic (y)	-0.002	0.310	0.996	0.132	0.149	0.401	-0.096	0.321
	duration	0.061	0.129	0.635	-0.064	0.061	0.295	-0.027	0.134
	redirection (y)	0.059	0.385	0.878	0.159	0.180	0.369	-0.819	0.432
	secondary aggression (y)	-0.248	0.254	0.329	-0.029	0.119	0.787		
control	focal (recipient)	0.041	0.243	0.866	-0.047	0.114	0.689	-0.105	0.667
random	agg./group	0.000	0.000		0.028	0.168		0.013	0.106
	rec./group	0.001	0.013		0.000	0.000		0.000	0.000

b)		Model 2a: aff.opp			Model 2b: prox.opp			Model 2c: aff. 3rd		
	LRT test full vs null	χ^2 = 124, df = 1,p < 0.001			χ^2 = 474, df = 1,p < 0.001			χ^2 = 124, df = 1,p < 0.001		
factors	variables	β	SE	p_{MCMC}	β	SE	p_{MCMC}	β	SE	p_{MCMC}
fixed	intercept	0.502	0.019	0.001	-0.403	0.009	0.001	2.367	0.047	0.001
	session (PC)	0.241	0.020	0.001	0.450	0.010	0.001	0.479	0.040	0.001
control	focal (recipient)	0.024	0.021	0.252	-0.017	0.011	0.133	-0.007	0.043	0.898
random	focal/group	0.001	0.024		0.000	0.000		0.029	0.170	

Table C.3 a) Influence of conflict and dyadic characteristics on the occurrence of affiliation between opponents (aff.opp., Model 3a) and the occurrence of affiliation with 3rd-party (aff.3rd., Model 3b); b) Influence of dyad characteristics on the dyadic number of reconciled conflicts (Model 4). When the full model is not different from the null model, only the estimates and standard errors are given. See Methods for details.

a)		Model 3a: aff. opp.			Model 3b: aff. 3rd		
	full vs null LRT test	χ^2 = 110, df = 16, p < 0.001			χ^2 = 55, df = 16, p < 0.001		
factors	variables	β	SE	p	β	SE	p
fixed	intercept	0.686	0.619	0.268	-0.471	0.584	0.420
	aff. opp (y)				0.595	0.311	0.056
	aff. 3rd (y)	0.557	0.313	0.076			
	CSI	0.253	0.193	0.190	0.086	0.182	0.637
	|Elo difference|	-0.277	0.179	0.122	-0.130	0.155	0.404
	Elo sign (+)	-0.814	0.432	0.061	-0.257	0.390	0.510
	ASI	0.352	0.166	0.033	0.135	0.152	0.375
	CV	-0.093	0.178	0.599	-0.206	0.156	0.189
	aggression	-0.015	0.162	0.926	0.150	0.149	0.314
	counter-aggression	-0.458	0.166	0.006	0.249	0.162	0.125
	support	0.011	0.182	0.951	-0.028	0.164	0.863
	context (social)	1.413	0.381	0.001	1.075	0.325	0.001
	intensity (n)	-0.484	0.420	0.249	-0.029	0.404	0.943
	decided (y)	-1.518	0.358	0.001	-0.136	0.355	0.702
	poly (y)	0.045	0.361	0.901	0.113	0.339	0.740
	duration	-0.304	0.153	0.047	0.139	0.144	0.334
	redirection (y)	-1.102	0.458	0.016	0.838	0.433	0.054
	secondary aggression (y)	-0.264	0.302	0.383	0.518	0.279	0.095
control	focal (recipient)	0.066	0.288	0.818	-0.059	0.263	0.821
random	agg./group	0.000	0.000		0.000	0.000	
	rec./group	0.016	0.125		0.000	0.000	

b)		Model 4		
	full vs null LRT test	χ^2 = 94, df = 7, p < 0.001		
factors	variables	β	SE	p
fixed	intercept	0. 562	0. 092	0.001
	CSI	0. 054	0.071	0.442
	|Elo difference|	-0.123	0.071	0.084
	CV	-0.169	0.073	0.020
	ASI	0.197	0.058	0.001
	aggression	-0.505	0.052	0.001
	counter-aggression	0.012	0.061	0.841
	support	0.114	0.077	0.135
random	dyad mb 1/ group	0.017	0.131	
	dyad mb 2/ group	0.033	0.182	

Appendix D –
Supplementary material to Chapter 4

Table D.1 Dyad Maximum Likelihood coefficient between female dyads in PB (N = 105).

	ap	bp	cp	dp	ep	fp	hp	ip	jp	lp	np	op	rp	sp	yp
ap		0.3	0.5	0.08	0	0.08	0	0.07	0	0	0	0	0	0.05	0
bp			0.11	0.07	0.14	0.27	0	0.11	0.06	0	0	0.07	0.06	0.5	0
cp				0.09	0	0	0.13	0	0	0	0.16	0.07	0	0	0
dp					0.1	0.14	0.11	0	0	0	0.41	0.5	0.02	0	0.01
ep						0.53	0	0.12	0.09	0	0.08	0	0	0.09	0.34
fp							0	0.14	0.12	0	0.06	0	0.03	0.29	0.2
hp								0	0	0	0	0	0	0	0.12
ip									0.34	0.31	0.01	0.09	0.06	0.32	0.34
jp										0.36	0	0	0.14	0.5	0.22
lp											0.03	0	0.41	0.06	0.1
np												0.05	0.25	0	0.05
op													0.24	0.12	0.03
rp														0	0
sp															0.22
yp															

Table D.2 CSI scores of female dyads in PB (N = 105)

	ap	bp	cp	dp	ep	fp	gp	hp	ip	jp	lp	np	rp	sp	yp
ap		0.96	5.32	0.52	0.86	1.06	0.58	1.27	1.09	1.04	1.05	0.60	0.75	0.89	0.37
bp			0.59	0.97	0.69	0.71	0.51	0.89	0.74	1.64	0.72	0.96	0.81	2.00	0.44
cp				1.37	1.21	0.89	0.65	1.10	1.10	1.54	1.03	0.92	1.32	0.88	0.87
dp					1.91	1.28	0.4	0.98	0.54	1.11	1.63	2.27	0.57	0.92	0.74
ep						0.91	0.52	1.19	0.61	2.00	0.83	1.33	0.95	0.97	0.61
fp							0.62	0.49	0.65	1.49	0.66	0.66	0.81	0.96	0.50
gp								1.23	0.93	0.67	0.85	0.49	0.56	0.78	0.24
hp									0.82	0.67	1.95	0.80	1.05	0.95	0.57
ip										1.20	1.16	0.74	0.49	0.97	0.44
jp											1.37	1.19	0.72	1.65	1.03
lp												1.23	0.43	0.72	0.59
np													2.60	1.27	0.95
rp														1.39	0.86
sp															0.76
yp															

Table D.3 Dyad Maximum Likelihood coefficient between female dyads in R1 (N = 210).

	as	bs	cs	ds	es	gs	hs	is	js	ks	ms	ns	os	ps	qs	rs	ss	ts	us	xs	ys
as		0.08	0	0.5	0.18	0.23	0	0.2	0	0.34	0	0	0.21	0.5	0.5	0.02	0.3	0.01	0.65	0.02	0.11
bs			0	0.07	0.08	0.5	0	0.32	0.53	0.23	0.03	0	0	0	0	0	0.07	0.45	0.25	0.08	0
cs				0	0.06	0.2	0	0.09	0.02	0	0	0	0.38	0.12	0.07	0	0.24	0	0.07	0	0.23
ds					0.01	0.19	0.01	0.13	0.23	0.02	0.25	0.1	0.25	0	0.22	0.01	0.24	0.2	0.18	0.1	0
es						0.09	0	0.04	0.12	0	0.07	0	0.14	0.19	0.05	0	0	0.37	0.5	0.37	0.08
gs							0	0.09	0.35	0	0.05	0	0.23	0	0.08	0	0.3	0.17	0.52	0.02	0
hs								0.06	0	0	0.03	0.36	0	0.06	0	0.48	0	0.2	0	0	0
is									0.17	0.14	0.17	0	0	0	0.04	0	0.18	0.07	0.14	0.01	0
js										0	0.05	0	0.14	0	0	0	0	0.3	0.15	0.35	0
ks											0	0	0	0.05	0.34	0.01	0.32	0.03	0.38	0	0
ms												0	0.13	0	0.04	0	0.18	0	0	0	0.5
ns													0	0.01	0	0.17	0.1	0	0	0.09	0
os														0.27	0	0	0.51	0	0.5	0	0.25
ps															0.5	0	0	0.13	0	0	0.19
qs																0	0.34	0.06	0.29	0	0.18
rs																	0	0	0	0.07	0
ss																		0	0.5	0	0.5
ts																			0.24	0.51	0
us																				0.07	0
xs																					0
ys																					

Table D.4 CSI scores of female dyads in R1 (N = 210)

	as	bs	cs	ds	es	gs	hs	is	js	ks	ms	ns	os	ps	qs	rs	ss	ts	us	xs	ys
as		0.8	1.5	2.5	0.2	1.8	1.3	0.6	3.2	1.4	1.3	0.6	1.4	0.8	1.2	0.7	0.5	0.9	1.3	0.8	1.5
bs			0.5	0.8	0.5	3.4	0.4	0.6	2.2	1.3	0.5	0.7	0.4	0.3	0.8	0.3	0.9	0.8	0.7	1.7	0.9
cs				1.3	0.2	0.8	0.7	1.3	0.7	0.5	1.5	1.6	0.9	1	1.2	0.4	0.6	0.5	0.9	0.4	1.1
ds					0.6	1.3	1.1	1.5	1.8	1.2	1.2	0.8	0.8	0.9	0.8	0.5	0.4	0.8	1	0.7	2.1
es						1.4	0.3	1.3	0.2	0.2	0.4	0.3	0.4	0.1	0.2	0.2	0.4	0.3	0.9	0.2	0.3
gs							0.7	0.9	2.4	1.6	0.5	0.8	1	1	0.5	0.6	1.2	1.7	1.4	1.6	1.3
hs								0.6	1.4	0.9	2.3	1.3	0.9	1	1.1	0.7	0.6	1.3	1.2	0.5	0.8
is									1.3	0.9	1.2	1.5	1.6	0.7	0.9	0.6	1.1	0.4	1.4	0.9	1
js										1.9	1.4	0.8	1.7	0.7	0.9	0.5	0.7	1.3	1.1	1.1	1.4
ks											1.1	0.7	1.2	1.2	1.1	1	1	1.6	1.1	0.4	0.7
ms												2.5	2	0.8	1.6	1.1	0.6	1.2	1.3	0.4	0.9
ns													1.7	0.6	1.2	2.3	0.5	0.6	0.9	0.5	0.7
os														0.7	1.6	2.7	0.4	1	1.3	0.6	1
ps															0.6	0.4	2.5	0.5	0.9	0.3	1.8
qs																0.6	0.7	0.9	0.6	0.3	0.9
rs																	0.5	0.5	0.9	0.3	0.7
ss																		0.9	0.5	1.3	3.3
ts																			0.8	0.9	1.2
us																				0.5	1.8
xs																					1.1
ys																					

Table D.5 Summary of results of GLMMs on the influence of Elo difference (Elo Δ), degree of relatedness (DML), age difference (age Δ) on CSI scores (Model 1) and on the influence of all previous factors plus CSI on support, feeding in proximity and reconciliation (Models 2-4), N = 315.

1/ CSI					2/ support			
red. vs. full	χ^2 = 3.737, d.f. = 1, P = 0.053				red. vs full	χ^2 = 0.612, d.f. = 1, P = 0.434		
null vs. full	χ^2 = 40.955, d.f. = 4, P < 0.001				null vs red.	χ^2 = 14.765, d.f. = 4, P = 0.005		
main	β	SE	t value	$p_{(mcmc)}$	β	SE	z value	p
Intercept	0.093	0.106	0.875	0.580	-1.088	0.437	-2.486	0.013
Elo **Δ**	-0.308	0.056	-5.496	0.001	-0.361	0.153	-2.392	0.017
DML	0.070	0.053	1.32	0.212	-0.131	0.139	-0.947	0.344
age **Δ** (distant)	-0.175	0.112	-1.554	0.095	0.858	0.304	2.824	0.005
Elo **Δ** : DML	-0.103	0.053	-1.942	0.048				
CSI					0.125	0.149	0.835	0.406
3/ reconciliation					4/ feeding in proximity			
red. vs full	χ^2 = 6.958, d.f. = 4, P = 0.138				red. vs full	χ^2 = 7.312, d.f. = 1, P = 0.006		
null vs red.	χ^2 = 3.455, d.f. = 5, P = 0.485				null vs full	χ^2 = 9.061, d.f. = 5, P = 0.107		
main	β	SE	t value	$p_{(mcmc)}$	β	SE	t value	$p_{(mcmc)}$
Intercept	0.043	0.161	0.268	0.953	-0.033	0.137	-0.246	0.938
Elo **Δ**	-0.114	0.093	-1.223	0.212	0.004	0.063	0.067	0.930
DML	0.002	0.085	0.029	0.971	0.055	0.057	0.961	0.343
age **Δ** (distant)	-0.051	0.181	-1.280	0.908	0.128	0.123	1.046	0.330
CSI	0.075	0.092	0.823	0.346	0.101	0.069	1.451	0.145
approaches proximity					-0.010	0.071	-0.153	0.806
Elo **Δ** : DML					0.140	0.058	2.413	0.014

Curriculum vitae

Julie Duboscq
Born 30th of May 1981 in Flers, France
French nationality

Education

Current	**Doctoral degree** in Natural Sciences – University of Göttingen & University of Strasbourg Doctoral thesis "Social tolerance: novel insights from wild female crested macaques, *Macaca nigra*" – German Primate Centre & CNRS-IPHC
2005	**Master's degree** in Biology and Psychology – University of Tours & Rennes II Master's thesis "Early vocal recognition between ewes and new-born lambs in domestic sheep, *Ovis aries*" - INRA-CNRS.
2003	**Bachelor's degree** in Organismal Biology –University of Nantes Bachelor's practical "Social and environmental enrichment of the enclosure of a group of Diana monkeys, *Cercopithecus diana roloway*" - Doué-la-Fontaine zoological park.
1999	**A level** (baccalaureat) in Sciences, option Biology

Work / Field experience

2012	**Genetic analyses for doctoral thesis**. • mtDNA and microsatellite specific analyses from DNA extracted from faecal samples supervisor: Antje Engelhardt & Christian Roos, DPZ.
2008-2010	**Field work for doctoral thesis.** • behavioural data & faecal sample collection • team & project management supervisor: Antje Engelhardt, DPZ.
2007	**Camp manager and research coordinator** for the Macaca Nigra Project. • daily cores, budget & team management, discussions with Indonesian authorities, • supervision of data and faecal sample collection, preliminary analyses

2006-2007 **Field assistant** for the Macaca Nigra Project.

- behavioural data & faecal sample collections, vocalisation recordings, play-back experiments

supervisor: Antje Engelhardt, DPZ.

2005-2006 **Research assistant** for a PhD project on collective moves in two species of macaques, *Macaca tonkeana* and *M. mulatta*.

- behavioural data video recording and coding.

supervisor: Odile Petit & Cedric Sueur, CNRS-IPHC- University of Strasbourg.

2004-2005 **Data collection and analysis for MSc thesis**

- play-back experiments, vocalisation recording and manipulating, behavioural data video recording and coding.

supervisor: Pascal Poindron & Frederic Sebe, INRA-CNRS-Tours University.

2003 **Data collection and analysis for BSs practical**

- behavioural data collection, design and set-up of enrichment

supervisor: Brice Lefaux, Doué-la-Fontaine zoological park.

Skills

Language: French (native), English (fluent), German (intermediate), Indonesian (basic), Italian (basic).
IT: MS Office, R, relatedness analysis software (Peakscanner, Coancestry).
Lab: DNA extraction, PCR, sequencing, genotyping.
Others: project and budget management.

Grants

2009	PhD funding: Volkswagen Stiftung "Evolutionary Biology" Initiative	148 000€
2008	field funding: Primate Conservation Incorporated	2 400$

Teaching & Seminars

2011-2012 2 practical Bachelor projects: data processing, behavioural analysis, scientific methods (design, collection, analyses, writing).

2010-2012 Member of the DPZ colloquium committee: invitation of guest speakers, organisation of colloquia & lab visits.

2011 Organisation of the 2nd PhD workshop of the Courant Research Centre for the Evolution of Social Behaviour.

2010 Environmental and conservation education seminars in primary schools in Indonesia.

2008-2009 Field assistant training in behavioural observation and data collection.

Ad-hoc reviewer

Behavioral Ecology and Sociobiology, Behavioural Processes, Integrative Zoology, Peerage of Science

Publications

Duboscq J., Agil M., Engelhardt A., Thierry B. The function of post-conflict interactions: novel insights from a tolerant species of primate. Accpeted, Animal Behaviour.

Duboscq J., Micheletta J., Agil M., Hodges J. K., Thierry B., Engelhardt A. (2013). Social tolerance in wild female crested macaques, *Macaca nigra*, in Tangkoko-Batuangus Nature Reserve, Sulawesi, Indonesia. *American Journal of Primatology*, 75: 361-375, doi: 10.1002/ajp.22114.

Micheletta J., Waller B.M., Panggur M.R., Neumann C**., Duboscq J**., Agil M., Engelhardt A. (2012). Social bonds affect anti-predator behaviour in a tolerant species of macaques, *Macaca nigra*. *Proceedings of the Royal Society B: Biological Sciences*, 279: 4042-4050, doi: 10.1098/rspb.2012.1470.

Neumann C., **Duboscq J.** , Dubuc C., Ginting A., Irwan A. M., Agil M., Widdig A., Engelhardt A. (2011). Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo rating. *Animal Behaviour*, 82: 911-921, doi: 10.1016/j.anbehav.2011.07.016.

Sebe F., **Duboscq J**., Aubin T., Ligout S., Poindron P. (2010). Early vocal recognition of mother by lambs: contribution of low- and high-frequency vocalizations, *Animal Behaviour*, 79: 1055-1066, doi: 10.1016/j.anbehav.2010.01.021.

Duboscq J., Neumann C., Perwitasari-Farajallah D., Engelhardt A., 2008. Daytime birth of a baby crested black macaque (*Macaca nigra*) in the wild. *Behavioural Processes*, 79: 81–84, doi: 10.1016/j.beproc.2008.04.010.

Conference contributions

Duboscq J., Thierry B., Engelhardt A. More valuable and more secure dyads form stronger bonds in wild female crested macaques, *Macaca nigra*. (Poster at the 13th meeting of the German Primatological Society, Hamburg, Germany, 2012)

Duboscq J., Engelhardt A., Thierry B. Social trait covariation in macaques: a within-species perspective. (Talk at 105th meeting of the German Zoological Society, Constance, Germany, 2012)

Duboscq J., Agil M., Engelhardt A., Thierry B. Costs of aggression and reconciliation in wild female crested macaques. (Talk at the 10th graduate student meeting of the Animal Behaviour Section, German Zoological Society, Göttingen, Germany, 2012).

Duboscq J., Engelhardt A., Thierry B. Social trait covariation in macaques: a within-species perspective. (Talk at Evolution, 1st joint congress of Evolutionary Biology, Ottawa, Canada, 2012)

Duboscq, J. Tolerant social style in macaques: parameters and influential factors in a wild population of female crested macaques, *Macaca nigra*. (Talk at the 3rd Status Symposium of the Volkswagen Foundation in Evolutionary Biology, Sylt, Germany, 2011)

Duboscq J., Perwitasari-Farahjallah D., Agil M., Engelhardt A., Thierry B. Post-conflict affiliations in wild female crested macaques, *Macaca nigra*. (Talk at the 4th meeting of the European Federation of Primatology, Almada, Portugal, 2011).

Duboscq J., Perwitasari-Farahjallah D., Agil M., Thierry B., Hodges K., Engelhardt A. Dominance and social relationships in females of a tolerant macaque species, *Macaca nigra.* (Talk at the XXIIIrd congress of the International Primatological Society, Kyoto, Japan, 2010)

Duboscq J., Sebe F., Levy F., Poindron P. Mechanisms of vocal recognition between ewes and new-born lambs in domestic sheep, *Ovis aries*. (Talk at the annual meeting of the French Society for the Study of Animal Behaviour, Boult-aux-Bois, France, 2006).

UNIVERSITÉ DE STRASBOURG

Julie Duboscq

Nouvelles perspectives sur la tolérance sociale à travers l'étude des femelles macaques à crête, *Macaca nigra*, dans leur milieu naturel.

Résumé

La socialité diverse des femelles primates reflète une combinaison de stratégies compétitives et coopératives. Différentes théories expliquent cette diversité. Les macaques sont un bon exemple de variation sociale. L'objectif de ma thèse est d'approfondir la connaissance des sociétés de macaques par l'étude d'une espèce peu connue, les macaques à crête, Macaca nigra, dans son milieu naturel, la réserve de Tangkoko à Sulawesi, Indonésie. 2600 heures de données comportementales ont été prises sur 42 femelles adultes d'Octobre 2008 à Juin 2010. En combinant une analyse compréhensive des variables comportementales, je confirme le style social tolérant des femelles. En examinant la fonction des interactions post-agression par l'analyse des liens entre agression, anxiété, caractéristiques des conflits et de celles des dyades impliquées et les interactions post-agression, je détermine que celles-ci ne servent pas à réduire l'anxiété ou à "raccommoder" les relations sociales mais fonctionnent plutôt pour signaler l'intention pacifique ou pour réaffirmer le statut social. En étudiant l'influence des relations de dominance et de parenté sur les interactions sociales, je détermine que la force des liens sociaux n'est pas forcement liée a la dominance ou la parenté et que les coalitions sont formées entre femelles proches en dominance, mais pas entre apparentées ou proches affiliées. Ces résultats contrastent avec d'autres sociétés animales et mettent en évidence la complexité des sociétés tolérantes. Ma thèse apporte de nouvelles bases empiriques sur la variation sociale dans une perspective comparative et apporte un nouveau cadre théorique sur l'évolution des sociétés animales.

Mots-clés : comportement social, femelle, primate, mammifère, relations sociales, dominance, parenté, résolution des conflits, style social.

Résumé en anglais

The diversity in female primate sociality reflects a combination of competitive and cooperative strategies. Different frameworks explain such diversity. The genus Macaca is a good example of social variation. The aim of my thesis is to foster our understanding of macaque societies by studying one little-known species, the crested macaque, Macaca nigra, under natural conditions, the Tangkoko Reserve, in Sulawesi Indonesia. From October 2008 to June 2010, I gathered 2600 hours of behavioural data on 42 adult females. By quantifying a comprehensive set of behaviours, I confirm the females' tolerant social style. I investigate the function of post-conflict interactions by analysing the relationship between aggression, anxiety, characteristics of conflicts, of dyads involved in conflicts, and the occurrence of post-conflict interactions. Post-conflict interactions did not serve to reduce stress or to "repair" relationships but function as a signal of benign intent or to reassert social status. I analyse the hierarchical and nepotistic influence on social relationships and show that social bonds are not entirely shaped by kinship or dominance. Coalitionary support occurred amongst females close in rank but not amongst close kin or strong affiliates. These patterns represent meaningful contrasts to other animal species and highlight the complexity of social life in tolerant societies. By combining behavioural and genetic data, my thesis brings an empirical basis to theoretical frameworks on the evolution of social diversity, reflects on the interplay between different factors in a comparative perspective and provides a general framework for the evolution of animal societies.

Key words: social behaviour, female, primate, mammal, social relationships, sociality, dominance, kinship, conflict resolution, social style.