Within- and between-group feeding competition in Siberut macaques (*Macaca siberu*) and Assamese macaques (*Macaca assamensis*)

Dissertation

for the award of the degree
"Doctor rerum naturalium" (Dr.rer.nat.)
of the Georg-August-Universität Göttingen

within the doctoral program Biology
of the Georg-August University School of Science (GAUSS)

submitted by
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Göttingen, 2014

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Date of oral examination: 11. Feb. 2014

This thesis
is dedicated to
Siberut and its people

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Acknowledgements

This thesis would not have been possible and successful without the great help of many people. First of all, I would like to thank Oliver Schülke and Julia Ostner for their supervision, trust and support, and for accompanying and shaping my scientific career during the last seven years since the start of my Diploma thesis. Thanks for all your valuable comments, and for always pointing me towards the right directions, to see and understand the bigger picture. I thank Peter M. Kappeler for his support and for becoming a co-supervisor of my thesis. I thank Eckhard W. Heymann for helping me out in the last minute to become my second reviewer for my thesis. I am thankful to Antje Engelhardt, Michael Mühlenberg and Matthias Waltert for their willingness to become members of my examination board.

I am grateful to Keith Hodges and Christophe Abegg for allowing me to conduct my study within the premises of the Siberut Conservation Programme (SCP), and to Pak Agil for his collaboration. I thank the Indonesian authorities (LIPI, RISTEK, DEPDAGRI, DIKTI, PKSDA Padang) for granting me the research permits to conduct my study. Thanks to all SCP members for their help: Thomas Ziegler, Christophe Abegg, Siti Aminah, Edith Sabara, Fauzan, Pak Dodi and Dodo. Thanks especially to Marcel Quinten for his great coordination and management.

My deepest gratefulness goes to all the people in Siberut who helped me that Siberut became my home during these 2.5 years. Masura bagatta! Especially thanks to Pak Tarzan, who became my second dad and always took care for me. Thanks for your loyalty and help, even during the most difficult times, when flood and epidemic hit Politcioman, and the massive earthquake cut off all logistics. Thanks for still helping me during this time as best as possible, while everybody else was just caring for his own survival. I am grateful to my guides Pak Safrizal, Bang Risel, Pak Tongam, Pak Teiba, Pak Bitcar, Pak Mathias and Pak Mitchen, and also Peator, Pak Hermanto and Pak Lucian who kindly helped out when needed. Without you I would have lost bokkoi more quickly, and would have stepped on a cobra several times, while being focused on the monkeys in the trees. Thanks to Pak Safrizal and Pak Mathias for carrying me several kilometers back to camp, over hills and through rivers, when I got bitten by a viper on my last day. A great thank you goes to Ibu Ripe for coming so quickly to camp, to provide me with local medicine to heal me from the poisonous bite. Sincere thanks to Pak Nauli and Pak Tarzan for assisting me with plant identification and herbarium sample collection.

I am deeply grateful to my assistants Adi Nugroho, Marliana Chrismiawati, Rahayu Oktaviani, Azhari Purbatrapsila, Ahmad Taufiq, Rima Lamhatul Mikrimah and

Betty Millyanawati. Thanks for all your hard work and efforts, for many long days in the forest, walking up and down the hills, through rain and storm, and for keeping the motivation high even when bokkoi were sleeping at T3-T22 1700, T2 or T26, "dan kalau bokkoi lagi gila". Thanks for all the fun times with you in the forest and in camp! I am very grateful to Pierre Gras who did so much more than was necessary for his Master thesis. Thank you for leading the guides and keep the data collection going, while I was lying in hospitals for weeks on end. Most particular I thank Ahmad Taufiq, for becoming such a close friend, a wonderful and enthusiastic colleague, and finally my soulmate. Thank you for being on my side during one of the most difficult times in my life, when being severely sick for 2 months, not knowing whether there will be a future. Thanks also to all your family members, who brought me so delicious food to the hospital. Thanks Taufiq, because without you I would never have finished my study in Siberut - you gave me all the strength I needed!

I thank everybody who made life and especially the weekends in camp so special, with "bioskop Pungut", nice cooking experiments ("ayo, kita cobar"), swimming in the river, singing songs, dancing and playing games. Thanks to all who taught me Mentawaian and Indonesian songs, and for sharing your culture. I particularly thank Vera, Susilo, Deden, Yulia, Arul, Lim, Yandhie, Emma, Richard, Husnul, Andrea, Jojo, Ika, and of course Lia, Adi, Ayu, Ai, Rima, Taufiq and Betty for all the great moments we shared in camp. I also thank Jane and Tony Whitten for a nice few days together, and for sharing some of your stories how life was in Siberut some decades ago. Thanks to the BR film crew, who brought a lot of fun to camp. I am very grateful to Deden, the best camp manager ever. Thanks for accompanying me to the forest when I had no guides, and for swimming out of camp through the flood when all porters refused to bring food to Pungut! I like to thank Husnul for being on my side when we had to evacuate camp, and when trying to find something edible in Padang amongst all the ruins, being surrounded by the smell of dead people everywhere. Thanks for being with me during this horrible earthquake disaster. Thanks to your family who received me so cordially once we got out of that nightmare.

I thank all people in Politcioman for celebrating Christmas and New Year together, and for nice times in the church. Especially thanks to Mba Ros, Yohanna, Yuyun, Yohann, Feri and Bang Potan for many nice weekends in Betaet, which always felt like a little holiday. Thanks for organizing the logistics for Pungut. I also like to acknowledge the brave young men of Politcioman, who protected all of us with weapons against the "organ hunters" by patrolling night after night around Betaet, so that we could sleep safely. Thanks to Pak Parulian for driving us safely with the speedboat even through the highest waves and craziest storm.

I am very grateful to Mas Padi and Mba Mis, for always being so welcoming and friendly, making me feel like at home in your house in Pokai. Thanks for incredibly delicious food, ginger tea, and for many nice conversations. Thanks for your help with organizing porters, and finding out when and whether there will be a ferry. Thanks for your great effort in finding the last gasoline for me on the island after the earthquake, when there was no incoming logistics for the next months and everybody was fighting over the last resources.

I like to thank all current and former members of my research group: Marlies Heesen, Chris Young, Sally Macdonald, Miranda Swagemakers, Mathias Franz, Annie Bissonnette, Claudio de la O, Lisann Heyse, Nadine Müller, Josefine Kalbitz, Andreas Berghänel, Sarah Wibbeke, Christin Minge, Markus Port, Barbora Kubènová. Thanks for discussions, advice, comments, many nice refreshing Mensa breaks and your aid during all the computer problems. Thanks to the other CRC and DPZ PhD students, especially to Cédric Girard-Buttoz and Pascal Marty. I am grateful to all who helped improving the content and language of parts of my thesis: Julia, Oliver, Marlies, Keith, Chris, Sally, Brandon Wheeler and my parents. In addition, I thank all people who contributed to the data set I used on Assamese macaques.

I would like to express my gratitude to all my friends, in particular Anja Dhinagaran, Andrea Höing, Kai Weinhold, Sabine Heitmann, Anita K. Hansen, Nicole Werner and Kathleen Kästner. I thank you for your deep friendship, your trust and support, all the emails, letters and presents you sent me while being in Indonesia. I thank you for so many wonderful and ever-lasting moments in my life.

I am deeply grateful to god, for giving me the strength to finish this project successfully, for giving me new optimism when I needed it most, for protecting me from a tsunami when the earthquake epicenter was right under me while waiting for the ferry in MuaraSiberut, and for saving our lives during the massive storm which destroyed several hectare of forest at once, when everybody else in camp thought we would not have survived.

Ich danke meinen Eltern Ingrid und Conny Richter, die mich mein Leben lang beschützt und behütet haben, mir alles notwendige mit auf meinen Lebensweg gegeben haben, und immer für mich da waren. Ich danke euch für all die Kraft und das Vertrauen das ihr mir geschenkt habt, und dass ihr mich immer unterstützt habt. Danke, dass ihr immer für mich da wart, auch wenn ich am anderen Ende der Welt war.

This study would not have been possible without the funding provided by Max-Planck Society, the German Initiative of Excellence to the Georg-August University Göttingen, and a scholarship provided by the Evangelisches Studienwerk e. V.

Summary

Feeding competition creates one of the major costs of group living and remains a central focus of research interest, as it affects female reproductive success, individual and population growth, survival of individuals, sets an upper limit to group size and shapes the social structure of animal groups. It is well recognized that feeding competition should be largely determined by food resource characteristics, such as food abundance, distribution, quality and food patch size relative to group size. Other environmental factors, like the risk of predation, can influence feeding competition as well, as individuals form larger groups and become more cohesive if predation risk is high. Feeding competition in turn is thought to determine social relationships, such as dominance relationships and the degree of tolerance and nepotism between individuals. The influence of these ecological factors and some additional social factors (e.g. infanticide risk) on the competitive regime and in turn on social relationships has resulted in the formulation of various generations of the socioecological model. Female mammals are usually more limited by food in their reproductive success than males, therefore these models have focused on explaining female social relationships. Testing the predictions of the socioecological models has largely influenced ecological research during the last decades.

My thesis addresses two major gaps related to the feeding competition aspects of the socioecological models. Firstly, it addresses the lack of empirical data examining feeding competition under low predation risk to test the model predictions that groups become less cohesive and feed in small feeding parties or even alone, if predation risk is low, resulting in reduced contest competition. Secondly, it addresses the often neglected role of males within socioecological models that usually focus on feeding competition between females. However, there is some evidence that males can also actively defend food resources and thus can play an important role in between-group feeding competition.

To address the first research gap, I studied within-group feeding competition in Siberut macaques (*Macaca siberu*), a species endemic to Siberut island in West Sumatra, Indonesia, where predation risk is low as carnivore predators have been absent for at least 0.5 m years. I conducted my research at the field site of the Siberut Conservation Programme (SCP), run by the German Primate Center (DPZ), Göttingen, Germany, and the Bogor Agricultural University (IPB), Bogor, Indonesia. After habituation to human presence (Dec. 2008 – Mar. 2010), I collected behavioral, ecological and botanical data of one group of Siberut macaques (29 individuals) between March 2010 and March 2011, with the help of two field assistants and four local guides.

My study is the first quantitative study on the ecology of Siberut macaques, making it necessary to first describe the general ecology of this species. I a) conducted group scan observations to describe the diet, activity budget, forest structure use, home range use and group spread, b) established 12 permanent botanical plots (á 50m x 50m) to describe the habitat and the distribution and density of food resources, and c) carried out focal tree observations to describe the use of food patches, food patch characteristics (size, food abundance, patch depletion) and the frequency of aggression as a measure of contest competition.

My study revealed that Siberut macaques are largely frugivorous and semi-terrestrial, and are ecologically most similar to their sister species *Macaca nemestrina* (Chapter 2). Siberut macaques fed on tree, palm tree, rattan, strangler and liana fruit, mostly occurring in small to medium sized food patches (Chapter 3). Palm tree and rattan fruit constituted important food resources due to their long temporal availability (Chapter 2, 3). Most food species occurred at low densities within the area of average group spread, offering few possibilities to use alternative food resources to avoid aggression. In addition, fruit was spatially clumped within the crown in several species. All these conditions provide a high potential for contest competition, but observed aggression rates were low (Chapter 3). Compared to other primate species living in medium or high predation pressure environments, aggression rates in food patches were lowest in Siberut macaques, confirming the prediction of socioecological models that feeding competition is reduced when predation risk is low. Group spread was highly variable in Siberut macaques, and even when group spread was large, no sub-grouping occurred as is common in other macaque species (*Macaca nemestrina*, *Macaca fascicularis*) that co-occur with felid predators (Chapter 5). Low predation risk should also influence feeding group size. In accordance with model predictions, average feeding group size was small, and more importantly, both adults and juveniles were able to feed alone in food patches (Chapter 3, 5). Thus, I found support for all predictions of socioecological models tested.

I addressed the second gap of research using Assamese macaques (*Macaca assamensis*) as study species to evaluate the role and consequences of male group size on between-group competition, by investigating the influence of male group size on home range size. Assamese macaques are an ideal species for this study as they form large multi-male multi-female groups and males actively participate in intergroup contests. As home range size determines access to food resources, home range size before the start of the breeding season should directly influence female reproductive success. I used an existing long-term data set of ecological and ranging data of one group of Assamese macaques (40-64 individuals, including 6 to 16 males), collected between October 2007 and October 2012, at Phu Khieo Wildlife Sanctuary in Northeastern Thailand, as part of a long-term field project. To control for other factors known to influence home range size, I included data on total group size, daily travel distance, food availability, food distribution, temperature, and precipitation in the multivariate analysis. I found that, as predicted, the number of males positively influenced monthly home range size (Chapter 4). Furthermore, home range size in August, a critical time period determining female fertility, was positively correlated with the proportion of females conceiving in the following mating season (Chapter 4). This indirectly indicates that male Assamese macaques defend food resources during intergroup encounters, and that male resource defense is an important part of between-group competition in that species. A literature review revealed that there is direct or indirect evidence for male resource defense in 17 primate species (Chapter 5), suggesting that male resource defense may be more common than previously assumed. Future studies should therefore not only consider male mate defense, but also male resource defense, when investigating the role of males in intergroup-encounters. Furthermore, I examined various conditions suggested by Fashing (2001) to predict in which species and under which conditions male resource defense is likely to occur. More data are needed before we can draw proper conclusions. If future studies can demonstrate that male food resource defense influences between-group feeding competition in many species, we should consider including males as an explanatory factor in future socioecological models.

In sum, my thesis fills two major gaps relating to feeding competition aspects of socioecological models. It contributes to the debate about the merit and validity of socioecological models by confirming model predictions for a species living under low predation risk, and shows that it is important to measure food resource characteristics on a scale relevant to the study animals. A comparison of Siberut macaques and Sulawesi macaques shows that their competitive regimes differ largely, although they all live on oceanic islands under low predation risk and feed mainly on fruits. This shows the importance of detailed measurements of behavior, food resource characteristics and other ecological conditions, and prompts us to be careful with generalizations based on coarse dietary categorizations. More detailed data on a wide range of species and populations, including other non-primate vertebrate species, are needed to test the predictions of socioecological models, and to evaluate the relative importance of their main factors in comparative tests. Various factors have been previously proposed to be added to the socioecological models, to improve their explanatory power. I would suggest that males could be one of them, as male food resource defense may be more important than previously assumed.

Zusammenfassung

Die negativen Auswirkungen von Nahrungskonkurrenz stellen eines der bedeutendsten Nachteile des Gruppenlebens dar. Nahrungskonkurrenz ist seit jeher von zentralem Forschungsinteresse, da sie den Fortpflanzungserfolg von Weibchen, das Wachstum von Individuen und Populationen sowie das Überleben von Individuen limitiert. Außerdem begrenzt Nahrungskonkurrenz die maximale Größe einer Gruppe und beeinflusst die Sozialstruktur von gruppenlebenden Tieren. Es ist allgemein anerkannt, dass Nahrungskonkurrenz durch die Charakteristika der Nahrungsressourcen bestimmt werden sollte, wie die Verfügbarkeit, Verteilung und Qualität von Nahrung, sowie die Größe von Nahrungsquellen (food patches) relativ zur Gruppengröße. Andere Umweltfaktoren wie das Prädationsrisiko können Nahrungskonkurrenz ebenfalls beeinflussen, da Tiere bei hohem Prädationsdruck größere Gruppen bilden und dichter beieinander bleiben, was den Wettbewerb um Nahrung verstärkt. Die Nahrungskonkurrenz wiederum sollte die Sozialbeziehungen wie Dominanzverhältnisse, den Grad an Toleranz und Nepotismus (Bevorzugung von Verwandten) zwischen Individuen beeinflussen. Der Einfluss dieser ökologischen Faktoren und einiger zusätzlicher sozialer Größen (z.B. Infantizidrisiko) auf unterschiedliche Formen der Nahrungskonkurrenz und weiter auf die Sozialbeziehungen führte zur Formulierung von verschiedenen Versionen des sozioökologischen Modells. Da bei Säugetieren der Fortpflanzungserfolg der Weibchen generell stärker durch Zugang zu Nahrung limitiert ist als der von Männchen, konzentrierten sich die Modelle auf die Erklärung weiblicher Sozialbeziehungen. Die letzten Jahrzehnte ökologischer Primatenforschung wurden weitesgehend davon geprägt, die Vorhersagen der sozioökologischen Modelle zu testen.

Meine Doktorarbeit befasst sich mit zwei großen Lücken in unserem Verständnis der Rolle von Nahrungskonkurrenz in sozioökologischen Modellen. Erstens wurden bisher nur wenige Studien zur Nahrungskonkurrenz an Arten, die unter geringem Raubdruck leben, durchgeführt, um die Modellvorhersagen für diese Bedingungen zu testen. Genauer wird vorhergesagt, dass der Gruppenzusammenhalt loser wird, d.h. dass sich die Tiere in größeren Abständen voneinander aufhalten, und dass die Tiere in kleinen Gruppen oder sogar allein fressen können wenn das Prädationsrisiko gering ist. Dadurch wird die Nahrungskonkurrenz geringer. Zweitens wurde bisher die Rolle von Männchen in sozioökologischen Modellen oft ignoriert, und der Fokus auf die Nahrungskonkurrenz zwischen Weibchen gerichtet. Allerdings gibt es einige Hinweise, dass Männchen ebenfalls aktiv Nahrungsressourcen verteidigen können und somit eine bedeutende Rolle für die Nahrungskonkurrenz zwischen Gruppen spielen können.

Um die erste Forschungslücke zu füllen, habe ich die Nahrungskonkurrenz innerhalb einer Gruppe von Siberut-Makaken (*Macaca siberu*) untersucht. Das Vorkommen von Siberut-Makaken ist auf die indonesische Insel Siberut begrenzt, die vor der Küste Westsumatras liegt. Der Prädationsdruck auf Siberut ist gering, da es seit über 0.5 Mio. Jahren keine Raubkatzen gibt. Meine Arbeit wurde an der Forschungsstation des Siberut Conservation Programmes (SCP) durchgeführt, die gemeinsam von dem Deutschen Primatenzentrum (DPZ) in Göttingen (Deutschland) und der Landwirtschaftlichen Universität Bogor (Indonesien) geleitet wird. Nachdem die Affen an die Anwesenheit von Menschen gewöhnt wurden (Dez. 2008 – Mär. 2010), habe ich zusammen mit einem Team von zwei Feldassistenten und vier einheimischen Führern ökologische, botanische und Verhaltensdaten von einer Gruppe von 29 Tieren im Zeitraum von März 2010 bis März 2011 gesammelt. Da meine Studie die erste quantitative Untersuchung zur Ökologie von Siberut-Makaken ist, war es notwendig, zuerst die allgemeine Ökologie dieser Art zu beschreiben. Um die Nahrungszusammensetzung, das Aktivitätsbudget, die Nutzung der Waldstruktur, des Streifgebietes und die Gruppenausdehnung (group spread) zu beschreiben, habe ich Gruppenscanbeobachtungen (group scan observations) durchgeführt. Außerdem habe ich 12 dauerhafte botanische Plots angelegt (von je 50m x 50m), um das Habitat, die Verteilung und die Dichte der Nahrungsressourcen zu beschreiben. Weiterhin führte ich Fokusbaumbeobachtungen (focal tree observations) durch, um die Nutzung von Nahrungsquellen, ihre Eigenschaften (Größe, Nahrungsverfügbarkeit, Nahrungsverbrauch (patch depletion)) und die Häufigkeit von Aggressionen als Maß für direkte Nahrungskonkurrenz (contest competition) zu beschreiben.

Meine Studie zeigte, dass Siberut-Makaken sich vorwiegend von Früchten ernähren und semi-terrestrisch leben. Hinsichtlich ihrer Ökologie sind Siberut-Makaken im Vergleich zu anderen Makaken ihrer Schwesternart, den Südlichen Schweinsaffen (*Macaca nemestrina*), am ähnlichsten (Kapitel 2). Siberut-Makaken ernährten sich von Früchten von Bäumen, Palmen (baumförmige Palmen und Rattan), Würgefeigen und Lianen. Diese Nahrungsquellen (food patches) waren, relativ zur Gruppengröße, vorwiegend klein bis mittelgroß (Kapitel 3). Palmfrüchten kommt aufgrund ihrer langen zeitlichen Verfügbarkeit eine besondere Bedeutung zu (Kapitel 2, 3). Die meisten Nahrungspflanzen kamen im Verhältnis zur durchschnittlichen Gruppenausdehnung in einer geringen Dichte vor. Dadurch gibt es nur wenige alternative Nahrungsressourcen, um Aggressionen zu vermeiden. Außerdem waren die Früchte einiger Arten innerhalb der Krone stark geklumpt. All diese Bedingungen liefern ein großes Potential für direkte Nahrungskonkurrenz (contest competition), aber die beobachteten Aggressionsraten waren niedrig (Kapitel 3). Im Vergleich zu Primatenarten, die unter mittlerem bis hohem

Prädationsdruck leben, waren die Aggressionsraten bei Siberut-Makaken am geringsten. Daher ist die Vorhersage sozioökologischer Modelle, dass sich die Nahrungskonkurrenz verringert, wenn der Prädationsdruck gering ist, bestätigt. Die Gruppenausdehnung (group spread) von Siberut-Makaken war sehr variabel. Selbst wenn die Distanz zwischen Gruppenmitgliedern groß war, so bildeten sie nie Untergruppen, so wie es bei anderen Makakenarten (*Macaca nemestrina*, *Macaca fascicularis*) die in Gebieten mit Raubkatzen leben, der Fall ist (Kapitel 5). Ein geringer Prädationsdruck sollte außerdem die Anzahl der Tiere, die zusammen fressen, beeinflussen. In Übereinstimmung mit den Modellvorhersagen war die durchschnittliche Anzahl von Tieren, die zusammen in Nahrungsquellen fressen, gering. Viel wichtiger noch ist die Beobachtung, dass nicht nur erwachsene Tiere, sondern auch Jungtiere Nahrungsquellen alleine nutzen konnten (Kapitel 3, 5). Daraus ergibt sich eine Bestätigung aller überprüften Modellvorhersagen.

Um die zweite Forschungslücke zu schließen, habe ich Assam-Makaken (*Macaca assamensis*) studiert und die Rolle von Männchen für die Nahrungskonkurrenz zwischen Gruppen untersucht, indem ich den Einfluss der Anzahl der Männchen auf die Größe des Streifgebietes bestimmt habe. Assam-Makaken sind dafür besonders geeignet, da sie in großen Mehr-Männchen-Mehr-Weibchen-Gruppen leben und Männchen aktiv in aggressiven Gruppenbegegnungen teilnehmen. Da die Größe eines Streifgebietes generell den Zugang zu Nahrungsressourcen bestimmt, sollte die Streifgebietsgröße vor der Paarungszeit direkt den Reproduktionserfolg der Weibchen beeinflussen. Um diese Frage zu untersuchen, stand mir ein Langzeitdatensatz von ökologischen und räumlichen Verhaltensdaten von einer Gruppe von Assam-Makaken (40-64 Tiere, inklusive 6-16 Männchen) zur Verfügung, der im Zeitraum von Oktober 2007 bis Oktober 2012 im Naturschutzgebiet Phu Khieo im Nordosten von Thailand im Rahmen eines Langzeitprojektes gesammelt wurde. Um für andere Faktoren zu kontrollieren, die die Streifgebietsgröße ebenfalls beeinflussen können, habe ich Gruppengröße, Tageswanderstrecke der Gruppe, Nahrungsverfügbarkeit, Nahrungsverteilung, Temperatur und Niederschläge als weitere erklärende Variablen in die multivariate Analyse miteinbezogen. Es zeigte sich, dass im Einklang mit den Vorhersagen, die Anzahl der Männchen einen positiven Einfluss auf die monatliche Streifgebietsgröße hat (Kapitel 4). Außerdem korrelierte die Streifgebietsgröße im August, eine kritische Zeitspanne, die die Fruchtbarkeit von Weibchen bestimmt, positiv mit dem Anteil der sich in der darauffolgenden Paarungszeit erfolgreich fortpflanzenden Weibchen (Kapitel 4). Dadurch wird indirekt gezeigt, dass Assam-Makaken-Männchen Nahrungsressourcen gegenüber anderen Gruppen verteidigen, und dass Männchen dadurch eine bedeutende Rolle für die Nahrungskonkurrenz zwischen Gruppen spielen können. Eine Literaturrecherche zeigte, dass es direkte oder indirekte Beweise für

Ressourcenverteidigung durch Männchen bei 17 Primatenarten gibt (Kapitel 5). Daraus lässt sich erkennen, dass diese Art von Ressourcenverteidigung häufiger vorkommen könnte, als bisher angenommen. Zukünftige Studien, die die Rolle von Männchen in aggressiven Gruppenbegegnungen untersuchen, sollten daher nicht nur die Verteidigung von Weibchen, sondern auch die Verteidigung von Ressourcen in Betracht ziehen. Weiterhin untersuchte ich die von Fashing (2001) vorgeschlagenen Bedingungen, unter denen Ressourcenverteidigung durch Männchen wahrscheinlich ist. Es zeigt sich, dass die Datenlage momentan keine belastbaren Schlußfolgerungen zulässt. Falls die benötigten zukünftigen Studien weitere Hinweise finden, dass Ressourcenverteidigung durch Männchen verbreitet ist und die Nahrungskonkurrenz zwischen Gruppen in vielen Arten beeinflusst, dann sollten wir in Betracht ziehen, Männchen in zukünftige sozioökologische Modelle miteinzubeziehen.

Zusammenfassend lässt sich sagen, dass meine Doktorarbeit dazu beiträgt, zwei große Lücken hinsichtlich der Rolle von Nahrungskonkurrenz in sozioökologischen Modellen zu schließen. Sie trägt zur Debatte um den Wert und die Gültigkeit sozioökologischer Modelle bei, indem sie die Modellvorhersagen für eine Art, die unter geringem Prädationsdruck lebt, bestätigt. Weiterhin wird in meiner Arbeit die Wichtigkeit verdeutlicht, die Eigenschaften von Nahrungsressourcen auf einer Skala zu messen, die der untersuchten Tierart angemessen ist. Ein Vergleich von Siberut-Makaken mit Sulawesi-Makaken zeigt, dass deren Nahrungskonkurrenz stark verschieden ist, obwohl alle Arten auf ozeanischen Inseln unter geringem Prädationsdruck leben und sich von Früchten ernähren. Dies verdeutlicht die Bedeutung detaillierter Messungen von Verhaltensweisen, Charakteristika von Nahrungsressourcen und anderer ökologischer Faktoren, und fordert uns auf, mit Verallgemeinerungen vorsichtig zu sein, die auf groben Kategorisierungen von Nahrungszusammensetzungen basieren. Weitere detaillierte Daten von einer Vielzahl von Arten und Populationen, inklusive anderer Vertebraten außerhalb der Primaten, sind notwendig, um die Vorhersagen der sozioökologischen Modelle in vergleichenden Analysen zu testen, und die relative Bedeutung der Hauptfaktoren zu untersuchen. Eine Reihe von Faktoren wurde bereits vorgeschlagen, um die sozioökologischen Modelle und deren Aussagekraft zu verbessern. Mein Vorschlag wäre, dass Männchen eine dieser zusätzlichen erklärenden Variablen sein könnten, da die Ressourcenverteidigung durch Männchen häufiger und wichtiger sein könnte, als bisher angenommen.

Chapter 1

General Introduction

When multiple individuals exploit the same limited food resource, they become competitors and feeding competition arises (Davies et al. 2012). Feeding competition has been a topic of interest for decades, as it influences individual growth and survival (Magnuson 1962; Parker et al. 2009; Parr and Gibb 2010; Nislow et al. 2011), female reproductive success through shorter inter-birth intervals, more offspring per litter, faster growth rates and higher survival of offspring (reviewed in Stockley and Bro-Jørgensen 2011). It is also thought to set an upper limit on group size through increased ranging costs (Janson and Goldsmith 1995; Chapman and Chapman 2000b; Majolo et al. 2008; Schülke and Ostner 2012), and to shape the social system, especially social structure (sensu Kappeler and van Schaik 2002), of many species (Wrangham 1979; Wrangham 1980; van Schaik 1989; Sterck et al. 1997; Koenig 2002; Koenig et al. 2013).

The present thesis will focus on feeding competition between socially foraging animals. Social foraging theory implies an economic interdependence of an individual's benefits and costs (Giraldeau and Caraco 2000). Social foragers, i.e. members of social groups or non-social individuals aggregating around resources (Giraldeau and Caraco 2000), like individual foragers, try to maximize their own net intake, but the most efficient strategy depends on the decisions of the other competitors (Maynard Smith 1976).

It is well recognized that local ecological conditions, such as food resource characteristics, influence feeding competition and social interactions between individuals and groups (Clutton-Brock and Janson 2012; Schülke and Ostner 2012). This knowledge led to the ecological and later socioecological models which set the framework of my thesis (van Schaik 1989; Koenig 2002; Koenig et al. 2013). The power and validity of the socioecological models has been recently debated, as certain discrepancies between the models' predictions and empirical data have been found (Thierry 2008; Koenig and Borries 2009; Clutton-Brock and Janson 2012). However, this is argued to mainly come from inaccurate testing and measurements, and from ignoring important factors (Koenig and Borries 2006; Koenig and Borries 2009; Schülke and Ostner 2012). In my thesis, I address two major gaps of research regarding the socioecological models: firstly, the lack of feeding competition studies on species in low predation pressure environments, and secondly, the neglected aspect of male resource defense.

Socioecological theory is of course embedded within general ecological theory. Thus, I will give a general theoretical overview on concepts important to understand feeding competition (section 1.1) before I present some background for within- and between-group feeding competition (section 1.2 and 1.3). I will clarify various terms used to describe different types of feeding competition (Box 1.1), as this varies between research disciplines and researchers. After identifying empirical gaps within socioecological theory, I will present the objectives of my thesis in detail (section 1.4).

1.1 Theoretical background

The intensity of feeding competition depends on the amount of resources available and the distribution of competitors. One classic theory to predict the distribution of individuals among available food patches is the “ideal free distribution” (Fretwell and Lucas 1970; Fretwell 1972). It states that animals distribute themselves according to the resources available in different patches, so that the distribution of individuals matches with the proportion of resources (Fretwell 1972). The model assumes that individuals are all equal in their competitive abilities, have a perfect knowledge of how resources are distributed, and are free to choose which patch to use (Fretwell 1972; Parker and Sutherland 1986). These assumptions rarely fit with empirical data, where competitive interactions and asymmetries between individuals are quite common, individuals lack perfect knowledge regarding resource distribution and can have constraints in discriminating between resource values, and travel costs between sites can influence decisions (Abraham 1986; Kennedy and Gray 1993; Kennedy and Gray 1997; Hugie and Grand 1998). For these reasons, many studies have found a systematic deviation from predicted values, with individuals under-using richer sites and over-using poorer sites (Kennedy and Gray 1993; Tregenza 1995). The ideal free distribution can thus only explain one form of competition sufficiently, exploitation or scramble competition (for terminology see Box 1.1). Under scramble competition, all individuals get more or less equal access to resources, and intake rates decline in direct proportion to the number of competitors depleting a patch (Fretwell 1972; Johnson et al. 2006). The second form of competition is termed interference or contest competition (Ens and Goss-Custard 1984; Stillman et al. 1997; Johnson et al. 2006) (for terminology see Box 1.1), where competitors are unequal, and some individuals have higher competitive abilities than others (Parker and Sutherland 1986; Korona 1989; Hugie and Grand 1998). To explain this type of competition, the model was adapted to include interference between individuals, resulting in the “interference ideal free distribution” (Sutherland and Parker 1992; Tregenza et al. 1996; Johnson et al. 2006). Interference or contest competition is a common type for many vertebrates and some invertebrates (Sutherland and Parker 1992). Under contest competition, certain individuals can defend resources and even exclude other individuals from resources altogether (Fretwell 1972), so that at very high levels of interference the distribution of foraging individuals can become independent of the resource distribution (Johnson et al. 2006).

Whether or not individuals behave aggressive and defend resources can be predicted by Brown’s theory of economic defendability (Brown 1964). Only if the benefits of priority of access to resources outweigh the costs (energy expenditure, risk of injury) or if net benefits exceed the net costs of alternative strategies, like scrambling for food, individuals should engage in resource defense (Brown 1964; Grant 1993). Several factors are important for this decision of whether or not to engage in aggressive competition, including the density of resources and competitors, and the temporal and spatial distribution of resources (Brown 1964; Grant 1993; Dolman 1995; Cresswell 1998; Robb and Grant 1998).

Another theoretical model which can help to understand and predict the occurrence of aggression among foraging individuals is the game theoretical approach (von Neumann and Morgenstern 1944; Maynard Smith 1982). If animals compete over resources, the best strategy for an individual depends on what other individuals are doing (Maynard Smith 1976), resulting in various possible strategies with different pay-offs. The two most extreme strategies are the “hawk” strategy, where an individual always fights and may injure the opponent (but may also get injured itself), and the “mouse” or later called “dove” strategy, where the individual never fights and immediately retreats upon escalation to avoid injuries (Maynard Smith and Price 1973; Maynard Smith 1976). Game theoretical models showed that the pure dove strategy can never be an evolutionary stable strategy (ESS, Maynard Smith and Price 1973), whereas a pure hawk strategy can be an ESS if the density of competitors is high and food availability is low (Sirot 2000). The model showed that aggressiveness should vary with ecological conditions, with higher levels of aggressiveness with decreased food availability and increased density of foraging animals (Sirot 2000).

Box 1.1 Terminology of feeding competition

Many different terms are used in the literature to describe competition for resources in general, and feeding competition in particular. This terminology has been used inconsistently as different researchers and different research areas use the same labels with different meanings, complicating cross-taxa comparisons. The terms exploitation and interference competition (Birch 1957; Park 1962) and scramble and contest competition (Nicholson 1954) have been either used independently, describing competition on different levels (de Jong 1976), or have been used as synonyms, with exploitation/-scramble competition (or indirect competition: Janson and van Schaik 1988) describing food depletion within a resource patch without any interactions between animals, and interference/-contest competition (or direct competition: Janson and van Schaik 1988) referring to situations where some individuals interfere in the foraging decisions of others, usually by direct aggression by dominants or avoidance by subordinates, so that dominant individuals gain a higher proportion of the resources (Ens and Goss-Custard 1984; Alatalo et al. 1987; Janson and van Schaik 1988; van Schaik 1989; Kotrschal et al. 1993; Giraldeau 2008). Others have argued that exploitation and interference competition should be distinguished from scramble and contest, with exploitation describing situations where individuals use a common resource independently of the actions of the other individuals, direct interference competition describing situations where individuals actively restrict the access of other individuals to the resource, and indirect interference competition describing situations in which the past utilization of resources influences the present food acquisition (de Jong 1976). Scramble and contest are then seen as the way resources are utilized (i.e. under scramble part of the food is wasted as those individuals which did not acquire enough food died and do not produce biomass), and they can both occur under exploitation and interference competition (de Jong 1976).

Adding further complications, scramble and contest have been used differently in ecology and behavioral ecology (Parker 2000). In ecology, the meaning followed Nicholson’s original use (Nicholson 1954) to describe competition effects on a population level: In scramble situations, all individuals gain some share of the resources, and individuals try to increase their share by increasing their effort to harvest the resource, but where this is not enough, they die or do not breed so that these resources get wasted for the population, whereas in contest situations competitors get either all or nothing, and are either winners or losers (Parker 2000). In behavioral ecology, scramble and contest have been used to describe effects of competition on an individual level, with an interest in how individuals compete behaviorally and how the resource is divided among competitors (Parker 2000). In primate behavioral ecology, this latter view on an individual level has been adopted and became the prevailing use of the terms scramble and contest since then (van Schaik and van Noordwijk 1988; Isbell 1991; Sterck et al. 1997). Thus, I follow this terminology throughout this thesis.

Table 1.1 Summary of the two types of feeding competition, scramble and contest, for both within- and between-groups (Janson and van Schaik 1988; van Schaik 1989; Isbell 1991; Sterck et al. 1997; Isbell and Young 2002; Koenig 2002; Snaith and Chapman 2007; Koenig et al. 2013). Note that gregarious animals generally experience a mixture of all four components (Sterck et al. 1997).

	Scramble competition		**Contest competition**	
	Within-group (WGS)	**Between-group (BGS)**	**Within-group (WGC)**	**Between-group (BGC)**
Food patch characteristics				
quality	low	low	high	high
distribution	highly dispersed (or clumps > group size)	highly dispersed	clumped	clumped
size	very large relative to group size	very large relative to population density	intermediate (< group size)	intermediate (> group size); patches can be defended by a group
Food patch used by	all group members	several groups (not necessarily at the same time)	individuals assorted by rank	larger or more aggressive group
Energy gain (EG) and female reproductive success (RS)	EG and RS negatively related to group size (small groups favored); EG equally reduced for all individuals within a group	EG and RS decrease with increasing population density	RS can be negatively related to group size, EG positively related to dominance rank	EG and RS positively related to group size (large groups favored)
Aggression and avoidance	rare	rare	common (intragroup)	common (intergroup)
Effect on social behavior	little effect	little or no effect	dominance hierarchy; agonistic interactions	between-group agonism and hierarchy
Effect on ranging behavior	larger groups have longer daily travel distance	debated	no effect (apart from Isbell: effect on daily travel distance)	larger groups have larger home ranges

1.2 The concepts of within- and between-group competition

Many animals live and forage in social groups (Turner and Pitcher 1986). Living in groups can have important benefits like increased protection from predators (Siegfried and Underhill 1975; Treisman 1975; Pitcher 1986; Turner and Pitcher 1986; Nunn and van Schaik 2000; Krause and Ruxton 2010; Shultz et al. 2011), reduced infanticide risk (van Schaik and Kappeler 1997) and advantages in between-group competition (Wrangham 1980). However, there are also inevitably costs, with within-group feeding competition being one of the major costs of group-living (Clutton-Brock and Harvey 1978; Janson and Goldsmith 1995; Chapman and Chapman 2000b; Silk 2007) (but see Johnson et al. (2002) for situations when group living is less costly). Feeding competition occurs whenever food limits female’s reproductive success and population growth (Isbell 1991; Koenig 2002; Stockley and Bro-Jørgensen 2011). Gestation and lactation in mammals are energetically highly demanding, and access to and competition over food are therefore thought to be more important for females than for males (Trivers 1972; Emlen and Oring 1977; Gittleman and Thompson 1988). Feeding competition is thus an important type of reproductive competition among females (Stockley and Bro-Jørgensen 2011). For males, food is at least important to the extent that it provides energy required for sexual activities (Wrangham 1979).

Although feeding competition is important in many mammalian taxa (e.g. spotted hyenas, *Crocuta crocuta*: Holekamp & Dloniak (2010), reindeer, *Rangifer tarandus*: Holand et al. (2004), Soay sheep, *Ovis aries* Robinson & Kruuk *(2007)*), its causes and consequences have been most intensively studied in primates, due to the fact that the majority of primates live in social groups (Terborgh and Janson 1986; van Schaik and Kappeler 1997) and show large variation between (and in some cases within) taxa in both in their ecology and social structure (Smuts et al. 1987; Kappeler 1999). The potential influence of environmental factors (food resource characteristics, predation risk) and social risks (infanticide) on grouping patterns and thus social relationships and the competitive regime resulted in the formulation of various generations of a verbal model, commonly called the “socioecological model” (Wrangham 1979; Wrangham 1980; Terborgh and Janson 1986; van Schaik and van Noordwijk 1988; Isbell 1991; Sterck et al. 1997; Janson 2000; Koenig 2002; Koenig and Borries 2006; Koenig et al. 2013). Contrary to the interference ideal free distribution model described above, which mainly focuses on the characteristics of the competitors (e.g. differences in phenotype: Sutherland and Parker (1992), costs of encounters and competitor density: Tregenza et al. (1996)), the focus of the socioecological model lies in the characteristics of food resources and how this shapes female social relationships (Wrangham 1980; van Schaik

1989; Koenig 2002). In the following, the concepts of the socioecological models will be summarized (see Table 1.1 for overview):

When individuals live together in groups and resources are limited, within-group feeding competition arises, either as scramble or contest competition (van Schaik and van Noordwijk 1988; van Schaik 1989; Sterck et al. 1997). Within-group scramble competition (WGS) occurs when food patches are of low quality, highly dispersed or very large relative to group size and are thus not monopolizable by certain individuals (Isbell 1991; Sterck et al. 1997). As a result, all animals will share the resource more or less equally (van Schaik 1989). The effect of WGS will be stronger in larger groups, as resources get depleted more quickly (van Schaik 1989; Koenig 2002). If WGS dominates, females are expected to have egalitarian social relationships with an unstable, nonlinear hierarchy (van Schaik 1989; Sterck et al. 1997). Within-group contest competition (WGC) arises when food occurs clumped in distinct patches which can be monopolized (or are usurpable: Isbell & Young (2002)) by some group members, which are generally high-ranking individuals, so that these individuals have a higher net food intake rate (van Schaik 1989; Sterck et al. 1997; Koenig 2002). Species with strong WGC are predicted to have despotic relationships and a stable, linear dominance hierarchy (Wrangham 1980; van Schaik 1989; Sterck et al. 1997; Koenig 2002). Although original socioecological theory predicted no group size effect for WGC (Janson and van Schaik 1988; Koenig 2002), later research found that larger groups show higher rates of agonism as a result of increased local competitor density (Koenig and Borries 2006; Wheeler et al. 2013). However, rates of agonism can but do not always correspond to energy gain and thus strength of contest competition (Koenig and Borries 2006). Similarly, larger groups can suffer from reduced female reproductive success (Silk 2007; Majolo et al. 2008), but it is not clear whether this is mainly caused by stronger scramble competition or negative effects of increased agonism. Both WGS and WGC are thought to occur to some extent in all primate species, but with the relative importance of each varying from species to species (van Schaik and van Noordwijk 1988; Koenig 2002).

Competition over resources is not limited to individuals within a group, but neighboring groups can also compete (Wrangham 1980). Whereas some argue it is mainly food abundance which is thought to determine between-group competition (Isbell 1991), other studies show that food distribution also plays a role (Kinnaird 1992; Kinnaird and O´Brian 2000). When groups overlap in their home ranges and individuals suffer from a reduced resource intake due to previous patch depletion by other groups, between-group scramble (BGS) competition is present (van Schaik 1989). In BGS, net food intake rates are influenced by population density, being lower when population density is high (van Schaik 1989). Whenever food patch characteristics allow, scramble competition will be replaced by contest (van Schaik 1989). Between-group contest (BGC) is predicted when food resources are defensible by a group, of high quality, and when general food abundance is low (Wrangham 1980; Isbell 1991; Koenig 2002), although some studies find more aggression between groups when food abundance is high (Kinnaird 1992). Aggression between groups generally leads to the larger group gaining access to the resources, thereby increasing their energy status and energy intake rates (Janson and van Schaik 1988; Isbell et al. 1990; Isbell 1991; Koenig 2002), which can positively affect their reproductive success (Cheney and Seyfath 1987; Robinson 1988; Suzuki et al. 1998). Some socioecological models have predicted that strong BGC combined with strong WGC leads to social tolerance in within-group relationships, because high-ranking individuals may be restricted in enforcing their dominance so as not to lose the coalitionary support of lower-ranking individuals during between-group competition (Sterck et al. 1997). However, a test of these assumptions in Hanuman langurs, *Semnopithecus entellus*, showed that social relationships are probably only weakly affected by BGC (Lu et al. 2008).

Evaluations of the predictive power of the socioecological models revealed a number of mismatches between predictions of the verbal models and empirical data (Isbell 1991; Janson 2000; Koenig 2002; Koenig and Borries 2006; Sussman and Garber 2011; Clutton-Brock and Janson 2012), which led to a call for abandoning the model (Thierry 2008). However, these mismatches may result from uncritical or inaccurate testing of the assumptions (Koenig and Borries 2009), like the uncritical use of the folivore-frugivore dichotomy (Snaith and Chapman 2007; Schülke and Ostner 2012; Sayers 2013; Wheeler et al. 2013). Another justified critique is the lack of control for phylogeny, which is important to consider because phylogenetic history explains some of the observed variation in social relationships between taxa (Rendall and di Fiore 1995; Koenig and Borries 2009; Kappeler and Kraus 2010; Clutton-Brock and Janson 2012; Koenig et al. 2013; Thierry 2013). Other mismatches may result from inaccurate ecological measurements (e.g. measuring food distribution on an inappropriate scale without considering group spread: Koenig and Borries (2006), Hirsch (2007)) and unclear definitions of relevant resource characteristics (Isbell and Young 2002; Koenig and Borries 2006; Snaith and Chapman 2007; Vogel and Janson 2007; Koenig et al. 2013). For example, what exactly constitutes a clumped or patchy distribution is not defined by the socioecological models (Isbell and Young 2002). Measures of patchiness are largely scale-dependent, i.e. food can be distributed at random on a small scale (“bite” level), but clumped on a larger scale (“meal” level), or vice versa (Kotliar and Wiens 1990; Johnson et al. 2002). The model needs more specific definitions to prevent different interpretations by different researchers, and we need more accurate measurements of relevant resource characteristics (Koenig and Borries 2006; Vogel and Janson 2007; Clutton-Brock and Janson 2012). One important measurement improvement was introduced by Vogel and Janson (2007), by suggesting to measure feeding competition, its rank related costs and benefits and food abundance from the perspective of the study animal, rather than from a botanical perspective (focal-tree method: Vogel and Janson (2007)). This approach was used in my current thesis. Another factor which might account for some of the observed discrepancies might be an overly-strong focus on feeding competition in many studies, without considering the influence of predation risk (see below under 1.4.), which might hamper the interpretation of results. Overall, attempts to improve the model should be implemented before we give up and abandon it entirely (Isbell 1991; Koenig 2002; Koenig and Borries 2006; Clutton-Brock and Janson 2012; Schülke and Ostner 2012).

1.3 Feeding competition and ranging behavior

Feeding competition has direct effects on ranging behavior, i.e. on daily travel distance and home range use (Isbell 1991; Chapman and Chapman 2000b). Most important and well accepted is the group size effect (Chapman and Chapman 2000b; Schülke and Ostner 2012). Larger groups have higher total nutritional requirements and deplete food patches more quickly, and so may be required to increase their daily travel distance and expand their home range size in order to exploit more food patches (Milton and May 1976; Clutton-Brock and Harvey 1977; Janson 1988b; van Schaik and van Noordwijk 1988; Isbell 1991; Janson and Goldsmith 1995; Chapman and Chapman 2000b; Majolo et al. 2008; Isbell 2012; Schülke and Ostner 2012). This requires that food is distributed in discrete patches, which is generally the case for frugivorous and at least for some folivorous primates (Koenig et al. 1998; Chapman and Chapman 2000b; Gillespie and Chapman 2001; Isbell 2012). Such an increase in time and energy spent traveling in larger groups sets an upper limit to group size, an idea which forms the foundation of the ecological constraints model (Wrangham 1979; Wrangham 1980; Chapman et al. 1995; Chapman and Chapman 2000b; Gillespie and Chapman 2001). The predictions of this model were recently tested and confirmed by a meta-analysis on non-human primates, where larger groups indeed showed larger daily travel distances and spent more time feeding per day than smaller groups (Majolo et al. 2008). The group size effect described by the model is due to exploitation competition and patch depletion, i.e. due to within-group scramble competition (Chapman 1988; Wrangham et al. 1993; Chapman and

Chapman 2000b). Whereas all authors agree on this effect of WGS on day range, only Isbell indirectly predicts an additional effect of WGC on day range (Isbell 1991; Isbell and Young 2002). She found that in species with strong dominance hierarchies, which she takes as evidence of WGC, increased group size was significantly related to increasing daily travel distance, whereas no relationship existed in species with weak dominance hierarchies (Isbell 1991).

Apart from the day range effect described above, feeding competition can also act on home range size. When neighboring groups contest for food, larger groups have higher competitive abilities (Wrangham 1980; Janson and van Schaik 1988; Crofoot and Wrangham 2010) and can thus obtain a larger home range size (Cheney and Seyfath 1987; Isbell et al. 1990; Isbell 1991; Isbell and Young 2002). Whether between-group scramble also affects home range size is debated. Some authors argue that BGS results in larger home ranges with increased group size (Isbell 1991; Isbell and Young 2002), whereas others doubt this effect as BGS is dependent on population density and not on group size (van Schaik 1989; Snaith and Chapman 2007).

Competition between groups can be generally solved in two ways. Where it is economically feasible and cost-efficient (Brown 1964), territories are established, which are areas within a home range where the territory holder(s) have exclusive or priority of access to resources (Noble 1939; Burt 1943; Hixon 1980; Powell 2000). These territories are defended from others of the same species by aggression, scent marking, calls or displays (Powell 2000). Territories commonly exist in birds, certain fish and insects (Gerking 1953; Odum and Kuenzler 1955; Brown 1969; Alcock and Houston 1987; Parr and Gibb 2010), in some reptiles (Simon 1975; Smith 1985; Baird 2013), bats (Bradbury and Vehrencamp 1976; Winkelmann et al. 2003), rodents (Ostfeld 1985), ungulates (Alvarez et al. 1990; Balmford et al. 1992), carnivores (Bekoff and Wells 1982; Lindström 1986; Heinsohn 1997) and some primates (Mitani and Rodman 1979; Lowen and Dunbar 1994; Crofoot and Wrangham 2010).

Defending a territory is not always economically feasible, especially not for species living in habitats with high temporal and spatial variability of food resources, where large home ranges are needed (Johnson et al. 2002). Under these conditions, or when food is superabundant (Carpenter and MacMillen 1976; Powell 2000), home ranges are not defended and home ranges overlap largely between neighbors. Competition is then solved during more or less frequent aggressive intergroup encounters. Based on the strong asymmetry in reproductive effort by females and males (Trivers 1972), competition over food and thus food resource defense was for a long time assumed to be a female affair, whereas males were thought to primarily defend mates (Trivers 1972; Emlen and Oring 1977). This principal has been used to argue that females should be the primary participants in between-group contests over food (Wrangham 1980; van Schaik 1989; Sterck et al. 1997). However, mate defense can indirectly lead to defense of critical food resources for females, whereby males act in the females' interest as "hired guns" (Wrangham 1980; Wrangham and Rubenstein 1986). Direct male resource defense, however, also exists in various taxa throughout the animal kingdom, e.g. in bees (Alcock and Houston 1987), beetles (Forsyth and Alcock 1990), bats (Winkelmann et al. 2003), hummingbirds (Wolf and Stiles 1970), deer (Clutton-Brock et al. 1988) and primates (Harrison 1983; Fashing 2001; Cooper et al. 2004; Williams et al. 2004; Koenig et al. 2013). Male resource defense can increase the reproductive rate of females (Robinson 1988; Williams et al. 2004), and thus also indirectly benefits males' reproductive success.

Socioecological theory suggests that strong between-group contest competition should favor larger groups as they have a higher competitive ability and are more likely to win an encounter (Wrangham 1980; Janson and van Schaik 1988; Majolo et al. 2008). The suggested higher competitive advantage of larger groups is however not always confirmed by empirical data (wild dogs: Bonanni et al. (2010); primates: Crofoot et al. (2008), Crofoot and Gilby (2012)). One major reason is that larger groups are more likely to suffer from a collective action problem (Olson 1965; Nunn 2000; Willems et al. 2013), as individuals have a higher temptation to flee or not to participate in aggressive encounters (Kitchen and Beehner 2007; Crofoot and Gilby 2012). Effective territory defense can break down and home range overlap with neighbors can increase (Willems et al. 2013). Whether individuals defect or cooperate is largely influenced by the encounter location, showing a "home-field" advantage with higher readiness to engage in encounters and higher chances of winning in the center of a home range (Crofoot et al. 2008; Crofoot and Gilby 2012; Scarry 2013). Such a "home-field" advantage also exists in territorial living pairs of birds (Krebs 1982).

1.4 Neglected aspects of socioecological theory and aims of the study

In most socioecological models, predation risk constitutes an important factor in determining social relationships and feeding competition (van Schaik and van Hooff 1983; Terborgh and Janson 1986; Janson 1988b; van Schaik 1989; Sterck et al. 1997; Nunn and van Schaik 2000; Koenig et al. 2013). Primates are generally threatened by three main types of predators: large carnivorous mammals, raptors and snakes (Cheney and Wrangham 1987; Miller 2002; Miller 2007; Fichtel 2012). Especially in primates, group cohesiveness seems even more important than group size *per se* for an individual's perception of predation risk (Treves 1998; Treves 2000). Based on Hamilton's model (Hamilton 1971) of the selfish herd, individuals are predicted to seek a close distance to other individuals to reduce the chance of being predated ("domains of danger"), therefore increasing spatial cohesion (Treves 1999b). A comparison between folivorous primates indeed showed that the risk of aerial predators increases a group's cohesiveness (van Schaik and Hörstermann 1994), and also other taxa like birds form more compact and larger flocks when predation pressure by raptors is increased (Carere et al. 2009). When the number of close conspecific neighbors increases, feeding competition should equally increase, therefore posing a cost on individual food intake rates (Janson 1988b; van Schaik 1989; Ron et al. 1996; di Bitetti and Janson 2001; Carbone et al. 2003). In contrast, if species face low predation risk, individuals can avoid competition without costs by a) foraging more dispersed, and b) using alternative food patches, which should be reflected in a larger total group spread (Janson 1988b; van Schaik 1989; Koenig 2002; Koenig and Borries 2006). Low predation risk may also allow individuals to feed in smaller parties (Terborgh and Janson 1986). So far, empirical studies on feeding competition have rarely considered predation risk (but see e.g. Mitchell et al. 1991; Kohlhaas 1993; Cowlishaw 1997; Wittig and Boesch 2003), which might explain some of the mismatches between the socioecological models' predictions and empirical results (Isbell 1991; Janson 2000; Koenig 2002; Koenig and Borries 2006; Sussman and Garber 2011; Clutton-Brock and Janson 2012). Also, few studies have been conducted in low predation pressure environments (but see studies on Japanese macaques, *Macaca fuscata*, e.g. Agetsuma (1995b), Saito (1996), Hanya et al. (2008), Majolo et al. (2009) and Sulawesi macaques, e.g. Matsumura (1998), Kohlhaas (1993); see also Nunn and van Schaik (2000) for predation risk categories).

To address this gap of research, I studied within-group feeding competition in one group of Siberut macaques (*Macaca siberu*) endemic to a small oceanic island called Siberut, situated offshore of West Sumatra. Oceanic islands are, in contrary to continental islands, not connected to continental shelves (Whittaker and Fernandéz-Palacios 2007). Due to their small size and history, these islands typically lack felid predators, e.g. clouded leopards, tigers and golden cats which occur on mainland Sumatra are absent on the islands off West Sumatra (van Schaik and van Noordwijk 1985; Wilting et al. 2012). I conducted my study at the field site of the Siberut Conservation Programme (SCP), run by the German Primate Center (DPZ), Göttingen, Germany, and the Bogor Agricultural University (IPB), Bogor, Indonesia. After habituation of a group of Siberut macaques (Dec. 2008 – Mar. 2010), I collected ecological, behavioral, and botanical data from March 2010 until March 2011, with the help of various field assistants and local guides.

Before testing some of the predictions of the socioecological models under low predation risk, it was necessary to first describe the basic ecology of Siberut macaques. No quantitative ecological data on Siberut macaques existed before the start of my study, due to their limited distribution on just one very remote island. Comprehensive ecological data are also urgently needed because of the rapidly progressing habitat loss and their population decline (Whittaker 2006). Thus, as a baseline for conservation strategies and a first step to study feeding competition, I described the group's diet and activity budget, the forest structure and habitat use, and studied their ranging behavior and requirements (**Chapter 2**).

Socioecological models predict that under low predation risk, within-group feeding competition is reduced as individuals can a) disperse more during foraging and feeding, i.e. the group spread can be flexibly adapted to the resource characteristics, and b) individuals can feed alone or in small feeding groups, with minimal risk of predation (Terborgh and Janson 1986; Janson 1988b; van Schaik 1989; Koenig and Borries 2006; Schülke and Ostner 2012). To test these predictions, I investigated general food resource characteristics such as food patch size, density, distribution, depletion and availability to estimate first whether a potential for contest competition exists (**Chapter 3**). As the diet of Siberut macaques turned out to consist largely of fruits, I focused my study on the use of and competition over fruit resources. Food patches were defined as individual fruit plants. I adopted the focal tree method developed by Vogel and Janson (2007) to measure feeding competition from the perspective of the study animals. I described the group spread of Siberut macaques during their regular activities and investigated whether individuals form sub-groups or spread out continuously. I predicted that given the low predation risk on Siberut, individuals should be more flexible in their foraging strategies, being able to disperse more to avoid competition when necessary, expressed by occasionally large inter-individual distances for their group size (compared to available data for species under medium to high predation risk). I calculated food patch densities within the average group spread to achieve a more accurate measurement of food distribution from the animals' perspective (see critique of the socioecological models above). I used the focal tree method to calculate aggression rates in food patches and predicted that the aggression rate of Siberut macaques would be lower than in other primate species living in medium to high predation pressure environments. I furthermore investigated which social and ecological factors influence frequencies of aggression. I predicted that the frequency of aggression should increase with increasing feeding group size (the number of individuals feeding together in a patch), the number of total adult females and males using the patch, and feeding bout length as a measure of opportunity for aggression. I furthermore predicted that aggression frequency decreases with increasing fruit abundance, fruit availability in the forest, space per individual, and number of alternative resources close by (Chapter 3). Although my main focus was on the influence of low predation risk on within-group contest competition, I also investigated patch depletion as a measure of within-group scramble competition (Chapter 3).

A second gap in socioecological research concerns the role of males in between-group competition. So far, male food resource defense during intergroup encounters has been overlooked and was ignored in socioecological models (Koenig et al. 2013), mainly because only females were thought to be responsible for food defense (Emlen and Oring 1977; Sterck et al. 1997). Accumulating evidence shows that males also engage in food resource defense in chimpanzees, *Pan troglodytes* (Williams et al. 2004; Wilson et al. 2012); black-and-white colobus, *Colobus guereza* (Fashing 2001; Harris 2010), *Colobus vellerosus* (Sicotte and Macintosh 2004) and *Colobus polykomos polykomos* (Korstjens et al. 2005); grey-cheeked mangabeys, *Lophocebus albigena* (Brown 2011); green monkeys, *Cercopithecus (aethiops) sabaeus* (Harrison 1983); redtail monkeys, *Cercopithecus ascanius* (Brown 2011); wedge-capped capuchins, *Cebus olivaceus* (Robinson 1988); white-faced capuchins, *Cebus capucinus* (Crofoot 2007); tufted capuchins, *Sapajus nigritus* (Scarry 2013); brown titi monkeys, *Callicebus brunneus* (Lawrence 2007); black howler monkeys, *Alouatta pigra* (Chaput 2001); white-handed gibbons, *Hylobates lar* (Reichard and Sommer 1997); bonnet macaques, *Macaca radiata* (Cooper et al. 2004) and Japanese macaques, *Macaca fuscata* (Saito et al. 1998). For pig-tailed langurs, *Simias concolor*, no direct evidence exists yet, but males give loud calls more frequently when fruit availability is low, indicating that males also might defend food resources in this species (Erb 2012). In addition, males of other well-studied species might defend food resources as well, but this may have been overlooked because multiple aspects of food characteristics (e.g. food abundance, distribution, patch size, frequency of feeding site use) were not considered (Brown 2011; Brown 2013). Overall, this suggests that male resource defense is more common than previously believed (Fashing 2001). If groups with more males are dominant and win the contest between groups, they should have larger home ranges and preferred access to food resources in overlapping areas, which should translate into long-term benefits for female reproductive success (Williams et al. 2004; Scarry 2013). In **Chapter 4** I aim to investigate the consequence of male group size on home range size in Assamese macaques (*Macaca assamensis*). Assamese macaques are an ideal study species because large variations exist in male and total group size, and males are known to participate in intergroup contests. In order to address this question, I used a data set of more than 6 years of ranging data coming from the long-term field project at Phu Khieo

Wildlife Sanctuary in Northeastern Thailand, run by Julia Ostner and Oliver Schülke. I predicted that monthly home range size is positively influenced by male group size. If this determines the amount of food resources which can be accessed (Scarry 2013), larger home ranges are predicted to increase female reproductive success, from which males will benefit as well. The size of a home range is well known to be linked to group size, daily travel distance, and to ecological variables like food availability and distribution, temperature, and precipitation (Clutton-Brock and Harvey 1977; Isbell 1983; Isbell 1991; Newton 1992; Janson and Goldsmith 1995; Chapman and Chapman 2000b; Peres 2000; Kaplin 2001; Yiming 2002; Ganas and Robbins 2005; Wallace 2006; Baoping et al. 2009), which therefore need to be controlled for. To control for variations in habitat quality, which is known to influence the size of a home range (Takasaki 1981), I investigated the group's site fidelity, i.e. the stability of home range boundaries over different years. In addition, I evaluate and discuss the possible motivation of Assamese macaque males to participate in between-group contests and resource defense, and why the collective action problem, which is apparent in most primates (Willems et al. 2013), does not constitute a problem in this species.

Chapter 2

Ecology of an endemic primate species (*Macaca siberu*) on Siberut Island, Indonesia

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SpringerPlus 2013, 2:137

2.1 Abstract

Logging and forest loss continues to be a major problem within Southeast Asia and as a result, many species are becoming threatened or extinct. The present study provides the first detailed and comprehensive ecological data on the Siberut macaque (*Macaca siberu*), a primate species living exclusively on the island of Siberut off the west coast of Sumatra. Our results show that *M. siberu* is ecologically similar to its closest relative *M. nemestrina* occurring on the mainland, both species being semi-terrestrial, mainly frugivorous (75-76%), exhibit a large daily travel distance for their group size and spend more time on traveling than any other macaque species. The habitat of Siberut macaques was floristically very diverse (Simpson's index D=0.97), although somewhat impoverished in tree species richness, and had a lower tree basal area and a lower rattan density compared to other forests in Malesia (both rattan and palm tree fruit being an important food resource for *Macaca siberu* due to their long fruiting periods). These factors may lead to a lower diversity and abundance of fruit resources, and coupled with a high degree of frugivory of Siberut macaques, may explain the large amount of traveling observed in this species. The large home range requirements and strong dependence on fruit are important factors that need to be considered when developing conservation measures for this IUCN-listed (Category Vulnerable) species.

Keywords

macaque ecology, species comparison, Southeast Asian rainforest, endemic species, conservation

2.2 Introduction

Tropical rainforests occupy only 7% of our Earth’s land surface but are home to over half of all the species on the planet (Thomas and Baltzer 2002). They are of great importance for the world’s economy and ecology by providing timber, food products and pharmaceuticals, and because they play a major role in the global carbon cycle (also as carbon sinks) and shape local climate patterns (Laurance 1999; Thomas and Baltzer 2002; FAO 2010). While the area of planted forest and conservation efforts are steadily increasing, forest loss and conversion still continue globally at high rates (1990-2000: 16 million ha, 2000-2010: 13 million ha; FAO 2010). Especially in Southeast Asia, which has experienced fast development in the last decades, deforestation rates increased drastically (1880-1980: 0.3%, 1990-1997: 0.91%, 2000-2010: 1%; Flint 1994; Achard et al. 2002; Miettinen et al. 2011), with Indonesia being one of the most critical countries (FAO 2010), and Sumatra among the most critical regions (1985-2007: 48% forest cover loss; Achard et al. 2002; Hansen et al. 2009; Laumonier et al. 2010; Miettinen et al. 2011). While forest loss continues, many of the species existing in these tropical habitats still remain to be discovered or described. The role of these species within the ecosystem is still unknown, and reduction in species diversity may lead to the loss of important services for the ecological community (Díaz et al. 2006).

In this environmentally critical region lies the Mentawai Archipelago, consisting of four small islands 85 to 135km off the west coast of Sumatra, Indonesia (Whitten 1982c; Fuentes 1996/1997; Whittaker 2006). It is part of the biodiversity hotspot Sundaland, which covers Malaysia, Brunei, Singapore and the western half of Indonesia (Mittermeier et al. 1999; Myers et al. 2000; Myers 2001; Mittermeier et al. 2004). Among all 34 biodiversity hotspots worldwide, Sundaland has the highest number of endemic plant species (15,000 - same as Tropical Andes) and the highest number of endemic mammal species (173), of which 81% are already listed as threatened by IUCN (Mittermeier et al. 2004: p. 32-33, 64). This high species richness and endemism in Sundaland cannot be attributed to the amount of habitat alone, as Sundaland only ranks twelfth among all hotspots, with 100,571 km² of moist broadleaf forest (Mittermeier et al. 2004: p. 32). Rather, it is most likely the result of a dynamic geological past of Quaternary glaciations and episodic sea-level changes, during which Sundaland was repeatedly connected to the Asian mainland, enabling species migrations from the mainland to the islands of Sundaland (Gathorne-Hardy et al. 2002; Meijaard 2003; Sodhi et al. 2004; Woodruff 2010; Gower et al. 2012). Additionally, the rise in sea-level and increased isolation of islands which occurred during interglacial periods facilitated the speciation process (Sodhi et al. 2004). Furthermore, during the Pleistocene, some parts of Borneo and the northern and western part of Sumatra, including the Mentawai Islands, acted as rainforest refugia, enabling the survival of these rainforest biota (Gathorne-Hardy et al. 2002; Meijaard 2003).

The Mentawai Islands, of which Siberut is the largest and northernmost island, have been separated from the mainland for over 0.5 m years (Mitchell and Tilson 1986; Voris 2000; Bird et al. 2005). Even at times when sea level was so low that the rest of Sundaland was connected, the 1,700m deep Mentawai Basin maintained the separation of the islands from the mainland (Brune et al. 2010). In fact, the Mentawai Islands were never connected to Sundaland directly, but were linked to Sumatra via a land bridge from Siberut through the Batu Islands (Whittaker 2006). As a result of this long period of geographic isolation, the Mentawai Archipelago has evolved a distinct flora and fauna with a high level of endemism, and allowed the survival of a number of “primitive” forms of considerable evolutionary interest (WWF 1980).

The flora of Siberut is estimated to comprise about 15% endemic plant forms, but the figure is out of date and new research is needed (WWF 1980). Of those species also known from other areas in Southeast Asia, some developed distinct traits on Siberut (WWF 1980: p. 13). The Mentawaian fauna includes 43 mammal species, of which 42% are endemic to Mentawai, and without bats, the endemism level increases to 71% (Thorington Jr. et al. 2012; Wilting et al. 2012). That the fauna of Siberut still remains understudied was recently shown by Kemp (2000), who recorded 28 new bird species for the island.

The ecosystems on small isolated islands such as Siberut are usually shaped by a range of different factors: Firstly, small islands often have an impoverished flora and fauna compared to the mainland, since species richness has been shown to decrease with land area (MacArthur and Wilson 1967; Simberloff 1974; Heaney 1984; Burkey 2002; Kreft et al. 2008; Nijman and Meijaard 2008). Usually the poorly dispersing species or large animals with large home range requirements are absent on small islands (Simberloff 1974; Heaney 1984). Secondly, a lack of certain species or whole taxa is usually associated with increased density of a few other species (density compensation) and a broader niche of island species compared to their relatives on the mainland (niche expansion), where competition for the same resources is higher (MacArthur et al. 1972; Buckley and Jetz 2007; Yoder et al. 2010). Niche expansion or niche shifts between islands and the mainland can concern habitat, vertical foraging strata, altitudes, foraging techniques and diet (MacArthur et al. 1972; Yoder et al. 2010). On Siberut, such niche expansion has been demonstarted for the spangled drongo (*Dicrurus hottentotus*) and three squirrel species (*Callosciurus melanogaster, Sundasciurus (lowii) fraterculus, Lariscus obscurus*: Whitten 1981; Whitten 1982e). On islands, fewer species compete for the same niche, so that evolutionary pressure becomes lower and populations or species evolve less rapidly. Thus, more "primitive" (archaic) forms can be maintained than on the mainland (WWF 1980; Patou et al. 2010). Despite these general trends geographical isolation can also lead to the evolution of new forms (Yoder et al. 2010).

Primate species richness on Mentawai is unusually high. On a land surface area of only 6,549 km², Mentawai harbors five endemic primate species (Fuentes 1996/1997), the Kloss gibbon (*Hylobates klossii*), the Mentawai langur (*Presbytis potenziani*), the pig-tailed langur or pig-tailed snub-nosed monkey (*Simias concolor*), the Pagai island macaque (*Macaca pagensis*) and the Siberut macaque (*Macaca siberu*). Whereas the first three species occur on all four islands, *M. pagensis* only occurs on the three southern islands, and *M. siberu* exclusively on Siberut. All Mentawaian primates are included in the IUCN Red List of Threatened Species (IUCN 2012). They are threatened by habitat loss due to legal and illegal logging, conversion of the forest into oil palm plantations, forest clearing, extraction of forest products (such as rattan), hunting and pet trade (Whittaker 2006). In Siberut, forest cover has decreased to 60% (by 2005; Whittaker 2006), but part of it is protected by the national park, which includes 465 km² of protected "no-use" sanctuary zone where no hunting and logging is allowed (WWF 1980; Fuentes 1996/1997; Whittaker 2006).

Of the four primate species occurring on Siberut, the Kloss gibbons, the Mentawai langurs and the pig-tailed langurs have been reasonably well studied (e.g. Tenaza 1975; Tilson 1977; Watanabe 1981; Tilson and Tenaza 1982; Whitten 1982a; Whitten 1982b; Whitten 1982c; Tenaza and Tilson 1985; Fuentes 1996; Hadi et al. 2009a; Erb et al. 2012b; Hadi et al. 2012). In contrast, studies on the Siberut macaque are mainly limited to investigations on population size, acoustic traits, phylogenetic relationships and some preliminary observations on ecology (Whitten and Whitten 1982; Abegg and Thierry 2002b; Roos et al. 2003; Ziegler et al. 2007; Schneider et al. 2008; Waltert et al. 2008; Quinten et al. 2009). Initially, Siberut macaques were thought to be a subspecies of southern pigtail macaques (*Macaca nemestrina pagensis:* Fooden 1975) or of the Mentawai/ Pagai macaque of the southern Mentawai Islands (*Macaca pagensis siberu:* Fuentes and Olson 1995; Groves 1996). Recently, however, genetic and morphological studies have allowed their classification as a distinct species called *M. siberu* (Kitchener and Groves 2002; Roos et al. 2003), being more closely related to *M. nemestrina* on Sumatra and Malaysia than to *M. pagensis* on the neighboring Mentawai Islands (Ziegler et al. 2007). So far, no detailed and comprehensive systematic behavioral or ecological studies have been conducted on Siberut macaques.

The present study aimed to gather basic ecological knowledge about the endemic Siberut macaques, including home range requirements, habitat and forest structure use and feeding habits. The data will add substantially to what is known about the ecological range of the genus *Macaca*, which is among the most successful non-human primate genera with more than 20 species distributed from North Africa throughout Asia up to Japan (Abegg and Thierry 2002a). Siberut macaques, as part of the *silenus-sylvanus* lineage, are thought to represent a relict species from the earliest wave of macaque dispersal and thus may also help to understand the ancestral traits of this genus (Fooden 1980; Abegg and Thierry 2002a; Roos et al. 2003; Ziegler et al. 2007). We compared the new data on Siberut macaques with available data from other macaque species, in order to understand the range of ecological variations, and with data on Siberut's other primate species with the aim of investigating possible niche differentiations. In addition, we present data on the habitat of Siberut macaques to investigate whether the forest is impoverished as island biogeography theory would predict, which could have important impacts on the behavior of Siberut macaques. The data should also be useful in the development of much needed conservation guidelines for the species.

2.3 Methods

Study area

The study was conducted on Siberut Island, which comprises 4,030km² and a human population of ~25,000 people (Fuentes 1996/1997; Whittaker 2006). Siberut has a strongly dissected, rugged landscape of numerous steep slopes and ravines (highest elevation: 384m a.s.l.), and many rivers and streams (WWF 1980; Watanabe 1981). The island is covered by tropical lowland evergreen broadleaf rainforest (UNEP-WCMC classification) or tropical moist broadleaf forest (WWF classification). Different vegetation types can be distinguished: primary dipterocarp forest on high ridges (dominated by Dipterocarpaceae), primary mixed forest on slopes and lower hills (mixed composition of tree families with none being dominant), freshwater swamp forest, mangrove forest and Barringtonia forest on the West coast of Siberut (WWF 1980). The soil on Siberut is less fertile than on the Malay Peninsular (Whitten 1980b; Whitten 1982a). The study was conducted at the field site of the Siberut Conservation Programme (SCP; www.siberut-island.org), situated within the Peleonan Forest in North Siberut (Figure 2.1). The Peleonan Forest comprises 4,500ha rented by SCP for conservation purposes, surrounded by logging concessions and the Indian Ocean. It consists of undisturbed primary rainforest (i.e. with no signs of human impact) and some secondary forest at late successional stage. The climate is equatorial, with no seasonal changes in temperature. Temperature recorded during February 2010 and March 2011 ranged between 20.7°C and 35.2°C, with a monthly average of 25-27°C. There are only small seasonal changes in precipitation, and during our study, March was the driest month, and October to January the wettest period (max. precipitation per day: 150 mm/m³). Long-term climate data over 50 years show a mean annual precipitation of 3,601 mm at our study site, and every month of the year is perhumid, receiving at least 200 mm of rain (see Figure 1 in Erb et al. 2012a).

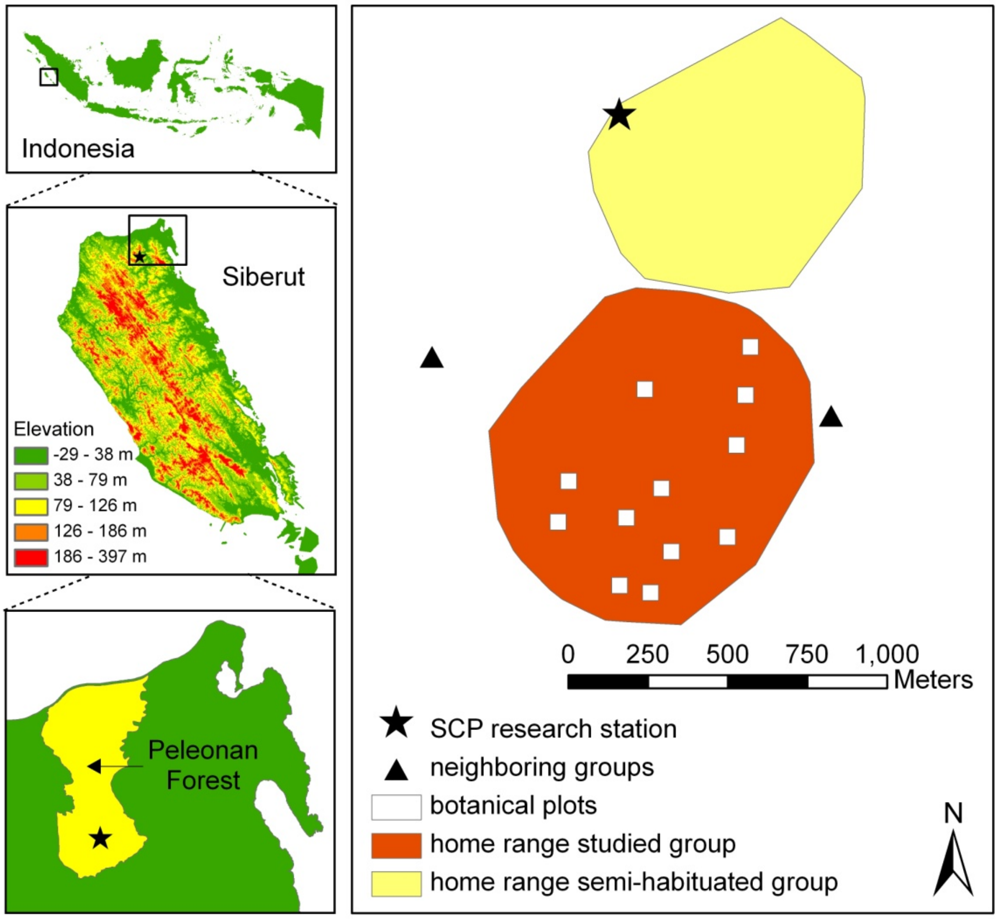

Figure 2.1 Location of Siberut, the Peleonan Forest (rented by SCP for conservation purpose) and the study site (SCP research station). The right map shows the 95% MCP home ranges of the studied group A (bottom), the semi-habituated group B (top) and locations of encounters with other neighboring groups of Siberut macaques. Small squares within the study group's home range indicate the 12 botanical plots.
Data source: 90m digital elevation data come from Shuttle Radar Topography Mission (SRTM) by USGS/ NASA (http://srtm.csi.cgiar.org).

Study group

The study group (group A) was habituated from December 2008 until March 2010. Habituation was done by searching the group silently from sunrise to sunset with two to four teams simultaneously on six days per week. Once macaques were encountered, geographical position, subgroup size and activity was recorded. Beginning of 2010, at the end of the habituation period and when data collection started, group size was 29. There were 3 permanent adult males and 8 adult females in the group. Adult individuals were the main focus of this study and were all identified, except two of the adult females which were first seen at the end of the study. We assume that they were already part of the group throughout the data collection period, but were never reliably identified before as they might have stayed very peripheral and shy. Adults were defined as those individuals who were sexually fully mature, i.e. had large testes in males and visible nipples in females. By the end of the study period, during the mating season in January and February 2011, 3 juvenile females developed their first sexual swelling. From the juveniles, only a few individuals were identified, the rest was recorded as age-sex category during data collection.

As this group of Siberut macaques is the first one ever studied in detail, we report some information on the life history and demography. Infants are born with white fur and reddish facial skin, hands and feet. After few weeks, their fur coloration changes to juvenile/adult like dark brown coat with only small white fur patches left around the temples and a slightly lighter breast fur. At an age of about 2.5 months, the coloration change is complete. During the course of this study several births occurred (Mar.-Apr. 2009 3 birth, Sep.-Oct. 2009 4 birth (1 died), Jan. 2010 1 birth, Jul. 2010 1 birth (died at 2 month age)).

The studied group was surrounded by several other groups of conspecifics (Figure 2.1), including one group (group B) which was habituated from May to November 2009 and occasionally came to the research station when trees were fruiting there.

Data collection

Group scan observations (scan sampling: Martin and Bateson 1993) were conducted from March 2010 until March 2011, from 6am until latest 7:30pm, by 1 to 3 observers simultaneously (69.3% by 1 observer, 27.0% by 2 observers, 3.7% by 3 observers). Scans were taken every full hour (sampling duration: 10min) in the first month, and were changed to every 30min at half and full hours for the rest of the time period (sampling duration: 5min per scan). Data in March 2011 were too scarce and were omitted for some analyses. During group scans, the following data were recorded: time, identity of the monkeys, type of habitat (forest, canopy gap, windthrow area, swamp), relative and absolute height of the monkey in the forest, activity and in case they were feeding, the food item and species, as well as the GPS coordinates.

To calculate the monthly percentage of habitat use, we scored for each scan the habitat type used by the majority (>50%) of individuals. Canopy gap was defined as a small open area within the forest caused by a treefall. Windthrow area was a forest area hit by a heavy storm, which destroyed nearly all trees in that specific area.

Forest strata use was measured as the absolute forest height used by the monkeys (in 5m steps) and the relative height used. Values for the whole group are based on the average of the values of each age-sex class (adult males, adult females, juveniles). The relative forest height describes the height of the monkey relative to the forest at a certain place in the forest, and was divided into 4 categories: ground (soil and leaf litter), lower-story (substrates on the ground, including fall-down trees, up to the mid-story), mid-story (either a tree that ends below the canopy at this place in the forest or the lower branches of a tree that make up the canopy) and canopy (the crown of the tree that makes up the canopy at this place in the forest).

The general activity of the monkeys at a scan time was classified as either traveling, resting, feeding (inserting food into the mouth, handling/ manipulating food; but not processing food which was already stored in the cheek pouch), foraging (searching for food), and social activities (allogrooming, mating, playing). Activity budget is given as the monthly average of 12 months, from March 2010 until February 2011.

Diet was based on the percentage of feeding time on different food items based on scan data. Food item categories were fruit, flower, arthropods, mushrooms, leaves, pith (soft core of palm stems), sap and shoot (young stems). The overall diet was calculated as the average over 12 months (Mar. 2010 – Feb. 2011). The dietary diversity index was calculated using the Shannon-Wiener index H’ (Pielou 1966; Krebs 1999). The index combines information on species richness as well as relative abundance. For calculation of H’, only food items of known species were used, which included fruit, flower, pith, sap and some of the leaves. Mushrooms and arthropods were not identified to species level and were thus not included in the index.

GPS points were recorded for 2,267 scans in a geographic coordinate system in a Lat/Lon format (Datum: WGS 84) and later converted into the projected coordinate system WGS 1984 UTM Zone 47 South. We only used GPS coordinates of permanent group members for home range analysis. Home range was calculated as Minimum Convex Polygon (MCP, Worton 1987; Harris et al. 1990; White and Garrott 1990; Börger et al. 2006) to allow comparison with older studies, and with Kernel methods using reference bandwidth h_{ref}, which equaled 63.85m (Silverman 1986; Worton 1989; Wand and Jones 1995; Worton 1995; Seaman and Powell 1996; Kenward 2001). We also applied the “ad hoc” bandwidth $h_{ad\ hoc}$ (Berger and Gese 2007; Jaques et al. 2009; Kie et al. 2010), but results were similar to h_{ref} and are not reported. For MCP calculation (with “fixed means”), we used 4,839 unique point locations (duplicate fixes removed) and calculated 100% (the maximum area in which the group was ranging), 95% (full home range, reducing the outlier effect), and 50% MCPs (core home range). For kernel polygons, average GPS coordinates were calculated for each scan as the center of the group, as GPS points of single individuals per scan are not independent, resulting in 2,410 point locations. Points were jittered by ±0.5m to avoid point duplicates, and kernels were constructed using fixed kernel approach, Gaussian (bivariate normal) kernels, a raster cell size of 20m and a buffer of 25m (the median distances to the group center). Although group center coordinates per scan were autocorrelated, we used all for kernel analysis because removing autocorrelation would also remove biologically significant information (Lair 1987; Reynolds and Laundre 1990; de Solla et al. 1999; Blundell et al. 2001; Cushman et al. 2005). We calculated the 95% contour as the full home range and the 50% contour as the core home range. Home range (and travel distance) calculations were done in ArcGIS® 9 (ArcEditor™ 9.3.1), using the Home Range Tools (HRT) extension (Version 1.1), except for the asymptote analysis of home range area, which was done with the extension HoRAE (Nov. 2011) in OpenJUMP 1.4.3.

The monthly average daily travel distance was calculated from group center coordinates per scan (see above). We only used days with ≥9h observation time per day (called “full day follows”). Travel speed (m/h) is calculated as the travel distance per observation day divided by the observation time on that day. As the active period of the group was usually about 12 hours, from 6:30am to 6:30pm, this calculated travel speed was multiplied by 12 to obtain the daily travel distance. Straight line distances of groups in 30min intervals can be different from actual travel distances of individuals (Isbell et al. 1999), so that we also report the average travel speed of single individuals. This is based on focal animal observations of all adult males and females, from August 2010 until February 2011, which aimed to be at least 30min long (mean 33min, max. 127min). For analysis, we only used observations of at least 20min.

For habitat analysis, we established 12 permanent botanical plots of 50m x 50m size (0.25ha each) within the group’s home range (Figure 2.1), in which 25 subplots of 10m x 10m were nested. A total of 3ha was sampled, covering 3.6% of the 95% kernel home range. Plots were distributed semi-randomly, while taking habitat variation, altitude and distance to rivers into account (top of hill: 1, slope: 2, slope/ riverine: 1, riverine/ level ground: 1, dry level ground: 6, edge of swamp: 1). Plots were mainly covering mixed forest, and to a low extent dipterocarp forest. We recorded all trees ≥10cm dbh (diameter at breast height), all palm trees ≥10cm dbh (*Oncosperma horridum*) or ≥5cm dbh respectively (A*renga obtusifolia*, Pinanga sp.), all lianas (woody vines) and stranglers (strangler figs) ≥5cm dbh and all rattan (i.e. climbing palms) longer than 5m. They were marked, measured for dbh, and height (or length for lianas and rattan) was estimated by eye after training with a measuring tape. For trees with buttress roots or prop roots, dbh was measured ~20cm above the rooting point. For clustering (rhizomatous) rattan and palm trees which produce multiple stems, we counted "apparent" genets, following Gerwing et al (2006). For the rhizomatous and very spiny palm tree *Oncosperma horridum*, we recorded the number of stems ≥10cm dbh (important for basal area calculation), and for height and dbh, a mean was estimated. For rhizomatous rattan, dbh and length was measured for each stem separately. We collected two specimen per species with the help of a local plant specialist (31% of species with fruit and/or flower), and described, photographed and dried them in a self-made herbarium oven at 60-75°C in the field. They were identified (using Kooders 1913; Sinclair 1955; Kostermans 1969; Kostermans 1970; van Steenis 1972; Polunin 1988; van Balgooy 1997; van Balgooy 1998; de Wilde 2000; Symington et al. 2004; Yoneda 2004; Berg et al. 2005; Min et al. 2006; Soepadmo et al. 2007) and stored at the Herbarium ANDA of the Andalas University Padang, W-Sumatra. For analysis, we classified species into trees, palm trees, lianas, stranglers and rattan to enhance comparability between plots and other studies (Hadi et al. 2009b). The dbh distribution of trees from botanical plots is compared to 235 sleeping trees (Dec. 2008 – Mar. 2011) and to 73 feeding trees (Mar. 2010 – Mar. 2011; palm trees excluded). Basal area (m^2) was calculated as 3.142 * (dbh in cm/ 200)^2. We measured species diversity with the Simpson's diversity index D, calculated as D = 1- (Σ n*(n-1)/ N*(N-1)), with n being the total number of individuals of a particular species, and N being the total number of individuals of all species. D ranges between zero (no diversity) and one (max. diversity).

Statistical analysis: Spearman rank correlations were conducted in Excel®, and p-values were based on 10,000 permutations. Mann-Whitney-U tests and Chi-Square tests were carried out in R 2.14.0© 2011. Species richness estimators as well as similarity indices were calculated using EstimateS 8.2.0© 2009 (R.K. Colwell). The species richness estimators ACE, ICE, Chao 1, Chao 2, Jack 1, Jack 2 and Bootstrap are reported as the mean of 10,000 randomizations, without replacement. For all analyses, we adopted an α-level of 0.05.

2.4 Results

Home range size and daily travel distance

The total area used by the group during one year was 134.9ha, based on 100% MCP. When excluding outliers, the area was 80.6ha (95% MCP), with a core home range of 26.1ha (50% MCP). Using the fixed kernel method with reference bandwidth, the 95% contour included 84.1ha, and the 50% contour 26.2ha (Figure 2.2). Excluding days with short contact times (<6h per day) did not change the shape or the size (average change of 0.1ha) of the home ranges. Home range size plateaued at ~900 fixes, i.e. 5 full months of observation.

The average travel speed of the group (from group scan data) was 169.6 m/h (SD ± 35.6 m/h, range: 87.8–280.0 m/h, n = 78 days), the average travel speed of single adult individuals (from focal observations) was 206.1 m/h (SD ±143.9 m/h, n = 120 focal follows). The monthly average daily travel distance of the group equaled 2,048.4m (SD ±205.5m, n = 10 months with 6-9 “full day follows” per months), with travel distances of single days ranging between 1,054m and 3,360m. Monthly average daily travel distances tended to increase with the percentage of fruit in the diet ($r_s = 0.64$, n = 10, p = 0.055; see Figure 2.3). The monthly average daily travel distance was 303m more than needed to cross the 100% MCP home range at its widest point. The largest observed distance moved between two consecutive group scan observations was 657m within 30min, and the largest distance moved of a single individual during a focal observation was 542m in 67min (by an adult male). Compared to other macaque species, Siberut macaques traveled more per day than other macaque species of similar group size, but they were similar to *Macaca nemestrina*, to whom they are genetically most closely related (Figure 2.4). Overall, group size was significantly correlated with the distance traveled per day in this comparative data set (Spearman rank: $r_s = 0.46$, n = 32, $p<0.01$).

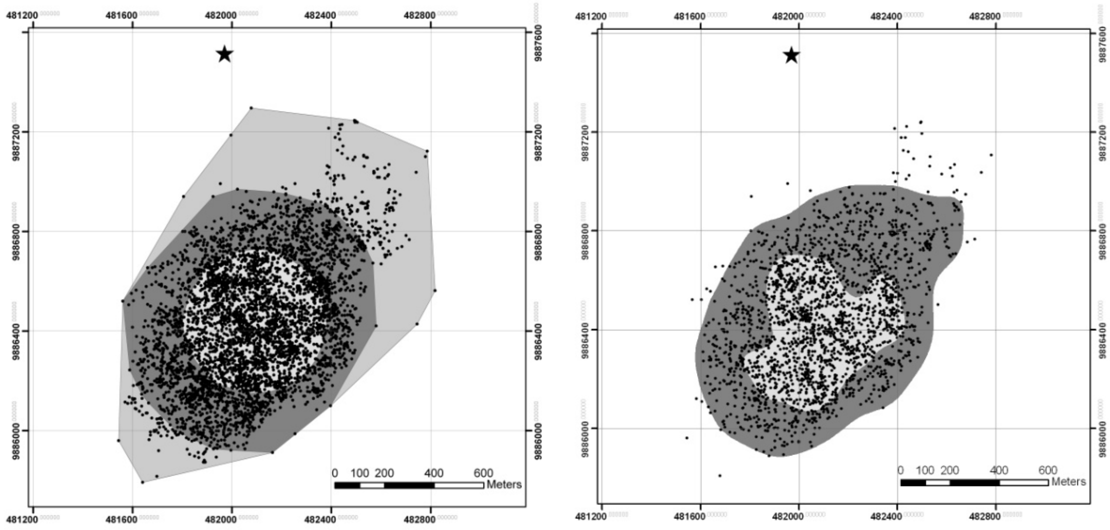

Figure 2.2 Home range areas of the study group. Left: 100%, 95% and 50% minimum convex polygons (MCP's). Right: 95% and 50% contour of the fixed kernel home range using reference bandwidth. The star is indicating the research station and the cloud of small dots represents the locations of group scan observations. Grid shows UTM coordinates (UTM Zone 47 South). One grid square equals 400m x 400m.

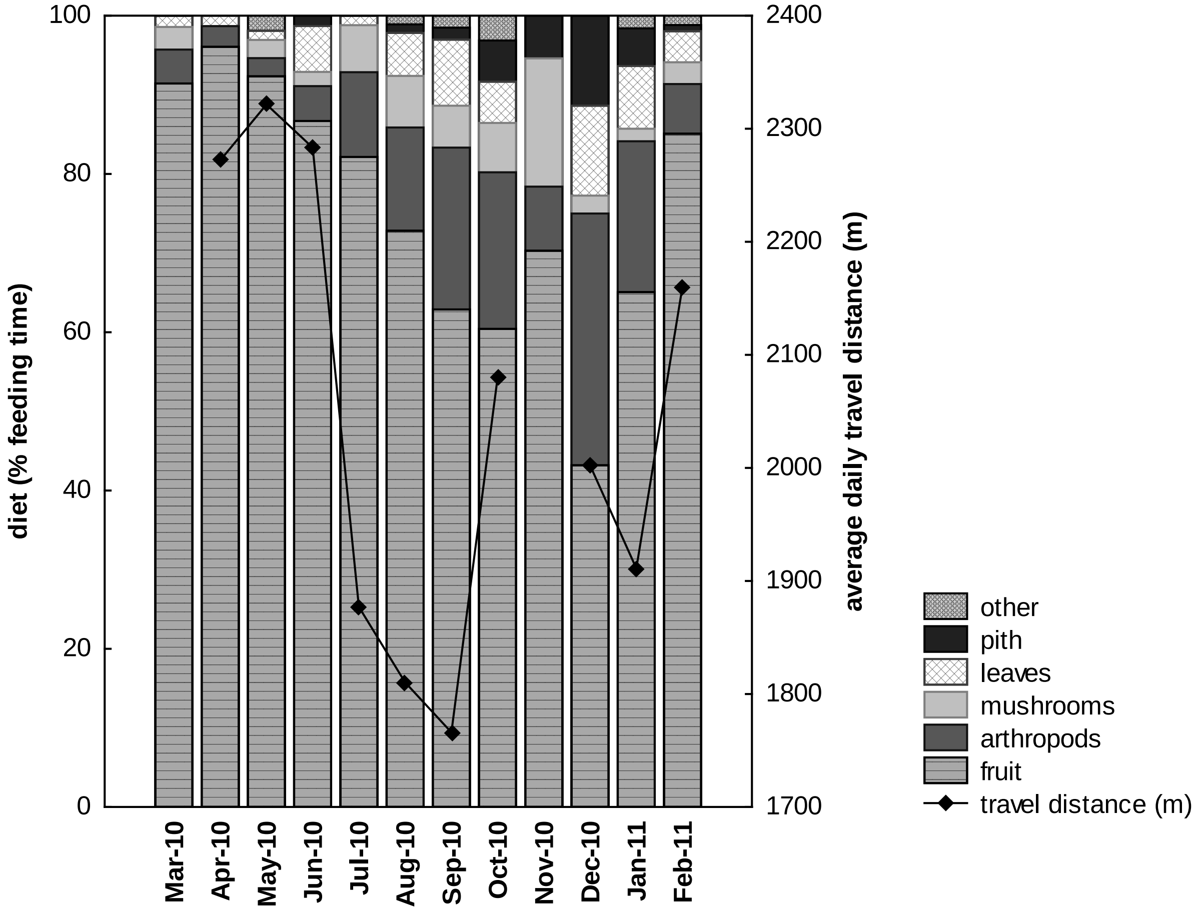

Figure 2.3 Diet and average daily travel distance per month. Diet is calculated as percent feeding time on fruit, arthropods, mushrooms, leaves (mainly young leaves and young leave petioles), pith (the soft core of the palm stem) and other food items, which includes flowers, sap and shoots. Data on travel distance for March 2010 and November 2010 were omitted because they were too scarce.

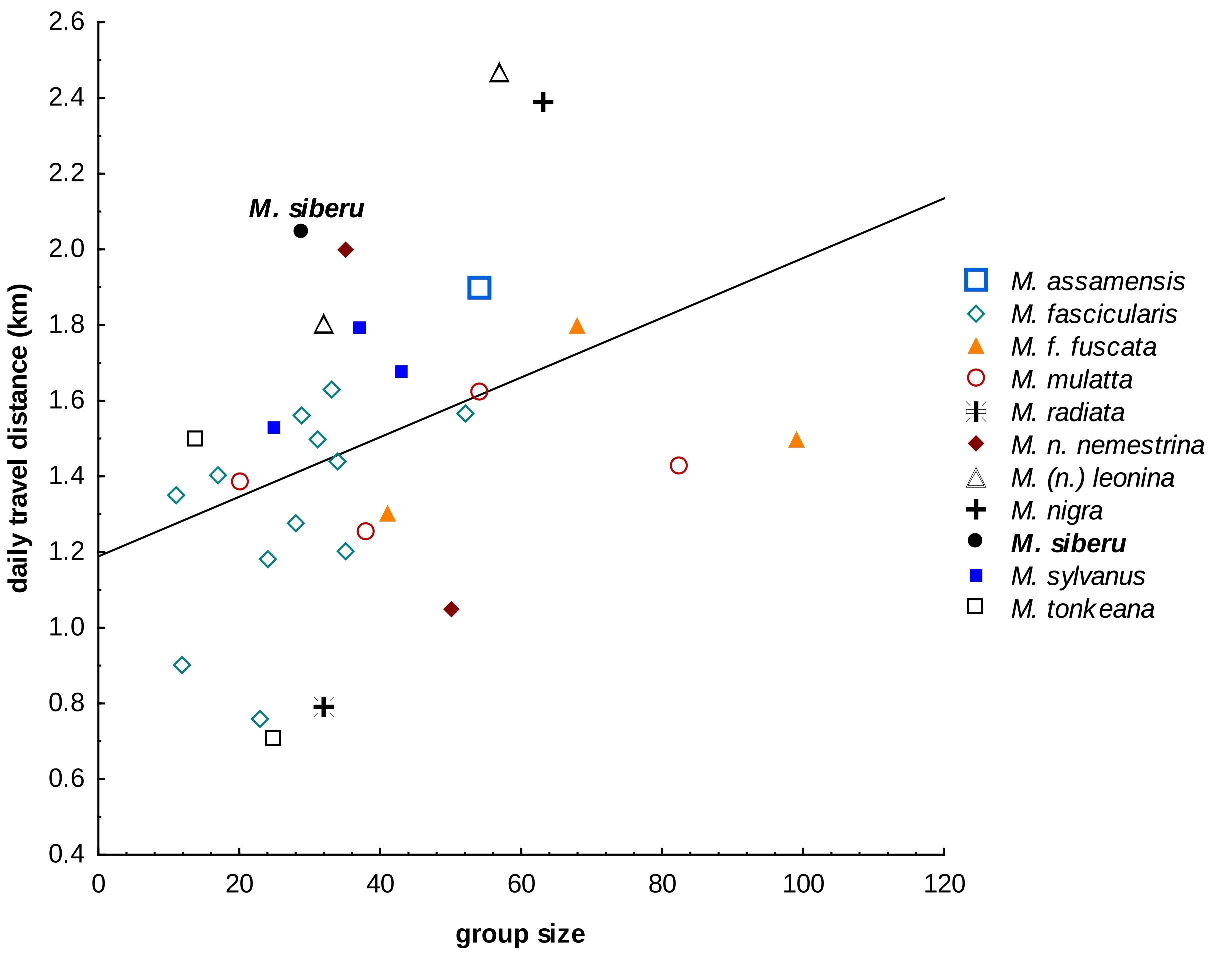

Figure 2.4 Mean daily travel distances (in km) of free-ranging macaque groups of different species in undisturbed habitats unless otherwise stated.

Sources and study sites: *M. assamensis*: Schülke et al (2011), Phu Kieo Wildlife Sanctuary,Thailand; *M. fascicularis*: 3 groups from C. Girard-Buttoz (pers. comm.), Ketambe, Sumatra, tropical lowland evergreen forest, Mar. ’10 – Apr. ’11, data only from 2 adult males per group; 7 groups (A, G, K77, H77, K, H, T, A) from van Schaik et al (1983a), Ketambe, Sumatra, 1 group (A) from Aldrich-Blake (1980), Kuala Lompat, Peninsular Malaysia; 1 group from MacKinnon & MacKinnon (1980), Kuala Lompat, Peninsular Malaysia; *M. f. fuscata*: data from the studies of Ikeda (1982) at Kawaradake, Japan, Wada (1979), Shiga heights, Japan, and Izumiyama (1999), Kamikochi, Japan, as appearing in Tsuji (2010) with values averaged from all seasons; *M. mulatta*: 3 groups (B, C, E) from Neville (1968), Uttar Pradesh, N-India, 1 group (Asarori II) from Lindburg (1971) and (1977), Uttar Pradesh, India; *M. radiata*: Sugiyama (1971), Dharwar, S-India; *M. n. nemestrina*: Caldecott (1986a), Lima Belas, Peninsular Malaysia, forest surrounded by oil palm plantations; MacKinnon & MacKinnon (1980), Kuala Lompat, Peninsular Malaysia; *M. (n.) leonina*: HQ troop from Albert (2012), Chapter 3, Khao Yai National Park, Thailand, close to human settlement, only day range data used from when the group was not using human food (high fruit abundance time); forest group (Ch troop) from J. M. José Domínguez (pers. comm.), Khao Yai National Park, Thailand, May – Jun. ’11 and May – Aug. ‘12; *M. nigra*: O’Brian & Kinnaird (1997), Tangkoko, Sulawesi; *M. siberu*: this study; *M. sylvanus*: 2 groups from Ménard & Vallet (1997) at Djurdjura and Akfadou, Algeria; 1 group (group 6) from Deag (1974), Ain Kahla, Marocco; *M. tonkeana*: 2 groups from Pombo et al (2004), Lore Lindu National Park, Sulawesi, 1 group in disturbed forest.

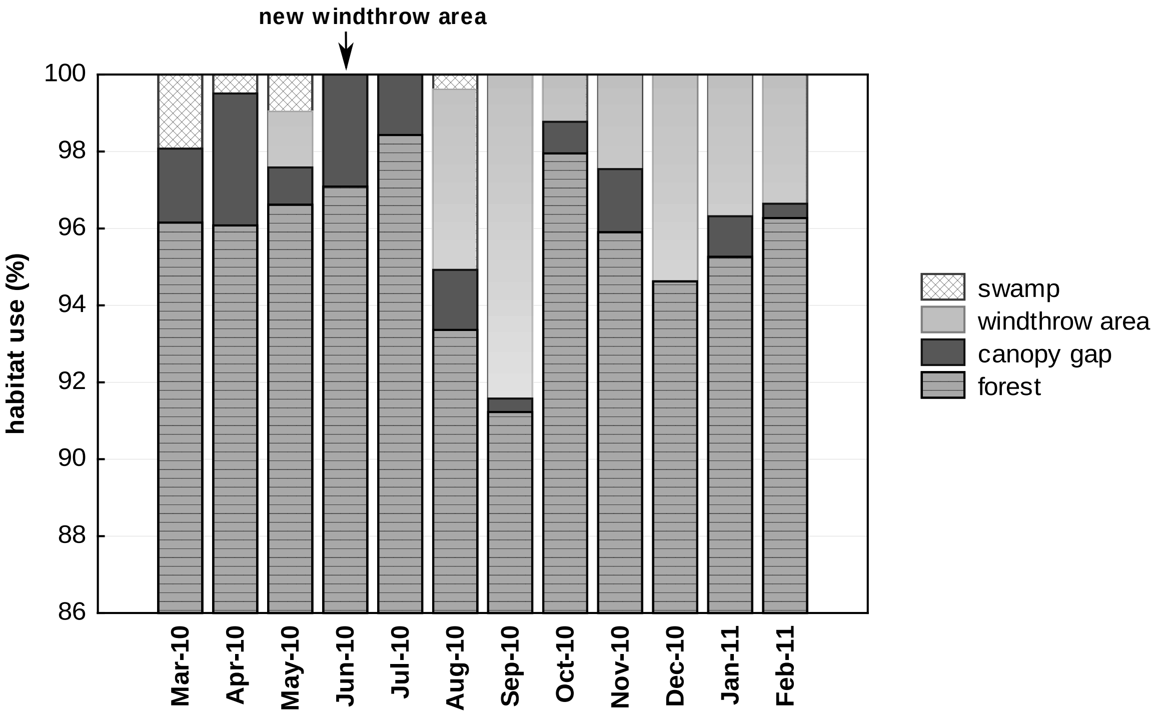

Figure 2.5 Percentage of habitat used, defined as forest, canopy gap, windthrow area and swamp. Windthrow areas were created by heavy storms, one in May 2009 (~4.5ha, at the SW edge of the home range), and another one beginning of June 2010 (~0.9ha, within the home range).

Habitat and forest structure use

Siberut macaques spent most of their time in the dense, continuous forest (average over all months: 95.7%), and used windthrow areas only 2.6%, canopy gaps 1.4%, and swamp areas 0.3% of their time. However, as can be seen in Figure 2.5, variation across months was high. The two windthrow areas were created by storms in May 2009 (before observations commenced; ~4.4ha) and June 2010 (~0.9ha). The use of windthrow areas and swamp were both correlated to the amount of fruit in the diet but in opposite ways. While windthrow areas were used more when less fruit was consumed ($r_s = -0.67$, n = 12, p = 0.02), time spent in swamp areas was positively related to the proportion of fruit in the diet ($r_s = 0.69$, n = 12, p = 0.02). The former effect may result from generally reduced fruit availability after the storm that created the second windthrow area while the latter effect suggests that swamps are only visited after sufficient amounts of fruit have been ingested.

In terms of the absolute forest height, Siberut macaques mainly used the lower strata of the forest (64.9% of their day-time activities in 0-10m height, with 53.0% being between 0-5m), and only to a much lesser extent the upper forest strata (16.5% in 11-20m, 11.5% in 21-30m, 5.8% in 31-40m, and 1.3% in >41m; see also Table 2.1 and Figure 2.9). Regarding the relative height of the forest, we find that the group spent

28.9% of their time on the ground, 36.2% in the lower-story, 23.5% in the mid-story, and only 11.4% in the canopy (values calculated as average of age-sex classes, Figure 2.6). When accounting for the number of individuals per age-sex class, these numbers change slightly (ground: 25.4%, lower-story: 38.4%, mid-story: 23.9%, canopy: 12.2%). Adult males spent more time on the ground than adult females and juveniles. The predominant activities on the ground were traveling (80.2%) and to some extent foraging (10.1%), with feeding, resting and social behavior only accounting for small proportions. Compared to other forest-living macaques in the tropics and subtropics, Siberut macaques fall on the side of more terrestrial macaque species (Table 2.2) and are more terrestrial than *M. nemestrina* on the Peninsular Malaysia (longterm study data), but similarly terrestrial than *M. nemestrina* in Sumatra (only survey data).

Table 2.1 Comparison of Siberut's sympatric primate species. Diet expressed as percent feeding time.

	S. concolor	***P. potenziani***	***H. klossii***	***M. siberu***
Group size	2-12	2-8	2-6	29
Home range size (100% MCP, ha)	4-20	25-40	5-35	135
Mean day range (m)	572	774	1,508[b]	2,048[c]
(range)	(189-1,200)[a]	(427-1,400)[a]	(885-2,150)	(1,054-3,360)[c]
Diet (%)[d]				
fruits	22.8	55.4 (32)	72.0	75.7
flowers	17.8	5.1	0	0.2
leaves	57.2	34.6 (55)	2.0	4.4
arthropods	0.6[a]	0.0	25.0	11.9
other	1.7	4.8 (13)	0	7.8
Activity budget (%)				
travel/ move	6.2	6.9	11	57.3
feed	30.8	35.3	34	10.1
forage	2.4	4.9		12.1
rest	55.4	50.8	54	14.6
social	2.3	0.7	x	5.9
other	2.8	1.4	2	
Forest strata use (%)[e]				
0-10m	13	14		64
11-20m	58	52		17
21-30m	28	33		12
>30m	1	1		7

[a] from S. Hadi (pers. comm.), [b] median range not mean range from Whitten (1982c), [c] mean day range is monthly average for 10 months, range means minimum and maximum of all single "full day follows" during this period, [d] diet for *P. potenziani* from Hadi et al (2012), with values from Fuentes (1996) in brackets, [e] forest strata use for the three species was recorded at the same study site of the Siberut Conservation Programme, in the Peleonan Forest, North Siberut

Data sources: *Simias concolor*: Erb (2012), Erb et al (2012b), Hadi (2012), Hadi et al (2012) and Tenaza & Fuentes (1995); *Presbytis potenziani*: Fuentes (1996), Hadi (2012) and Hadi et al (2012); *Hylobates klossii*: Tenaza (1975), Tilson (1981), Whitten (1980b), Whitten (1982a), Whitten (1982c); *Macaca siberu*: this study.

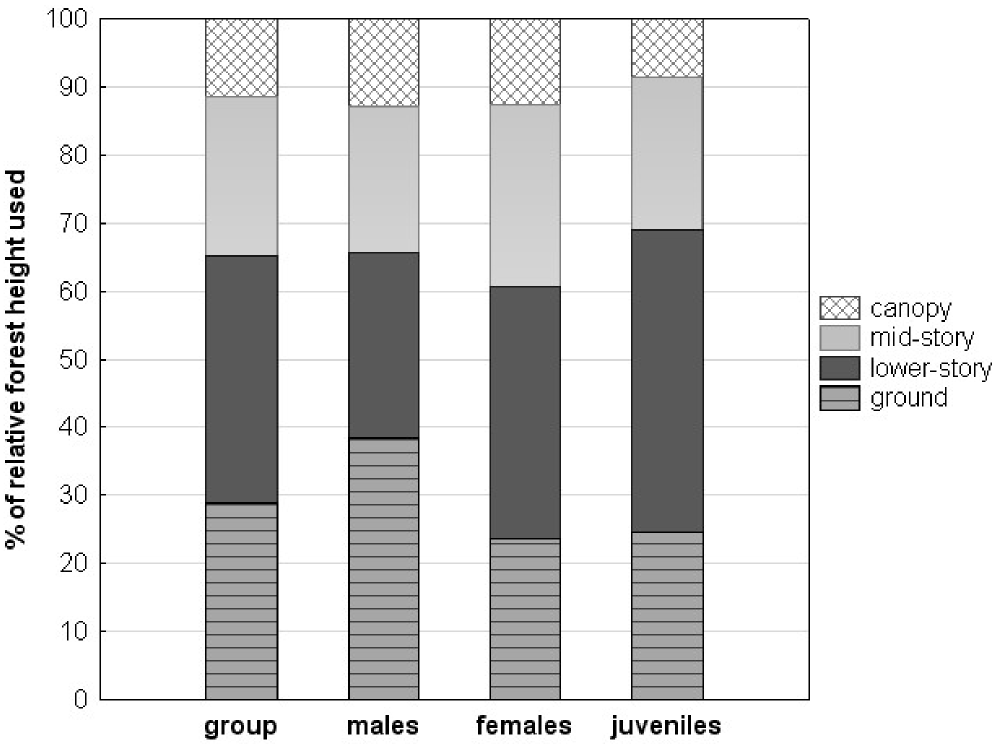

Figure 2.6 Percent frequency of the relative forest height used (ground, lower-story, mid-story, canopy) for the whole group (as average of all age-sex classes), and for adult males, adult females and juveniles separately.

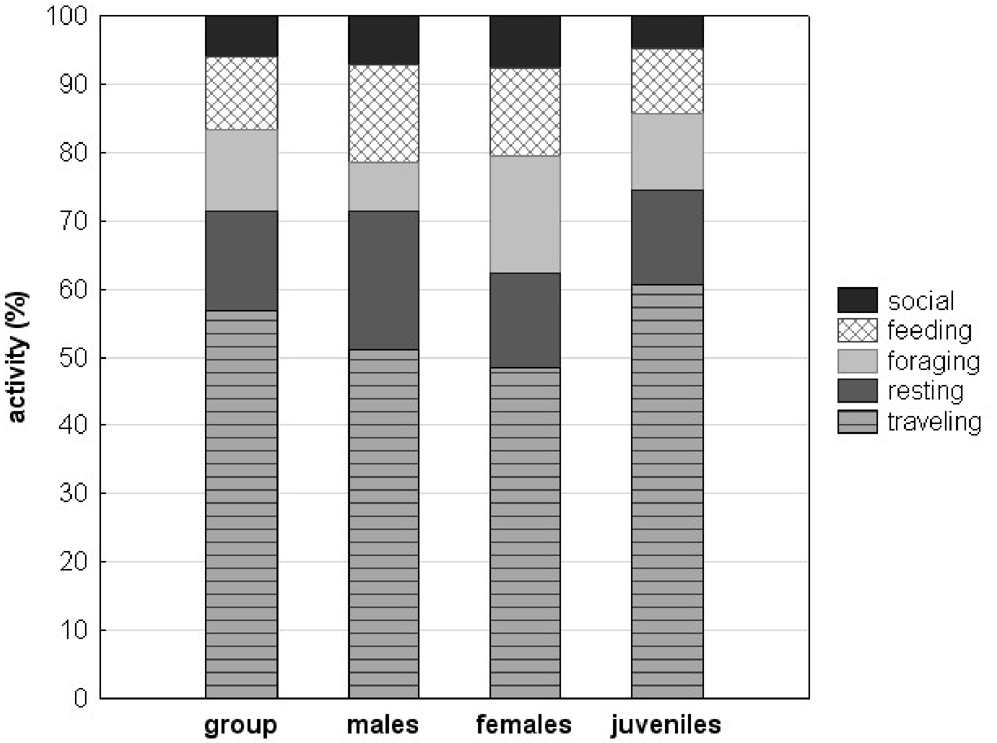

Figure 2.7 Activity budget based on group scan data, for the whole group, and for adult males, adult females and juveniles separately.

Table 2.2 Percent terrestriality of different free-ranging macaque groups and species, sorted by increasing terrestriality and species.

Species	Study site	Study period	% terrestrial	Source
tropical/ subtropical climate				
M. silenus	Western Ghats, India	1 year	0.4	1
M. silenus	Western Ghats, India	Sep '90 - Aug '91	4.9	2
M. (n.) leonina	Bherjan, E-India	1992-'94, 2004	1.5	3
M. (n.) leonina	Khao Yai NP, Thailand	Jul - Aug '12	48.5	4
M. (n.) leonina	Khao Yai NP, Thailand	Apr '09 - Nov '10	60.0	5
M. fascicularis	Kuala Lompat, W-Malaysia	Jul '74 - Jan '76	1.7	6
M. fascicularis	Kuala Lompat, W-Malaysia	Jan - Jul '73	2.0*	7
M. fascicularis	Sumatra, Indonesia		4.0*	7
M. fascicularis	Kutai NR, Kalimantan	Oct '74 - Jun '76	5.0	8
M. assamensis	Phu Khieo WS, Thailand	Jul '06 - Jun '07	10.0	9
M. n. nemestrina	Lima Belas, W-Malaysia	Jan '80 - May '81	9.0[a,b]	10
M. n. nemestrina	Lima Belas, W-Malaysia		15.0[c]	11
M. n. nemestrina	Sumatra, Indonesia		25.0[c,*]	7
M. n. nemestrina	Sumatra, Indonesia	Nov '71 - Jan '73	>30%[c]	12
M. cyclopis	Yushan NP, Taiwan	Mar '87 - Oct '88	15.4*	13
M. nigrescens	Dumoga-Bone NP, Sulawesi	Apr '89 - Jun '90	17.3*	14
M. s. sinica	Polonnaruwa, Sri Lanka	Sep '68 - early '72	24.1	15
M. siberu	Siberut island, Sumatra	Mar '10 - Mar '11	**25.4**	16
M. radiata	Dharwar, S-India	Mar - Sep '62	30.0	17
M. nigra	Tangkoko, Sulawesi	Jan '93 - Jun '94	>60	18
M. nigra	Tangkoko, Sulawesi	Jul '06 - Jun '07	72.0*	19
M. nigra	Tangkoko, Sulawesi	Jul '06 - Jun '07	76.7*	19
temperate climate				
M. f. fuscata	Takagoyama Area, Japan	1970 - '71	51.2[d]	20
M. f. fuscata	Tsubaki, Japan	Jun '95 - Jan '97	54.1	21
M. sylvanus	Akfadou, Algeria	Apr '83 - Feb '85	58.4[e]	22
M. sylvanus	Djurdjura, Algeria	Apr '83 - Feb '85	68.5[e]	22
M. mulatta	N-India (Kaluwala)	1981 - '86	61.4	23
M. mulatta	Murree hills, NW-Pakistan	1978 - '79	66.0	24
M. mulatta	N-India (Nagal Check Post)	1981 - '86	71.7	23

Terrestriality is defined as time spent on the ground, unless otherwise stated.
Abbreviations of study sites: NP = National Park, NR = Nature Reserve, WS = Wildlife Sanctuary
[a] 0-2m height, [b] mean of spot observations and activity assessment, [c] survey data, monkeys not really habituated, [d] only data for autumn and winter, [e] less than 1m height, * values estimated from figure
Sources and habitat type: 1) Kurup & Kumar (1993), undisturbed wet evergreen forest; 2) Menon & Poirier (1996), disturbed forest; 3) Choudhury (2008), tropical wet evergreen forest and decidious plantations; 4) J. M. José Domínguez (pers. comm.), seasonal wet evergreen forest, forest group Ch; 5) Albert et al (2011), seasonal wet evergreen forest, close to the national park's visitor center, group HQ; 6) Aldrich-Blake (1980), tropical lowland evergreen forest; 7) MacKinnon & MacKinnon (1980), site at Kuala Lompat: tropical lowland evergreen forest, site in Sumatra: habitat type not given by the authors; 8) Wheatley (1980), mixed lowland forest; 9) Schülke et al (2011), dry evergreen forest; 10) Caldecott (1986a), tropical broadleaf evergreen forest surrounded by oil palm plantations, value is the mean of spot observations and activity

assessments; 11) Bernstein (1967), tropical broadleaf evergreen forest, same study site as Caldecott (1986a); 12) Crockett & Wilson (1980), swamp, lowland, hill and submontane forest; 13) Lu et al (1991), mainly primary broadleaf forest; 14) Kohlhaas (1993), primary lowland rainforest, with some patches of secondary growth and grasses, 15) Dittus (1977), semi-evergreen forest, dry zone plain; 16) this study; 17) Sugiyama (1971), dry decidious forest; 18) O'Brian & Kinnaird (1997), some parts disturbed forest; 19) Giyarto (2010), Rambo I group (1st value) mainly primary forest, Rambo II group mainly secondary forest; 20) Yotsumoto (1976), secondary broadleaf decidious forest, some parts with broadleaf evergreen trees; 21) Chatani (2003), evergreen forest less than 5m high; 22) Ménard & Vallet (1997), temperate decidious oak forest at Akfadou, temperate evergreen cedar-oak forest at Djurdjura; 23) Chopra et al (1992), forest; 24) Goldstein & Richard (1989) and Goldstein (1984), temperate mixed coniferous decidious forest with disturbed areas.

Activity budget

The activity budget revealed that the group spent most of its time traveling, with a monthly average (±SD) of 57.3% (±6.6), 14.6% (±5.6) resting, 12.1% (±9.0) foraging, 10.1% (±4.0) feeding, and only 5.9% (±2.2) on social activities (Figure 2.7). There was a significant sex-difference in resting (Mann-Whitney-U: W = 18, p = 0.02), with adult males resting 6.4% more than their female counterparts. There was also a significant sex-difference in time spent foraging (Mann-Whitney-U: W = 0, p = 0.02), with females spending nearly two and a half times more on searching for food then males (Figure 2.7, Fisher's Omnibus Test to control for multiple testing: $X^2 = 19.6$, df = 10, p = 0.03). For feeding, traveling and social activities, males and females did not differ significantly. The most striking differences between juveniles and adults were the much higher amount of time spent traveling in juveniles (juveniles: 60.7%, females: 48.4%, males: 51.1%), a lower amount of time spent feeding (juveniles: 9.5%, females: 12.9%, males: 14.5%), and only very little time spent on social behavior (juveniles: 4.8%, females: 7.6%, males: 7.1%), which is surprising as playing is part of this category. However, these differences cannot be tested for significance as the majority of the juveniles were not identified. Most of the activities showed large variations throughout the months, and only social behavior was relatively stable (~5%, Figure 2.8). High variations in feeding time are probably driven by fruit availability in the forest, and as feeding time decreases, the time spent foraging (searching for food) increases, along with an increase of time spent traveling, both at the cost of time spent resting (Figure 2.8).

Compared to other macaque species, Siberut macaques spent more time traveling (Table 2.3), which is surprising, given their small group size, but is in accordance with the long daily travel distance observed (Figure 2.4). Among the 15 species examined in Table 2.3, only *M. nemestrina* travels more than Siberut macaques. Due to the large amount of time they have to devote to traveling, they only have very little time left for social activities (Table 2.3).

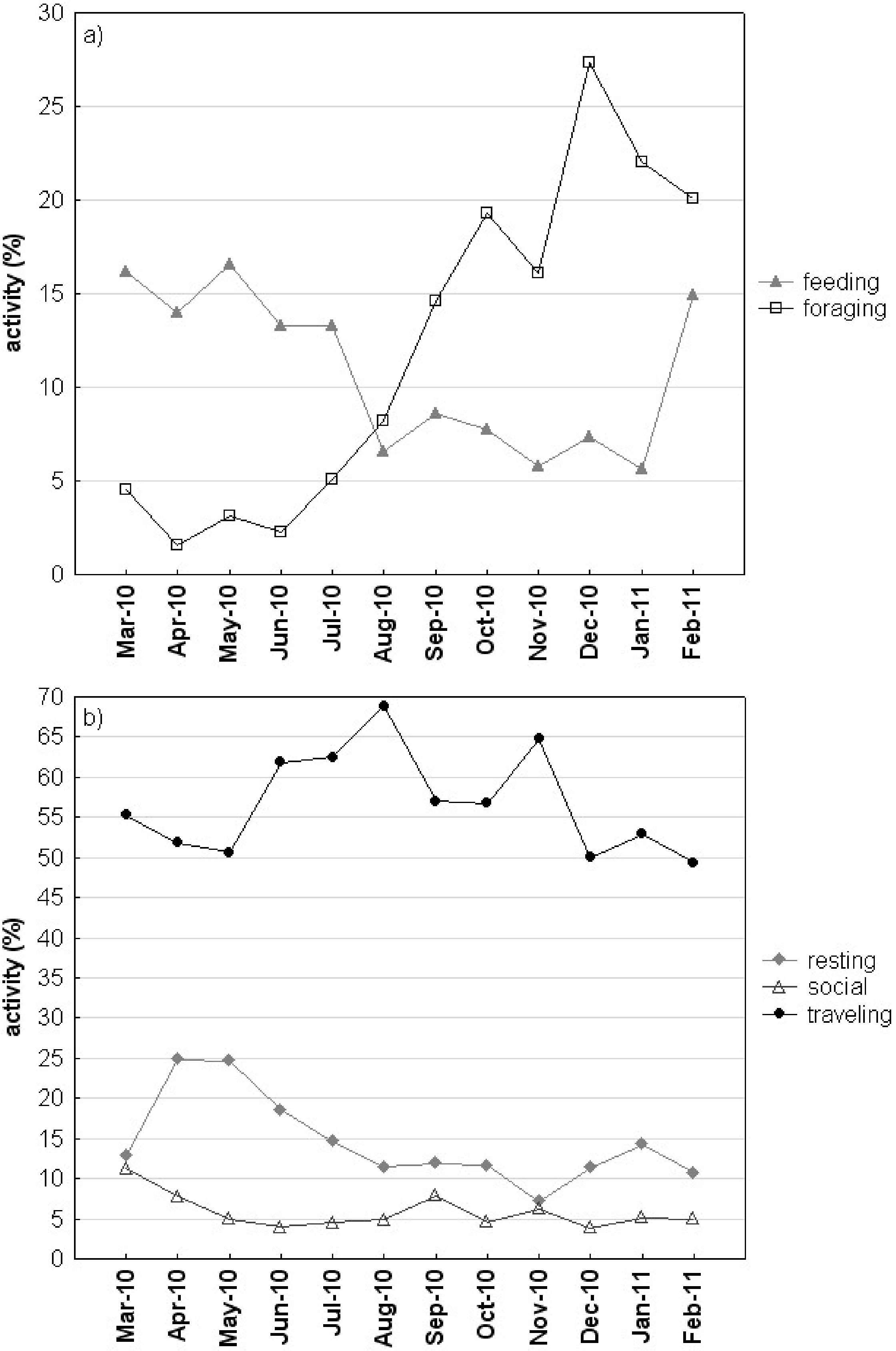

Figure 2.8 Variation in the activity budget (in percent) regarding a) time spent feeding and foraging and b) time spent resting, traveling and being social.

Diet

Across the study period, the diet of Siberut macaques was on average composed of 75.7% fruit (72.8% ripe fruit, 20.2% half-ripe fruit, 4.3% unripe fruit, 2.7% fruit of unknown ripeness), 11.9% arthropods (mainly ants, termites, spiders), 4.5% mushrooms, 4.4% leaves (59.7% young leaves, 13.4% young leave petioles, 25.4% leaves of unknown age, 1.5% mature leaves), 2.6% pith, 0.6% sap, 0.2% shoots and 0.2% flowers. Compared to other macaques, the degree of frugivory in Siberut macaques was high (third highest among the 14 macaque species examined) and the percentage of leaves eaten low (fifth lowest of the 14 macaque species, Table 2.4). According to local people, Siberut macaques also occasionally catch and consume crabs and shrimp from the rivers, but this was only observed once. In contrast to other macaque species, Siberut macaques were never observed to prey on bird eggs, birds, squirrels or other small mammals. Although the majority of the diet was comprised of fruit, the proportion of fruit varied largely from 43.2% (Dec. 2010) to 96.1% (Apr. 2010, Figure 2.3). With decreasing proportion of fruit eaten per month, the time spent feeding on arthropods, pith and leaves increased significantly (Spearman rank correlations: fruit vs. arthropods: $r_s = -0.97$, $p<0.01$, fruit vs. pith: $r_s = -0.86$, $p<0.01$, fruit vs. leaves: $r_s = -0.59$, $p<0.05$, for all $n = 12$ months). The correlation between fruit and mushrooms was not significant. The increase in pith eating was mainly due to adult males, since all males fed on pith whereas only 2 of the 6 adult females did. Pith was the only food item which was significantly different in the diet of males and females (Mann-Whitney-U: $W=18$, $p=0.02$). Observations suggested that only males were strong enough to break the palm trunks open to get access to the pith, whereas females were only observed feeding pith after they found a trunk already opened. In sum, when the abundance of fruit decreased, they used arthropods and (young) leaves as fallback foods (for annual availability of leaves and fruit see Erb et al. 2012a).

Dietary diversity, measured by the Shannon-Wiener index H', was low in months when the proportion of fruit in the diet exceeded 80% (average H': 1.1) and high in months when fruit only made up a smaller part of the diet (average H': 2.1). Overall average dietary diversity was 1.6. The monthly dietary diversity index was negatively correlated with the monthly feeding time (Spearman rank correlation: $r_s = -0.82$, $n = 12$, $p = 0.02$), indicating that the monkeys need to invest more time in feeding when the diversity of food items is low.

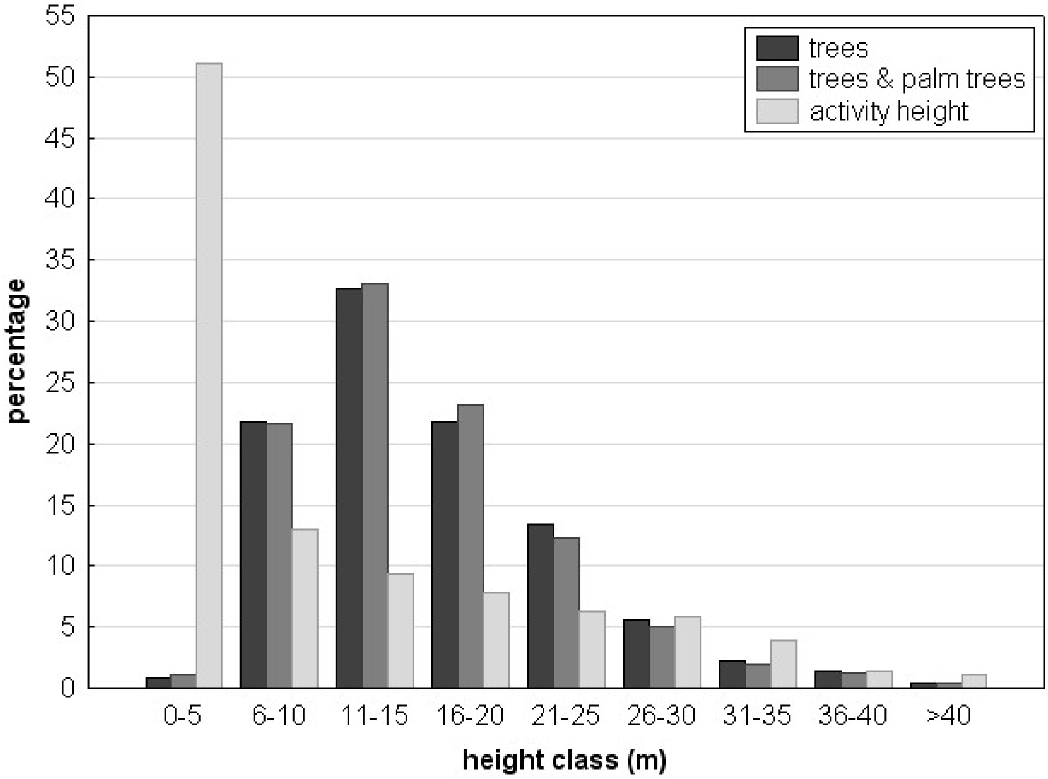

Figure 2.9 Distribution of height classes (in m) of trees, and trees and palm trees combined and the percentage of the daily daytime activity of the group of Siberut macaques per height class shown. Tree data are based on all 12 botanical plots.

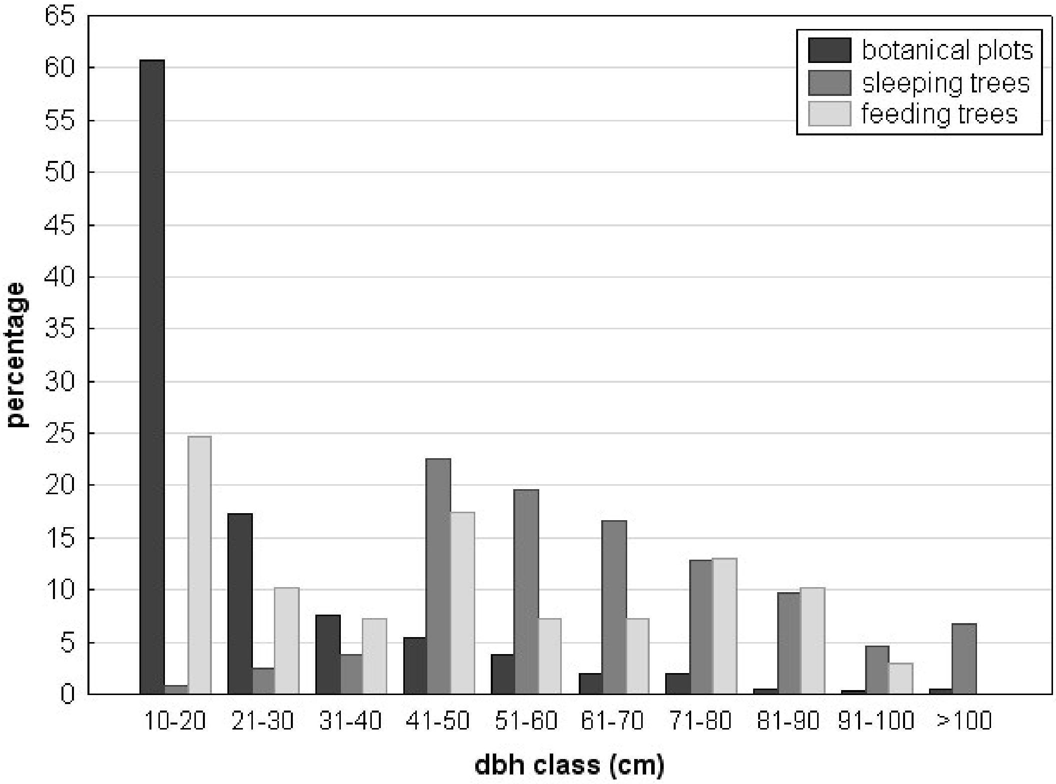

Figure 2.10 Distribution of dbh classes (in cm) of trees (without palm trees) of all botanical plots, of sleeping trees and of feeding trees.

Table 2.3 Activity budgets of free-ranging and unprovisioned macaque groups of different species, sorted by decreasing travel time and species.

Species	Study site	Study period	Group size (name)	Travel/ Move	Forage	Feed	Rest	Social	Other	Sou., Obs.
tropical/ subtropical climate										
M. n. nemestrina	Lima Belas, W-Malaysia	Jan '80 - May '81	50	61.0	16.0		19.0	4.0		1, O
M. siberu	Siberut island, Sumatra	Mar '10 - Mar '11	29	57.3	12.1	10.1	14.6	5.9		2, S
M. silenus	Western Ghats, S-India	Aug '94 - Mar '96	23	43.6	31.0		20.7	5.8		3, S
M. silenus [a]	Anamalai WS, India	Sep '90 - Aug '91	41-43	34	23.7	17.9	16	8.4		4, S
M. silenus	Anamalai WS, India	1 year	12-31	15	26.7	27.8	27	2.4	1.1	5, S
M. tonkeana (a),*	Lore Lindu NP, Sulawesi	Jun '02 - Apr '04	26-28 (Ch)	36.0	7.5	13.0	32.5	11.0		6, S
M. tonkeana [a,*]	Lore Lindu NP, Sulawesi	Jun '02 - Apr '04	6-9 (Anca)	29.0	10.0	14.0	36.0	11.0		6, S
M. tonkeana	Lore Lindu NP, Sulawesi		14	31.0		19.3	35.0	14.7		7, S
M. tonkeana [a,*]	Lore Lindu NP, Sulawesi		25	17.7		11.4	51.0	19.9		7, S
M. (n.) leonina [b]	Khao Yai NP, Thailand	Apr '09 - Nov '10	32-39 (HQ)	34.0	5	13.0	30.0	16.0	2.0	8, S
M. (n.) leonina *	Bherjan, E-India	1992-'94, '04	20-23 (2 groups)	19.5	23.5		45.0	8.0	4.0	9, S
M. assamensis	Chiang Rai, Thailand		x	27.2	16.8		31.2	24.8		10, U
M. assamensis [c]	Makalu-Barun NP, Nepal	Mar - Apr '97+ '98	27 (Wa.), 13 (Sa.)	27.0	45.5		16.5	11.0		11, S
M. assamensis [c]	Langtan NP, Nepal	Oct '00 - May '01	several groups	27.0	28.5		28.5	16.0		11, S
M. assamensis	Phu Khieo WS, Thailand	‘07-'08, ‘10-'11	49-53 (AS)[e]	24.7	4.9	27.2	32.0	11.1		12, F
M. assamensis	Jokai forest, Assam, India	Jun '97 - May '98	31	25.0	40		22	13.0		13, S
M. nigra	Tangkoko, Sulawesi	Jan '93 - Jun '94	42-50 (Mal.)	25.7	13.8	24.8	12.6	23.1		14, S
M. nigra	Tangkoko, Sulawesi	Jan '93 - Jun '94	57-61 (Dua)	23.5	15.2	20.8	17	23.5		14, S
M. nigra	Tangkoko, Sulawesi	Jan '93 - Jun '94	76-97 (Ram.)	18.3	9	25.1	28.9	18.7		14, S
M. nigra	Tangkoko, Sulawesi	Jul '06 - Jun '07	60 (Ram. I)	12.4	54.1		16.9	16.1	0.4	15, S
M. fascicularis	Kuala Lompat, W-Malaysia	Jul '74 - Jan '76	23	20.0	35.0		34.0	12.0	0.5	16, S
M. fascicularis	Ketambe, Sumatra	Mar '10 - Apr '11	28 (KA)[f]	6.1	3.8	38.7	48.2	5.9		17, F
M. fascicularis	Ketambe, Sumatra	Mar '10 - Apr '11	52 (C)[f]	3.8	2.3	36.3	47.2	10.7		17, F
M. fascicularis	Ketambe, Sumatra	Mar '10 - Apr '11	35 (KB)[f]	3.6	3.4	34.8	49.3	10.0		17, F
M. nigrescens	Dumoga-Bone NP, Sulawesi	Apr '89 - Jun '90	13.9	19.7	10.1		47.6	22.7		18, S
M. munzala	Arunachal Pradesh, India	Jul - Aug '05	13 (Ro.), 22 (Br.)	19.0	29.0		36.0	16.0		19, O
M. cyclopis	Mt. Longevity, Taiwan	Aug '03 - Jul '04	16-63 (Aa,C,E,F)	16.0	8.2	28.1	17.1	30.2		20, U
M. cyclopis	Yushan NP, Taiwan	Mar '87 - Oct '88	7.8	9.5	52.8		30.9	x	6.7	21, S

M. radiata *	Bandipur-Mundumalai, India	1 year	15	7.0		37.0	21.0	30.0	5.0	22, F
temperate climate										
M. mulatta	India	1981 - '84	31.5 (70 groups)	26.2		40.1	27.7	4.7	1.3	23, U
M. mulatta [b]	Kathmandu, Nepal	1974 - '75	x	25.0		27.0	8.0	21.0	21.0	24, S
M. mulatta	N-India	1981 - '86	43-70 (3 groups)	24.1		33.6	35.1	5.6	1.5	25, S
M. mulatta	Murree Hills, NW-Pakistan	1978 - '79	23-25 (Kong)	11.0		45.0	34.0	10.0	x	26, F
M. fuscata yakui	Yakushima, Japan	Jan '90 - May '92	5-19 (P)	23.0		32.7	22.6	18.9	2.8	27, S
M. fuscata yakui	Yakushima, Japan	Aug - Dec '76	47	22.8		23.5	22.1	31.6		28, S
M. fuscata yakui	Yakushima, Japan	1976, 1989-'92	5-19 (P, T, Ko)	22.6		30.8	22.1	20.7	3.7	29, S
M. fuscata yakui	Yakushima, Japan	Apr '00 - Mar '01	24 (HR)	16.0		38.0	32.0	14.0		30, F
M. f. fuscata	Kinkazan Island, Japan	1984-'87, '91-'92	20-51 (A)	16.8		53.9	17.6	11.5	0.3	29, S
M. f. fuscata [d]	Kinkazan Island, Japan	Sep - Dec '89	38 (A)	13.5		60.3	6.4	14.6	1.9	31, U
M. sylvanus	Akfadou, Algeria	Feb '83 - Mar '85	33-41	22.3	3.9	23.8	40.0	10.0		32, S
M. sylvanus	Ain Kahla, Marocco	1968 - '69	25 (6 groups)	21.8		50.1	16.7	10.8	0.6	33, S
M. sylvanus	Djurdjura, Algeria	Feb '83 - Mar '85	38-47	20.0	6.2	25.4	36.9	11.5		32, S

Obs. = Observation method (S = scan sampling, F = focal animal sampling, O = other method, U = unknown); Sou. = Sources (see below), NP = National Park, WS = Wildlife Sanctuary; [a] group was living in disturbed forest, [b] group was feeding to some extent on human food, [c] values averaged from both years, [d] values averaged from different age-sex categories, [e] data are only from adult females (12 in 2007/08; 15 in 2011/12), [f] data are only from the 2 adult males, * values were estimated from figure

Sources and habitat type: 1) Caldecott (1986a), tropical broadleaf evergreen forest surrounded by oil palm plantations; 2) this study, tropical lowland evergreen broadleaf rainforest; 3) Singh et al (2000), evergreen moist broadleaf forest; 4) Menon & Poirier (1996), disturbed forest fragment; 5) Kurup & Kumar (1993), undisturbed wet evergreen forest; 6) Riley (2007), lowland and hill forest, Ch group minimally altered, Anca group heavily altered with agricultural and agroforestry areas; 7) Pombo et al (2004), smaller group in undisturbed forest, larger group in disturbed forest; 8) Albert (2012), seasonal wet evergreen forest, close to human settlement; 9) Choudhury (2008), tropical wet evergreen forest, deciduous plantations; 10) Aggimarangsee (1992) in Chalise (1999); 11) Chalise (2003), at Makalu-Barun National Park steep slopes with patchy forest, for Langtan National Park habitat not mentioned; 12) M. Heesen (pers. comm.), dry evergreen forest; 13) Sarkar et al (2012), semi-evergreen forest; 14) O'Brien & Kinnaird (1997), different percentage of primary forest for the different groups (Mal.: 15%, Dua: 20%, Ram.: 4%), rest is secondary and burned forest; 15) Giyarto (2010), mainly primary forest; 16) Aldrich-Blake (1980), tropical lowland evergreen rainforest; 17) C. Girard-Buttoz (pers. comm.), tropical lowland evergreen rainforest; 18) Kohlhaas (1993), primary lowland rainforest, with some patches of secondary growth and grasses; 19) Kumar et al (2006), subtropical broadleaf evergreen forest, secondary scrub and agricultural fields; 20) Wang (2004); 21) Lu et al (1991), mainly primary broadleaf forest; 22) Singh & Vinanthe (1990), dry decidious forest; 23) Seth & Seth (1986), deciduous forest; 24) Teas et al (1980), open and wooded parklands, small tracts of forest, temple grouds; 25) Chopra et al (1992), forest; 26) Goldstein & Richard (1989) and Goldstein (1984), temperate mixed coniferous deciduous forest with disturbed areas; 27) Agetsuma (1995c), warm temperate broadleaf forest; 28) Maruhashi (1981), warm temperate broadleaf forest; 29) Agetsuma & Nakagawa (1998), Yakushima: warm temperate broadleaf forest, Kinkazan: mixed forest of deciduous and coniferous trees; 30) Hanya (2004b), coniferous forest; 31) Hashimoto (1991), deciduous broadleaf forest; 32) Ménard & Vallet (1997), Akfadou: temperate deciduous oak forest, Djurdjura: temperate evergreen cedar-oak forest; 33) Deag (1985), temperate cedar forest.

Table 2.4 Diet (as percent of feeding time) of free-ranging and unprovisioned macaque groups of different species, sorted by decreasing percentage of fruit eaten and by species.

Species	**Fruits (Pods)**	**Flowers**	**Seeds**	**Leaves**	**Buds**	**Shoots**	**Herbs**	**Stem**	**Pith**	**Bark**	**Roots**	**Sap/ Resin**	**Fungi**	**Lichens**	**Invertebrates**	**Vertebrates**	**Other**	**Source**
tropical/ subtropical climate																		
M. tonkeana	85.8	0.8		4.2		3.1		0					0.3		5.6		0.4	1
M. tonkeana	78.1	0.8		2.9		1.8		0.3					1		14.6		0.4	1
M. nigrescens	85.1	y		3.5		y		y							8.9		2.5	2
M. siberu	75.7	0.2		4.4		0.2			2.6			0.6	4.5		11.9			3
M. n. nemestrina	74.6	1.1		7.0	3.0			1.9							12.2	0.4		4
M. fascicularis	66.7[a]	8.9	y	17.2											4.1		3.2	5
M. fascicularis	63.7	8.8		24.0											4.4			6
M. fascicularis	52.4	5.4		16.1							2.9				23.3			7
M. fascicularis	44.9	6.5		8.4				6.3		7.9			6.6		11.3		8.0	8
M. fascicularis	30.0	4.1		10.5				4.4		30.2			1.8		15.5		3.4	8
M. fascicularis	25.0	1	45[b]	9.0				13[c]							5.0		2	9
M. fascicularis	15.1	6.4		5.5				4.1		44.9			2.7		19.5		1.8	8
M. fascicularis	4.0			41.0					6.0[d]						46.0			10
M. nigra	66.0	y	y	2.5 (+ y)		y	y		y				y		31.5			11
M. nigra	61.5	0.1		8.1 (+ y)	y			y					2.5		27.6	0.2	0.1	12
M. nigra	56.9	0.1		9.0 (+ y)	y			y					1.1		31.7	0.1	0.8	12
M. (n.) leonina	65.9	2.1	6.1	7.7[e]	y	1.5		y			3.5[f]				11.7		1.5	13
M. silenus	59.5			2.0											18.0		20.6	14
M. cyclopis	53.8	7.3	0.0	14.9		2.4		11.8							9.8			15
M. cyclopis	42.2	10.3		26.2	9.1			11.8			0.03							16
M. assamensis	30.7	2.0	28.2	12.4		0.7				0.3	0.3		0.1		20.6	0.1	4.5	17
M. assamensis	22.9	31.4		45.7														18

M. assamensis	11.0	7.0		52.0	30.0											2.0		19
M. munzala	10.3	3.25	0	40.2					41.4								4.85	20
temperate climate																		
M. fuscata yakui	30.2	5.6	13.2	35.1^g		y			y	y		y	4.6			10.3	1.2	21
M. fuscata yakui	28.6	4.9	28.2	22.4											8.9		7.0	22
M. fuscata yakui	13.0	15.0	4.0	41.0									14.0			1.0	11.0	23
M. f. fuscata	10.2	3.3	43.6	14.4	2.9		15.1			5.0			2.3		2.1		1.3	24
M. mulatta	8.5	3.7		84.4 (+ y)			y	y			2.2	1.1						25
M. sylvanus	0.8	3.5	32.2	8.8			18.5				6.9		4.1	14.2	10.5		0.5	26
M. sylvanus	4.3	1.6	26.7	13.0			35.1				7.7		1.5	1.9	5.6		2.6	26

For more details of the studies see Table 2.5.
Leaves includes leaves of trees, shrubs and lianas of different stages of maturity or fallen leaves, leaf petioles and palm fronds. The category flowers also includes flower buds. The category buds usually means leaf buds, and in case it was not specified in the literature whether flower or leaf buds were meant, the values were included in this category as well.
y = yes this food item was eaten but exact value not given by the author, and was either summarized with another food item (mentioned there) or given in the category other, (+y) = this value includes all other food items for which y is entered, ^{a} includes seeds, ^{b} includes pods, ^{c} includes bracts, ^{d} includes nectar, ^{e} includes buds, ^{f} includes stem, ^{g} includes shoots
Sources: 1) Riley (2007), 2) Kohlhaas (1993), 3) this study, 4) Caldecott (1986a) and Caldecott (1986b), 5) Yeager (1996), 6) MacKinnon & MacKinnon (1980), 7) Aldrich-Blake (1980), 8) C. Girard-Buttoz (pers. comm.), 9) Sussman & Tattersall (1981), 10) Khan & Wahab (1983) in Ahsan (1994), 11) O'Brian & Kinnaird (1997), 12) Giyarto (2010), 13) Choudhury (2008), 14) Singh et al (2000), 15) Su & Lee (2001), 16) Wang (2004), 17) M. Heesen (pers. comm.), 18) Ahsan (1994), 19) Srivastava (1999), 20) Mendiratta et al (2009), 21) Hill (1997), 22) Agetsuma (1995a), 23) Hanya (2004a), 24) Agetsuma & Nakagawa (1998), 25) Goldstein & Richard (1989) and Goldstein (1984), 26) Ménard (2004)

Table 2.5 Details of the studies mentioned in Table 2.4.

Species	Study site	Habitat type	Study period	Group size (name)	Source
tropical/ sub-tropical climate					
M. tonkeana	Lore Lindu NP, Sulawesi	Lowland and hill forest, minimally altered	Jan '03 - Apr '04	26-28 (Ch)	1
M. tonkeana	Lore Lindu NP, Sulawesi	Lowland and hill forest, heavily altered	Jan '03 - Apr '04	6-9 (Anca)	1
M. nigrescens	Dumoga-Bone NP, Sulawesi	Primary lowland rainforest, secondary growth	Apr '89 - Jun '90	13.9	2
M. siberu	Siberut island, Sumatra	Tropical lowland evergreen broadleaf rainforest	Mar '10 - Mar '11	29	3
M. n. nemestrina	Lima Belas, W-Malaysia	Trop. broadleaf evergreen forest, plantations	Jan '80 - May '81	50	4
M. fascicularis	Tanjung Puting, Kalimantan	Freshwater peat swamp forest	Jan - Dec '85	(several)	5
M. fascicularis	Kuala Lompat, W-Malaysia	Tropical lowland evergreen rainforest	Jan - Jul '73	17	6
M. fascicularis	Kuala Lompat, W-Malaysia	Tropical lowland evergreen rainforest	Jul '74 - Jan '76	23	7
M. fascicularis	Ketambe, Sumatra	Tropical lowland evergreen rainforest	Mar '10 - Apr '11	52 (C)*	8
M. fascicularis	Ketambe, Sumatra	Tropical lowland evergreen rainforest	Mar '10 - Apr '11	35 (KB)*	8
M. fascicularis	Mauritius	Degraded savanna	Jun - Jul '77	67	9
M. fascicularis	Ketambe, Sumatra	Tropical lowland evergreen rainforest	Mar '10 - Apr '11	28 (KA)*	8
M. fascicularis	Naaf river belt, Bangladesh	x	x	20	10
M. nigra	Tangkoko, Sulawesi	Lowland rainforest	Jan '93 - Jun '94	42-97	11
M. nigra	Tangkoko, Sulawesi	Lowland rainforest	Jul '06 - Jun '07	60 (Ram. I)	12
M. nigra	Tangkoko, Sulawesi	Lowland rainforest	Jul '06 - Jun '07	58 (Ram. II)	12
M. (n.) leonina	Bherjan, E-India	Tropical wet evergreen forest, plantations	1992-1994, 2004	20-23 (2 groups)	13
M. silenus	Western Ghats, S-India	Evergreen moist broadleaf forest	Aug '94 - Mar '96	23	14
M. cyclopis	Jentse, NE-Taiwan	Sec. broadleaf evergreen forest, plantations	Oct '91 - Jun '92	≤31 (≥ 6 groups)	15
M. cyclopis	Mt. Longevity, Taiwan	x	Aug '03 - Jul '04	16-63 (Aa,C,E,F)	16
M. assamensis	Phu Khieo WS, Thailand	Dry evergreen forest	‘07-'08, ‘10-'11	49-53 (AS)	17
M. assamensis	Bangladesh	x	1979 - 1981	18	18
M. assamensis	Jokai RF, Assam, India	x	x	x	19
M. munzala	Arunachal Pradesh, India	Subtrop. broadleaf forest,disturbed open forest	Dec '05 - May '06	24	20
temperate climate					
M. fuscata yakui	Yakushima, Japan	Warm temperate (coastal) broadleaf forest	Dec '87 - May '89	15-17 (P)	21
M. fuscata yakui	Yakushima, Japan	Warm temperate broadleaf forest	Jan '90 - Apr '92	5-19 (P)	22
M. fuscata yakui	Yakushima, Japan	Cold temperate coniferous forest	Apr '00 - Mar '01	24-27	23

M. f. fuscata	Kinkazan Island, Japan	Mixed forest of deciduous and coniferous trees	Nov '84 - Aug '92	20-51 (A)	24
M. mulatta	Murree hills, NW-Pakistan	Mixed coniferous decid. forest, disturbed areas	1978-'79	23-25 (Kong)	25
M. sylvanus	Akfadou, Algeria	Temperate deciduous oak forest	Feb '83 - Mar '85	33-47	26
M. sylvanus	Djurdjura, Algeria	Temperate evergreen cedar-oak forest	Feb '83 - Mar '85	38-73	26

NP = National Park, RF = Reserve Forest, WS = Wildlife Sanctuary, * data are only from the 2 adult males, Sources: see footnotes of Table 2.4

Comparison of Siberut's primates

Of all four sympatric primate species on Siberut, Siberut macaques have the largest group size and by far the largest home range size (see Table 2.1 for data and references). The size of home range increases with the percentage of fruit in the diet across species, with Siberut macaques being the most frugivorous species. At similar proportions of fruit and leaves in the diet, Kloss gibbons spend twice as much time feeding on arthropods, and Siberut macaques included more other food items instead, thus having a broader diet (Table 2.1). The amount of frugivory also seems to be related to the daily travel distance, with both folivorous colobine species (*Presbytis potenziani* and *Simias concolor*) traveling the shortest distances, Kloss gibbons being intermediate and Siberut macaques having 3-4 times the travel distances of the two colobine species; the same pattern emerges for travel time (Table 2.1). For the forest strata use we find a niche differentiation. Whereas Siberut macaques mainly used the lower strata (0-10m) of the forest, the sympatric colobine species mainly stayed within heights of 11 to 20m (Table 2.1). For Kloss gibbons, no data are available for the same study site but data collected in Central Siberut indicate that the gibbons spent 94% of their time in the middle and upper canopy (Whitten 1982c).

Habitat analysis

Within the 3 ha of forest sampled within the home range, a total of 1,807 individuals of trees, palm trees, rattan and lianas, belonging to 167 species, 107 genera and 46 families were recorded. 107 individuals (5.9%; 5 lianas and 102 trees) could not be identified at the family level. From the remaining individuals, 83% could be determined to species level, the rest to genus level. Trees were the dominant growth form, with 40 families and 133 species. The liana flora comprised 12 families and 19 species. This natural and undisturbed forest had 3 species of palm trees (*Arenga obtusifolia*, *Oncosperma horridum*, *Pinanga* sp.) and 10 species of rattan (6 species of *Calamus*, 3 species of *Korthalsia*, 1 *Plectocomia* species). We found two strangler species (*Ficus annulata*, *Ficus sp.*, Moraceae). The estimated potential species richness for all categories (trees, palm trees, lianas, rattan and strangler) ranged between 186 and 225, with a mean of 200 species for the different estimators (ACE: 188, ICE: 203, Chao 1: 193, Chao 2: 200, Jack 1: 207, Jack 2: 225, Bootstrap: 186; MMMeans (1st run): 200). Estimated tree species richness ranged between 150 and 189, with a mean of 166 species for the different estimators (ACE: 154, ICE: 169, Chao 1: 164, Chao 2: 177, Jack 1: 170, Jack 2: 189, Bootstrap: 150: MMMeans (1st run): 160). For lianas, a mean of 22 species was estimated, with a range of 20 to 24 (ACE: 21, ICE: 22, Chao 1 & Chao 2: 20, Jack 1 & Jack 2: 23, Bootstrap: 21: MMMeans (1st run): 24). For palm trees, rattan and strangler, the estimated species richness was the same as the observed one. In sum, total species richness observed was 167 and expected was 200, which is mainly due to the tree community which was undersampled. These estimates were in line with field observations on species occurrence outside the plots.

Looking at species diversity, which combines the information of species richness and relative abundance, we found a Simpson's diversity index of 0.97 for all categories together (trees, palm trees, liana, rattan, strangler), or 0.98 when only considering trees. As this index ranges between 0 and 1, with 1 being the highest diversity, this indicates a very high species diversity of the studied forest habitat. The 12 botanical plots studied showed a mean similarity in terms of species composition ranging from 0.32 to 0.63, depending on the index (incidence based indices: Jaccard: 0.32, Sørensen: 0.49, but both are usually biased downward when species richness is large; abundance based indices: Morisita-Horn: 0.60, Bray-Curtis: 0.43, Chao-Jaccard: 0.47, Chao-Sørensen: 0.63), resulting in a mean of 0.49, which is a medium similarity within the indices possible range between 0 and 1.

The average total density of all recorded individuals per area was 602.3 per ha (±118.1 SD) (trees: 402.3 individuals/ha (±86.8), palm trees: 73.0 individuals/ha (±24.8), lianas: 41.0 individuals/ha (±19.9), rattan: 83.3 individuals/ha (±52.7), strangler: 2.7 individuals/ha (±3.1)).

The height distribution of the forest showed tree heights ranging from 2m (*Chionanthus glomerata*, Oleaceae) up to maximum 52m (*Sloanea javanica*, Elaeocarpaceae). Other high trees taller than 40m were *Nauclea* sp. (Rubiaceae), *Scorodocarpus borneensis* (Olacaceae), *Syzygium palembanicum* (Myrtaceae) and *Palaquium obovatum* (Sapotaceae). Most of the trees (76%) fall into the three height categories from 6 to 20m (Figure 2.9). When considering trees and palm trees together (as Siberut macaques often used palm trees as food resource), these three categories account for 78% (Figure 2.9). The category with the highest proportion of trees, 11-15m, accounted for one third of all trees (32.6% for trees, 33.1% for trees & palm trees). Only a small proportion of trees was higher than 30m (trees: 4.1%, trees & palm trees: 3.6%). The distribution of time the macaques spent in different height classes during their normal, daylight activities was different from the abundance of different height classes in the forest ($X^2 = 1841.5$, df = 8, $p<0.001$, Figure 2.9) The macaques spent 51% of their time at less than 5m height, and only 30% of their time between 6 and 20m, the three categories which comprise the majority of the forest trees.

The diameter distribution of trees showed an average of 99cm dbh in all plots together, which is mainly driven by the large trees characteristic for Plot A, the only plot on the top of a hill. After excluding this plot, the average dbh of trees decreased to 38cm.

The largest trees >100cm dbh belonged to the family Dipterocarpaceae (*Dipterocarpus elongates*, *Shorea ovalis*, *Shorea pauciflora*) in Plot A, and to the family Euphorbiaceae (*Endospermum malaccense*) and Moraceae (*Artocarpus maingayi*, *Ficus* sp.) in 2 plots on the dry level ground. The distribution of trees in the botanical plots per dbh class followed a negative exponential distribution, with trees of smaller diameters being the most abundant, with a gradual decrease with increasing diameter (Figure 2.10). The sleeping trees used by the study group showed a very different distribution from the actual forest tree distribution (Figure 2.10; $X^2 = 647.8$, df = 9, $p<0.001$). The majority of sleeping trees (85%) had a dbh between 40 and 90 cm. Nearly 7% of sleeping trees were larger than 100cm dbh, indicating that monkeys favored large trees as sleeping trees. As large trees occur at low abundance they are an important requirement for a suitable habitat of Siberut macaques.

The distribution of feeding tree sizes was more even (Figure 2.10). A large proportion of feeding trees were small trees between 10 and 20cm dbh (24.6%), but there was also a high percentage of feeding trees larger than 50cm dbh (40.6%). The distribution of feeding trees used by the group was significantly different from the distribution of the same tree species in the botanical plots ($X^2 = 74.3$, df = 9, $p<0.001$), thus indicating that large feeding trees are a critical key component for the survival of Siberut macaques.

The tree flora was clearly dominated by the family Euphorbiaceae, both in terms of number of individuals (156) and species richness (21 species). For Siberut macaques, this family was important because it included the most favorite species of sleeping trees (*Endospermum malaccense*). As fruit resource, Euphorbiaceae appeared to be less important, which may be due to the irregularity of fruit production. Five of the seven species used by the macaques were fruiting in one year (habituation period), but not in the other (data collection period). The second most important tree family in terms of number of individuals (119) was Myristicaceae. It had a high importance as fruit resource for Siberut macaques (*Knema* sp.), but not as much as sleeping trees. Other important families in the forest based on number of individuals were Dipterocarpaceae (78), Sapotaceae (68) and Myrtaceae (63). In terms of species richness however, Euphorbiaceae, the family with the highest species richness, was followed by Lauraceae (9), Myristicaceae (8), Annonanceae (7) and Rubiaceae (7).

Considering all studied plant categories in the botanical plots and not only trees, the species with the highest abundance was a rattan species, *Korthalsia echinometra* (Palmae), reaching an abundance of 158 individuals in the 3ha of forest examined, followed by the palm tree *Oncosperma horridum* (157 individuals). The most abundant tree species *Vatica pallida* (Dipterocarpaceae) was about three times rarer in number (61 individuals). Rattan and palm trees were very important for Siberut macaques because they provided fruit for a longer time period. This can be seen from the number of months each species was recorded as fruit resource during scan observations over a period of 1 year. In average, palm trees provided fruit during 6.0 months (n = 4 species), rattan during 3.3 months (n = 8), whereas lianas and trees only during 2.1 or 2.0 months respectively (n = 7; n = 17).

The importance of palms for the forest and their dominance can also be seen from the basal area per family: Palmae (or Arecaceae) was the top-ranking family in terms of basal area (4.86 m^2/ha), followed by Dipterocarpaceae (2.98 m^2/ha), Euphorbiaceae (2.68 m^2/ha), Myristicaceae (2.51 m^2/ha), Moraceae (2.46 m^2/ha), Myrtaceae (2.27 m^2/ha), and Sapotaceae (2.09 m^2/ha). All other families had a basal area less than 2 m^2/ha. Total basal area of trees, palm trees, lianas, rattan and strangler combined was 33.68 m^2/ha, that of trees alone 28.46 m^2/ha.

2.5 Discussion and conclusions

Interspecies comparisons: The genus Macaca

The present study provides first comprehensive data on the ecology of a new representative within the ecologically very diverse macaque genus. The study group comprised 29 individuals, which is twice the size suggested by the preliminary observations of Whitten & Whitten (1982). Our second semi-habituated group consisted of at least 13 individuals, which is probably an underestimate as the number of adult males (3) which were frequently seen and vocalized was the same as in our much larger study group. All these observations suggest that group size for Siberut macaques falls within the range reported for *M. silenus* (9-31 individuals; 9 groups: Kumara & Singh (2004)), *M. sinica* (5-47 individuals; 20 groups Dittus (1988)) and *M. radiata* (16-44 individuals; 12 groups: Sugiyama (1971)).

Our comparative data sets revealed that Siberut macaques are ecologically most similar to pigtail macaques, *M. nemestrina* (Caldecott 1986a; Caldecott et al. 1996), their sister taxa according to genetic analyses (Ziegler et al. 2007). Siberut macaques are semi-terrestrial, traveling large distances per day relative to their group size, spending a very high percentage of their daily activities on traveling and using a mainly frugivorous diet. In the following, we discuss these traits in more detail.

The Siberut macaques studied here spent a very large amount of their daily activities on traveling, ranking second among all 15 macaque species examined. These differences in traveling time appear to be true differences, as they cannot be attributed to different sampling methods (69% scan sampling, 21% other, 10% unknown observation method; Table 2.3) or different definitions, because even when taking both traveling and foraging time together, Siberut macaques are still different from other macaque species. Siberut macaques also traveled longer distances per day (highest value for their group size, but similar to *M. nemestrina*). The high amount and distance traveled may be linked to the degree of terrestriality. For pigtail macaques, ground foraging and traveling is an adaptation to the habitat of Sundaic dipterocarp forest with scarce food resources which are patchy and slow to renew (Caldecott 1986a). Ground traveling allows fast traveling between widely dispersed fruit resources, and additionally allows the exploitation of food resources on the ground (Caldecott 1986a; Caldecott et al. 1996). Similarly, Siberut macaques inhabit dipterocarp and mixed forest where food seemed to be dispersed and often in small patches, for example the various different rattan fruit or Aren (*Arenga obtusifolia*) fruit which were common fruit resources throughout the year (CR, unpublished data). Similar to pigtail macaques, Siberut macaques mainly used the ground for traveling and to some extent for foraging. They were usually searching for insects or spiders and mushrooms under old foliage or on fall-down trees, and were occasionally picking young leaves or leaf petioles of herbs from the ground vegetation (e.g. from *Curculigo latifolia*, Hypoxidaceae), while searching for fruiting trees within their home range. As adaptation to those scattered and often cryptic resources, they would often forage alone or together with only a few other individuals in close vicinity, with sometimes large group spreads of ~200m, or in rare cases of over 400m. A similar pattern was reported for pigtail macaques (Caldecott 1986a; Caldecott et al. 1996). Another explanation for the high amount of traveling in Siberut macaques could be the lower percentage of trees bearing fruit (max. 5% in Central Siberut (median 3.5%) compared with max. 16% (median 4%) in Malay Peninsula (Whitten 1980b)).

Comparison of the diets of macaques revealed that Siberut macaques were mainly frugivorous, which is similar to *M. nemestrina*, *M. nigrescens* and *M. tonkeana* (Table 2.4). Ménard (2004) suggested that the most frugivorous macaque species also spend the most time moving. We tested this using the comparative data sets from Table 2.3 and 2.4 and by only including those groups and species for which both the time spent feeding on fruit and the time spent moving/ traveling were available for the same study site or group, we avoided potential confounding effects of habitat differences. There was a positive significant correlation (Spearman rank: $r_s = 0.53$, $n = 20$, $p<0.02$), i.e. the more frugivorous a species (or group) is, the more time of its daily activities it has to spend traveling, which could partly explain the large amount of time spent traveling in Siberut macaques.

Figs (Ficus spp.) are a common food source for many primates (Shanahan et al. 2001) and can make up a large percentage of the fruit diet of macaques (20-40% for *M. fascicularis* (Ungar 1995; Kinnaird and O'Brien 2005), 44% for *M. nigra* (Kinnaird and O'Brien 2005), 47% for *M. nigrescens* (Kohlhaas 1993); see also Riley (2007) for the importance for *M. tonkeana*). For Siberut macaques however, figs only accounted on average for 6.9% of the total amount of known fruit eaten per month. The abundance of figs (≥ 10cm dbh) on Siberut was relatively low, with a density of 2.7 figs/ha, similar to the figure for South Sumatra (1.4 figs/ha, Kinnaird & O'Brian (2005)), but very different to Sulawesi (11.8 figs/ha in the habitat of *M. nigra* in North Sulawesi (Kinnaird and O'Brien 2005), 33.2 figs/ha in the habitat of *M. tonkeana* in Central Sulawesi (Riley 2007)). As figs are not so abundant in the habitat of Siberut macaques, they are of lesser importance than, for example, rattan or palm fruit (rattan fruit: 8.5%, palm tree fruit: 22.3% of the monthly fruit diet). A high degree of frugivory and thus dependence on fruiting trees within the forest has important conservation consequences for *Macaca siberu*, which will be discussed below.

In addition, as island biogeography theory would predict, we may expect a possible niche shift or niche expansion in Siberut macaques, since longtail macaques which are the main competitors of pigtail macaques on the mainland Sumatra (Crockett and Wilson 1980), are completely absent in Mentawai. However, as the activity budget and diet of Siberut macaques and pigtail macaques are very similar, there is no indication for a behavioral or dietary niche differentiation. For forest strata use, no detailed data are available for pigtail macaques, but judging from the degree of terrestriality, there is also no indication for a broadened niche.

Interspecies comparisons: Siberut's primates

Of all primate species on Siberut, Siberut macaques have the largest group size and the largest home range requirements (see also Whitten and Whitten 1982). Although Kloss gibbons and Siberut macaques are both mainly frugivorous, Siberut macaques have a broader diet (i.e. also feed on herbs, mushrooms, sap and resin, pith etc) and dietary overlap between the two species seems low (only 25.6%, i.e. 10 out of 39 fruit species recorded for Kloss gibbons (Whitten 1982a) were also used by Siberut macaques, but different species may fruit in different years). Our present findings showed that Siberut macaques consumed a remarkably small amount of leaves for a rainforest macaque species (Table 2.4) and in this respect they resemble Kloss gibbons which include a much lower proportion of leaves in their diet compared to Malaysian gibbon species (Whitten 1982a). One possible explanation may be that due to the high annual precipitation and a very nutrient poor soil on Siberut, competition between trees is especially high resulting in a high concentration of secondary compounds in (tree) leaves and thus in a decreased digestability for mainly frugivorous primates, leading to a decreased choice of leaves as food resource compared to other primate species (Whitten 1980b; Whitten 1982a). Quantitative data to test this, however, are missing. Siberut macaques still fed on more leaves than Kloss gibbons, probably because they also used young herbaceous leaves from the understory vegetation, as they frequently foraged and travelled on the ground.

Forest comparison

The behavior of every animal is closely linked and determined by its habitat (Krebs and Davies 1997). Differences in the behavior of Siberut macaques compared to other macaque species could be attributed to differences in the forest habitat. To investigate this possibility, we compared species, family richness and other important forest characteristics of the habitat of Siberut macaques with other forests in the same phytogeographical region of Malesia.

In our study, we recorded a tree species richness of 133, which is lower than in North-Sumatra (184 species, Kartawinata et al. 2004), and thus in line with island biogeography (MacArthur and Wilson 1967; Simberloff 1974), as islands usually have an impoverished flora. This impoverishment, however, was only seen at the species level, not at the family level, as we recorded a similar number of tree families as in North-Sumatra (40 families in this study; 41 in North Sumatra: Kartawinata et al. 2004). The basal area of trees in our study site was very similar to that recorded in Central Siberut (28.5 m²/ha of trees ≥10cm dbh in this study; 27.7 m²/ha of trees ≥15cm dbh in Central Siberut, Whitten (1982d)), indicating that our botanical plots are representative for the forest of Siberut Island. In North-Sumatra, however, basal area is much higher (40.6 m²/ha of trees ≥10cm dbh, Kartawinata et al (2004). The three most species rich families were Euphorbiaceae, Lauraceae and Myristicaceae, with Euphorbiaceae and Lauraceae also being among the three most species rich families in another study at the same site in Siberut (Hadi et al. 2009b), as well as in West and East Malaysia (Kochummen et al. 1990; Lee et al. 2002). The tree families with the highest richness of individuals were Euphorbiaceae, Myristicaceae and Dipterocarpaceae, which is the same as in Central Siberut but in a different order (Dipterocarpaceae, Myristicaceae, Euphorbiaceae: Whitten 1982d), and Euphorbiaceae and Dipterocarpaceae were also the two top-ranking families in terms of tree richness in mainland Sumatra, West and East Malaysia (Kochummen et al. 1990; Laumonier 1997; Lee et al. 2002).

Rattan, which are centered in their distribution on the Sunda Shelf (Whitmore 1984), were an important feature of the studied forest, reaching densities of 83.3

individuals (apparent genets) per hectare. Although this density is much lower than in West Malaysia (115 clumps/ ha, Abdul Hamid and Suratman 2010) or Sulawesi (314 mature genets/ha, Siebert 2005), rattan diversity (10 species in this study) was higher than in East Malaysia (6 species, Putz and Chai 1987) and similarly high in West Malaysia (11 species, Abdul Hamid and Suratman 2010). Apart from rattan, palm trees were a common element in the forest, as already noticed for Central Siberut before (Whitten 1982d), reaching relatively high densities (*Oncosperma horridum*: 52.3 palms ≥10cm dbh/ha, *Arenga obtusifolia*: 17.3 palms ≥5cm dbh/ha or 9.7 palms ≥10cm dbh/ha). They are no indicator of disturbance, as they are common in primary forests (Laumonier 1997). Densities of other species which are more light demanding and thus common in secondary forests (Kochummen et al. 1990) were all low or average, thus there was no floristic indication for disturbances in the plots (*Endospermum malaccensis,* Euphorbiaceae: 2.3 trees/ha, *Dillenia obovata*, Dilleniaceae: 3.0 trees/ha, *Macaranga sp,* Euphorbiaceae: 0.7 trees/ha, *Campnosperma auriculatum*, Anacardiaceae: 1 tree/ha; compared to a mean of all tree species of 2.7 trees/ha, or the maximum density of 20.3 trees/ha of *Vatica pallida*, Dipterocarcpaceae).

Our comparison has shown differences between the forest in Siberut and other forests in Malesia in terms of an impoverishment of tree species richness, lower tree basal area and lower rattan density. Collectively, this may lead to a lower diversity and abundance of fruit resources, and this could possibly explain the large travel distances and the high amount of time devoted to traveling in Siberut macaques.

Conservation and future of Siberut macaques

Based on the present results, we can give the following advice for future conservation action plans for Siberut macaques. First, it has to be taken into account that Siberut macaques need a much larger home range than any of the other primate species on Siberut. An appropriate conservation area would be an area large enough to sustain several groups to facilitate emigration processes and gene flow, and large enough to include sufficient fruit resources during seasons of low fruit availability. The area should consist of an intact, rather than fragmented, forest area as the dense, continuous forest was the most frequently used habitat type and was the basis of their food supply. Large forest trees in particular are important both as fruit resources and sleeping trees, as was already assumed by Whitten and Whitten (1982). Thus, selective logging of the large trees would immensely disturb their livelihood.

The future of Siberut macaques will unavoidably be closely connected to habitat degradation and loss. As macaques are generally omnivorous, they have the advantage of being able to adapt more easily to habitat changes than more specialized primates.

However, as fruit constitutes a large percentage of their diet, they are likely to raid crops on farms if their original forest habitat does not supply enough fruit anymore, and this would increase conflicts with local people. In Siberut, local people traditionally hunt and trap primates, and Siberut macaques are caught in ground traps baited with sago, with which they can trap a whole group at once (pers. comm. by C. Abegg). Thus, Siberut macaques will become more vulnerable with increasing habitat loss and degradation.

The habitat of Siberut macaques is decreasing continuously. From the total land area of Siberut probably all covered with rainforest in the past, 87% was left in 1980 and only 60% in 2005 (2,400 km², Table 1 in Whittaker 2006). From the remaining forest cover, 1,926 km² are assigned to the Siberut National Park, but only 465 km² are a protected no-use sanctuary zone where no hunting and logging is allowed (Fuentes 1996/1997). A recent investigation has shown that the density of Siberut macaques in the national park is about three times lower than in the SCP area where this study was conducted (data from M. Quinten, unpublished), which indicates that the national park alone might not be enough to conserve Siberut macaques in the long-term. Although the status of Siberut macaques is not yet listed as critical, their population decreased from ~39,000 individuals in 1980 to 17,000-30,000 individuals in 2005 (Whittaker 2006) and if this decline continues, their future may soon be at risk.

2.6 Acknowledgements

We are grateful to all Indonesian authorities (LIPI, DEPDAGRI, DIKTI, RISTEK, PKSDA Padang) for granting the necessary research permits (Permit No.: 2921/FRP/SM/XII/08). Thanks to the Siberut Conservation Programme (SCP) for allowance to work on their field station, and to all SCP staff for very valuable field and logistical support, especially to Marcel Quinten for his reliable help and enthusiasm for the project. We thank all the people who helped tremendously during habituation and data collection, namely all field assistants (Adi Nugroho, Marliana Chrismiawati, Rahayu Oktaviani, Azhari Purbatrapsila, Rima Lamhatul Mikrimah, Betty Millyanawati), Pierre Gras who joined for his Master thesis, all field guides (P. Safrizal, P. Mathias, P. Mitchen, Bang Risel, P. Tongam, P. Teiba, P. Bitcar) and Pak Tarzan and especially Pak Nauli who helped with their local plant knowledge with the identification of the vernacular names of all plants in the botanical plots, as well as all sleeping and feeding trees. We are thankful to Arthur R. Rodgers and John Kie for advice with the Home Range Extension Tool. We like to acknowledge 4 anonymous reviewers whose detailed and helpful comments greatly improved this manuscript. CR, JO and OS received funding by the Max-Planck Society and the German Initiative of Excellence to the Georg-August University Göttingen, and CR received funding by the Evangelisches Studienwerk e. V.

Competing interests

The authors declare that they have no competing interests.

Author’s contributions

JO, KH and OS conceived the study, CR and AT collected data, CR analyzed the data, AT identified the plant specimen, CR, JO and OS wrote the paper. All authors read and approved the final manuscript.

Chapter 3

Food resource characteristics and predictors of food-related aggression in wild Siberut macaques (*Macaca siberu*), an oceanic island species with low predation risk

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American Journal of Primatology (in revision)

3.1 Abstract

The socioecological model for the evolution of female social relationships has been criticized repeatedly. Mismatches between model predictions and empirical findings may result from neglecting predation risk or from inappropriate testing. We addressed this lack of studies in low predation pressure environments in an observational study on *Macaca siberu,* endemic to the oceanic island of Siberut that lacks large carnivores. If group cohesion does not reduce predation risk, individuals can react to contest competition by spreading out and feeding in smaller parties at low or no cost. We measured group spread during regular activities allowing us to base our measures of resource characteristics on a scale relevant to the animals. We quantified food resource size, depletion, availability and density to estimate contest competition potential and recorded behavior in food patches using a modified focal tree method. Food patches of most plant species (70%) were small to medium sized, occurred at low densities and well distributed, promoting contest competition. However, aggression rate in food patches was low (between adults: 0.13 bouts/ h) compared to other species and was predicted by social factors coding for opportunity for aggression and crowdedness, but not by ecological factors. Individuals fed in small feeding parties (average 3.1 individuals). In 49.8% of all observations, individuals fed completely alone or with nearly no temporal overlap with other individuals. Average group spread was 50m and highly flexible, with individuals spreading over more than 100m (max. 419m) in 9.4% of the observations. Our study confirms predictions of the socioecological model for species under low predation risk, and shows that conclusive tests of model assumptions and predictions require measures of resource characteristics (not just diet) on a scale relevant to the animals, and consideration of predation risk as a cost of avoiding contest competition over food.

Keywords: contest competition, aggression, patch depletion, feeding ecology, socioecology, predation risk

3.2 Introduction

The socioecological model for the evolution of female social relationships proposes that environmental factors, such as resource characteristics and predation risk, as well as social factors (infanticide risk), affect grouping patterns and feeding competition, which in turn affect female social structure (van Schaik 1989; Sterck et al. 1997; Janson 2000; Koenig 2002; Schülke and Ostner 2012; Koenig et al. 2013). The model has been criticized repeatedly (Janson 2000; Thierry 2008; Clutton-Brock and Janson 2012) because data do not always support the model (Isbell 1991; Koenig 2002; Koenig and Borries 2006; Clutton-Brock and Janson 2012) which led some to call for abandoning the model altogether (Thierry 2008). The opposing stand in the current debate is that many mismatches stem from imperfect and uncritical testing and that more data measured on relevant scales are needed to falsify the socioecological hypothesis (Isbell and Young 2002; Koenig and Borries 2006; Snaith and Chapman 2007; Vogel and Janson 2007; Koenig and Borries 2009; Schülke and Ostner 2012).

Apart from methodological issues, inconsistencies between the model predictions and empirical data may also stem from concentrating mainly on feeding competition in the past. Without considering predation risk, which is an integral part of socioecological theory (van Schaik 1989; Sterck et al. 1997; Koenig et al. 2013), results cannot be fully understood. If food resource characteristics promote contest competition, subordinates may only be willing to pay costs in terms of reduced net energy intake or increased rates of aggression received if increased predation risk at the periphery of the group keeps them from feeding elsewhere. So far, however, predation risk has often been neglected in socioecological studies (but see e.g. (Wittig and Boesch 2003)), and only few studies have been conducted on oceanic islands where predation pressure usually is reduced due to the lack of carnivores (van Schaik 1989; but see van Schaik and van Noordwijk 1985). The present study aims to address this gap by investigating feeding competition in Siberut macaques (*Macaca siberu*), a species endemic to a single small oceanic island (Siberut, West-Sumatra, Indonesia), and by measuring food resource characteristics and aggression at a scale relevant to the animals by adopting the focal-tree method (Vogel and Janson 2007).

Food resource characteristics such as abundance, quality and especially distribution, influence the competitive régime and social relationships in a wide range of taxa (Hourigan 1989; Kotschral et al. 1993; Travis and Slobodchikoff 1993; Sterck et al. 1997; Johnson et al. 2002; Archie et al. 2006). When food occurs in large patches relative to group size, or is highly dispersed and/ or quickly depleted and of low quality, within-group scramble competition prevails (Sterck et al. 1997; Steenbeek and van

Schaik 2001; Koenig 2002). Under scramble competition, food consumption by any individual reduces the net energy intake of all others (Koenig 2002). Social relationships are not expected to be directly affected by scramble competition (van Schaik 1989; Janson 2000), but a reduction in relative food abundance could intensify the other type of feeding competition (Isbell 1991). Within-group contest competition is expected when limiting food resources are of high quality, low density, and occur clumped into patches small enough to be monopolized by a part of the group or a single individual (van Schaik 1989; Isbell 1991; Sterck et al. 1997; Koenig et al. 1998; Isbell and Young 2002; Koenig 2002; Koenig et al. 2013). Contest competition is thought to promote the formation of dominance hierarchies and leads to skewed energy acquisition towards dominant individuals (Vehrencamp 1983; Janson and van Schaik 1988; van Schaik 1989; Barton and Whiten 1993; Vogel 2005), affecting individual fitness and female reproductive success (Whitten 1983; Harcourt 1987; Janson 1988a; McFarland Symington 1988b; Isbell 1991). Contest competition is usually linked to aggression, but can also be very subtle, i.e. avoidance behavior (Snaith and Chapman 2007).

The intensity of feeding competition is strongly influenced by predation risk and cohesiveness of the group (Terborgh and Janson 1986; Koenig and Borries 2006; Schülke and Ostner 2012). If predation risk is low, as on most oceanic islands where large carnivores are absent, inter-individual distances can be increased, reducing the strength of both within-group scramble and contest competition (Janson 1988b; van Schaik 1989; Koenig and Borries 2006). As groups become less cohesive, female bonds become weaker (van Hooff and van Schaik 1992). Predation risk was thus identified as an important factor influencing social relationships (van Schaik and van Hooff 1983; van Schaik 1989; van Hooff and van Schaik 1992; Sterck et al. 1997; Schülke and Ostner 2012).

On Siberut, primates are the most common large mammals, as large carnivores including felids are absent (WWF 1980; Tenaza and Tilson 1985). An experimental study showed that primates (*Simias concolor*) do not perceive felid models as predators (Yorzinski and Ziegler 2007; Yorzinski 2010). The reduced terrestrial predation risk allows Siberut macaques to frequently use the ground for travelling (Richter et al. 2013). Siberut's largest predator is the reticulated python, *Python reticulatus* (WWF 1980). One case of python predation on a juvenile Siberut macaque has been observed during the present study (CR, unpublished data; 2 additional cases outside the study period). Records of predation by raptors are lacking. Whether crested serpent eagles, *Spilornis cheela sipora* prey on macaques is debated (Whitten and Whitten 1982; Tenaza and Tilson 1985), but they generally avoid primary forest (Thiollay 1998), the primary habitat at the study site.

Based on the lack of terrestrial predators (humans excluded), we predicted that group members can spread out during foraging, i.e. flexibly adapt group spread to the resource conditions. We also predicted that group members frequently feed alone or in small feeding parties. As a result, we predicted that aggression rates among Siberut macaques are low compared to those reported for other primates in medium to high predation pressure environments. If aerial predators constitute a risk, we predicted that the top parts of the tree crowns are avoided during feeding (Isbell 1994). If there is no avoidance behavior of aerial predators, the upper vertical layers of the tree crowns should be preferred, as they have higher photosynthate production resulting in higher fruit densities, larger fruit and probably fruit of higher nutritional quality than lower vertical layers (Houle et al. 2007; Houle et al. 2010).

In order to assess feeding competition in Siberut macaques, in particular the potential for within-group contest competition, we first described the food resource characteristics, such as temporal and spatial food distribution, food patch size, density and patch depletion. We predicted that the potential for contest competition exists if high quality food occurs in small depletable patches, when food patch density is low, and when food patches are distributed in a dispersed or random manner (i.e. not clumped) so that no alternative resources are available close by. Since Siberut macaques are highly frugivorous (75.7% of feeding time, Richter et al. 2013), we focused on fruit patches, and expected that most feeding competition will be over fruit, generally a food of high quality (Schülke et al. 2006). In order to address the criticism that food distribution is rarely or inappropriately measured (Isbell et al. 1998; Isbell and Young 2002), we used two approaches that measure resource distribution from the perspective of the group. Firstly, we used botanical plots that cover the area usually covered by the group during their regular activities (group spread). Secondly, we used the distribution of the actual food plants visited within the monthly home range. The distribution and density of food resources will also help to understand the effects on the group's daily travel distance (Isbell et al. 1998; Chapman and Chapman 2000b), which has been reported to be much larger than for other macaque species of similar group size (see macaque comparison: Richter et al. 2013).

After describing resource characteristics, we investigated which ecological and social factors predicted aggression frequency in food patches. Previous studies have shown that aggression or agonism is higher in small patches (Sterck and Steenbeek 1997; Janson and Vogel 2006; Vogel and Janson 2007), when food abundance is low or ripe fruit is limited in the patch (Sterck and Steenbeek 1997), and when food distribution within the crown is clumped (Sterck and Steenbeek 1997). The amount of alternative resources available to subordinates in order to avoid aggression has been suggested as an influential factor (Vogel and Janson 2007; Vogel and Janson 2011). In addition to these ecological factors, social factors like feeding party size or composition have been linked to aggression frequency. More aggression is predicted under increased crowding, i.e. with an increased number of females, males and juveniles (Janson 1988a; Janson and Vogel 2006; Vogel and Janson 2007; Asensio et al. 2008). The time spent in a food patch, which increases the opportunity for aggression, should also be considered (Janson and Vogel 2006; Vogel and Janson 2007). In Thomas langurs, *Presbytis thomasi*, the feeding party composition affected aggression, with lower aggression rates among females if the resident male was present (Sterck and Steenbeek 1997). Based on findings of previous studies, we predicted aggression frequency to increase with increasing feeding group size, number of adult females, adult males and juveniles, increased crowdedness, i.e. less space per individual, and increased feeding bout length (time spent in a food patch). We further predicted aggression frequency to decrease with increased fruit abundance in the patch, increased number of alternative fruit resources outside of the patch (but within the area of a regular group spread), and with increased fruit abundance in the forest, measured as the number of visited feeding “trees” per day.

3.3 Methods

Study site and species

The study was carried out on Siberut Island, West-Sumatra, Indonesia, at the field site of the Siberut Conservation Programme (www.siberut-island.org), situated in North-Siberut (for map see Richter et al. 2013). Siberut is covered by tropical lowland evergreen broadleaf rainforest (UNEP-WCMC classification) or tropical moist broadleaf forest (WWF classification). The study site consists of undisturbed primary rainforest as well as some secondary forest at late successional stage (Richter et al. 2013; see there for a detailed description of the habitat). The climate on Siberut is equatorial without seasonal changes in temperature (Richter et al. 2013). Annual precipitation at the study site is high, with 3,601 mm per year, and every month is perhumid (Erb et al. 2012a).

Siberut macaques, *Macaca siberu*, are endemic to Siberut island. Siberut macaques are highly frugivorous (75.7% of total feeding time) and are relative terrestrial (28.9% of activity time on the ground) (Richter et al. 2013). The study group (group A) consisted of 29 individuals, including 3 adult males and 8 adult females. Adult individuals were all identified except two females which were first seen at the end of the study (Richter et al. 2013). Agonistic interactions between adults were too rare to construct a dominance hierarchy (no agonistic interactions in 115h of adult continuous focal observations; for aggression in food patches see below). Although the study group was surrounded by at least three neighboring groups (Richter et al. 2013), no between group encounters were observed during one year of observations. Groups usually advertised their position to the neighboring groups by frequent loud calls of the males.

Behavioral data collection

Data were collected between March 2010 and March 2011, by 1 to 3 observers simultaneously. We followed the group from sunrise to sunset, from sleeping tree to sleeping tree. We conducted group scan observations (Martin and Bateson 1993) every 30 min for 5 min. During group scans, we recorded the GPS locations of as many individuals as possible, and in case of feeding, we recorded focal plant observations (see below).

To record the use of food patches, we conducted focal tree observations by adapting the method proposed by Vogel & Janson (2007). A total of 439 observations equaling 135.8 hours of feeding time were collected (425 between March 2010 and March 2011, plus 14 additional ones by one observer between May and August 2011) every time one or more individuals were feeding from a plant resource. During these observations, Siberut macaques were co-feeding on the same fruit resource six times with *Hylobates klossii*, once with *Presbytis potenziani* and once with *Simias concolor*. In three cases, observations were conducted simultaneously on two different trees used by different group members (twice the same plant species was used within 15m distance, once different plant species were used within 56m distance). As food resources consisted of trees (49.2%), stranglers (0.9%), lianas (15.7%), rattan (15.3%) and palm trees (18.9%), we use the term focal plant observation in the following. All observations were fruit eating events apart from one, so for simplicity we refer to all plants as fruit plants. A food patch was defined as the focal plant itself and for one species it also included fruit that had fallen on the ground. These patches were usually well defined and crowns were not connected to other plant individuals of the same species. Observations started when the first individual entered the food patch, and lasted until the last individual left. We used continuous recordings (Martin and Bateson 1993) to record the time and identity of all individuals entering and leaving, and in case the identity was unclear, age/ sex class was recorded instead. To record agonistic behavior, we used all occurrence sampling (Altmann 1974; Martin and Bateson 1993) and recorded the time, identity of involved individuals and location in the crown. For analysis however, we excluded spontaneous submission and only focused on the occurrence of aggression (threats and contact aggression). To score the location of aggression, the tree crown was split into 3 equal vertical parts (y-axis) and 3 equal horizontal parts (x-axis) on each side of the tree, starting from the trunk. We thus distinguished crown bottom, middle layer and top on the y-axis and crown center, inner periphery and outer periphery on the x-axis. To compare the location of aggression with the location of feeding within the crown, we conducted instantaneous scans in 5 minute intervals (Altmann 1974; Martin and Bateson 1993), but only during the first five months of observations. For this we recorded for each individual the identity, activity and position in the crown. In order to investigate patch depletion, we used 1-minute focal animal sampling (Altmann 1974; Martin and Bateson 1993) to record bite rates of individuals of all age-sex classes. Both the feeding gain as bites per unit time (ideally 1 minute) and feeding effort as the distance moved during this time were recorded. If a second observer was close by, this one recorded the bite rates, otherwise the first observer recorded it parallel to the continuous data. After the last individual left the food patch, the total number of monkeys using the resource was recorded (if individuals entered multiple times they were counted only once). The focal plant was measured for diameter at breast height (dbh) using a diameter tape, height was estimated visually (or length for lianas and rattan) after training of all observers, and each focal plant was marked with flagging tape. For each plant a unique number was given and the position was recorded with a GPS device. In addition, the length, width and perpendicular height of the crown were estimated visually. Abundance of food items was recorded on a $\log_{10}$ scale (see below). Plant species identification was validated with herbarium specimen. To account for the quality of the focal plant observation, we recorded whether the observation was complete (i.e. started with the first individual entering, or incomplete, i.e. one or more individuals were already in the focal plant at the time the observer arrived), and the visibility of the whole crown (good visibility = whole crown visible, restricted visibility = parts of the crown were covered by branches from neighboring trees). For each focal plant observation, however, substantial effort was made to maximize visibility by moving around under the tree. From all observations used for the aggression analysis, 80% were complete observations, and 53% were of good visibility.

Group spread

Group spread was defined as the maximum distance between any two group members, including all age-sex classes, during scan observations with ≥5 individuals (n = 1,279 scans, mean ± SD: 9.4 ± 3.4 individuals). The maximum distance was calculated as the Euclidean distance, i.e. altitude was not taken into account.

Botanical data

We established 12 permanent botanical plots of 50m x 50m size (3ha in total) that were distributed semi-randomly within the group's home range, taking different altitudes (hill, lowland areas) and forest type (wind fall areas, distance to river) into account. We recorded all trees ≥10 cm dbh (diameter at breast height), all lianas and stranglers ≥5 cm dbh and rattan (climbing palms) longer than 5m (more details in Richter et al. 2013). Height for trees and palm trees, and length for lianas, rattan and strangler was estimated visually after training with a measuring tape. For each species, we collected two specimen with the help of a local plant expert. Specimen were identified and stored at the Herbarium ANDA of the Andalas University Padang, W-Sumatra (Richter et al. 2013).

Variables included in the analysis of aggression frequency

Average feeding group size: The average number of individuals in the focal plant during a focal plant observation was calculated from continuous enter/ leave data using 5 minute intervals. The average for all focal plant observations was 3.1 individuals, the maximum 18.6 individuals.

Total number of adult females, adult males and juveniles: The total number of individuals per age/ sex category who visited the plant resource was used, as an average number could not be calculated because the identity of the individuals was not always determined during both the entering and leaving.

Space per individual: The space available per individual (in m^3) was calculated as the crown volume divided by the average feeding group size. Crown volume was calculated as a product of average length, width and height of the crown (estimated visually), as this was more appropriate for most focal plants (especially lianas, rattan, strangler, palm trees, but also several tree species) than assuming an ellipsoid to estimate crown volume. If estimations were available from multiple observers, the average crown volume was used.

Fruit abundance: The abundance of fruit was measured on a $\log_{10}$ scale (1 = 1–9; 2 = 10–99; 3 = 100–999; 4 = 1,000–9,999; and 5 = 10,000–99,999; Janson and Chapman 1999) by counting the number of fruit in a small section of the crown, multiplied by the number of same sized sections within the crown.

Alternative resources: The number of alternative resources was defined as the number of plant individuals of the same species which were used as a food resource in the same month and were within a radius of 50m (the average group spread, see results section) to the focal plant. The number of alternative resources ranged between zero and two.

Visited feeding trees per day: We used the number of visited feeding trees per day based on focal plant observations as a measure of general fruit abundance in the forest. Each individual focal plant was only counted once, independently of whether this plant was revisited on the same day or not. The maximum number of different individual feeding “trees” used per day was 9.

Feeding bout length: This is the time (in minutes) the focal plant was visited from when the first individual entered until the last one left. In rare cases, if all individuals stopped feeding but remained in the plant, this time was subtracted from the feeding bout length. Focal plant observations lasted between a few minutes to maximum 92 minutes.

Measuring scramble competition

If food patch depletion and thus scramble competition occurs because food items become rarer within the patch as patch occupancy time increases, then the feeding gain of the individuals, measured as food intake rates (bite rates), should decrease. However, a decrease in intake rates could be either the result of patch depletion, or of the animals becoming satiated. To distinguish between both possibilities, we measured the feeding effort, defined as the movement within the patch (distance in meter). If food intake rates decrease while feeding effort stays constant or increases, satiation is unlikely and patch depletion is evident. Bite rates and distances moved were calculated down to units of 10 seconds to include as many data as possible. Only focal plant observations longer than 10 minutes were used, to allow for enough time to deplete a patch, for which a total of 705 individual observations on feeding gain and effort were available. For analysis, we compared the average feeding gain and effort of the first and last third of each focal plant observation, which included 53 matched observations from 13 different plant species. Analysis was done using a Wilcoxon matched pairs test.

Spatial distribution of plants and resources

To assess the potential availability of alternative fruit resources in close spatial proximity in order to avoid aggression, the variance-to-mean ratio was used as an index of dispersion (Ludwig and Reynolds 1988; Ganzhorn 2003). Importance was based on the number of focal plant observations for each species. The variance-to-mean ratio was calculated using the frequency of occurrence of each species in the botanical plots. However, this takes all individuals into account, and is not restricted to the ones actually bearing fruit. Thus, in order to assess if the distribution of fruit resources influences daily travel distance of the group, we calculated the spatial distribution of the fruit resources used. We conducted an average nearest neighbor analysis in ArcGIS$^{®}$ 9.3.1. (Spatial Statistics Toolbox) for which we used the geographical locations of the focal plants

(Shaffer 2013). The analysis yields a nearest neighbor index (NN ratio), expressed as the ratio of observed distance of each plant to the nearest neighbor, divided by the expected distance, i.e. the average distance between focal plants within the monthly home range area used by the group. Monthly home range was determined as 95% Minimum Convex Polygon, calculated using the Home Range Tools (HRT) Add-In for ArcGIS® 9.3.1. The underlying dataset included 4,839 unique point locations (without duplicates) collected during group scan observations (Richter et al. 2013). A NN ratio of 1 indicates random distribution, <1 indicates clustering (clumped distribution) and >1 dispersed or uniform distribution. Significant difference from a random distribution ($p<0.05$) was tested using a Chi² test (Ludwig and Reynolds 1988). To investigate a potential influence of resource distribution on daily ranging behavior, we calculated daily travel distances from 2,267 group scan observations in 30 min intervals, using group center coordinates and only days with ≥9 hours observation time per day (Richter et al. 2013).

Statistical analyses

To predict the frequency of aggression during focal plant observations, a subsample of 234 observations was used which were at least 5 min long and for which data were available for all predictor variables. Due to a high correlation of average feeding group size and total number of juveniles ($r_s = 0.7$, $n = 234$, $p<0.001$), the latter had to be excluded as a predictor from the analysis. All other predictors showed correlations of less than 0.6. Skewed predictor distributions were transformed and all predictors were standardized. As aggression was very rare and occurred in only 41 out of 234 observations, zero inflation was an issue. We thus applied a zero-inflated Poisson (ZIP) model (Zeileis et al. 2008), consisting of a binomial model to model the occurrence of false zeros versus all other data (true zeros and count data), and a Poisson model to model the frequency of aggression (allowing zeros). In the binomial model, we used completeness of observation (yes / no) and visibility of the crown (good / restricted) as predictor variables to account for the quality of the observations. In the Poisson model, we included average feeding group size, total number of adult females, total number of adult males, space available per individual, fruit abundance, number of alternative resources, number of visited feeding trees per day and feeding bout length as predictor variables. As overdispersion was an issue in the original data, we compared the ZIP model to a zero-inflated negative binomial (ZINB) model, but a likelihood ratio test indicated no significant difference between the two ($\chi^2 = 3.8$, $df = 1$, $p = 0.053$), thus favoring the ZIP model. Dispersion parameter of the ZIP model was 1.2, indicating no overdispersion after accounting for zero inflation. Plotting the Pearson residuals against all predictor variables showed no obvious pattern, thus all model assumptions were met. The ZIP model was significantly different from a null model (Wald test: $Chi^2 = 72.9$, df= 10, $p<0.001$).

All analyses were performed with the statistical software environment R© (version 3.0.0, R Development Core Team 2013), apart from the Wilcoxon matched pairs test which was done in Statistica© StatSoft Inc. 2011, version 10. In addition to the standard R packages, computations were performed with the R package ‘pscl’ (Jackman 2012).

The present study was completely non-invasive and complied with the regulations of the involved institutions, the legal requirements of Germany and adhered to the principles of the American Society of Primatologists for the ethical treatment of primates. Approval and permission to conduct the research was granted by the Indonesian authorities (LIPI, DEPDAGRI, DIKTI, RISTEK, PKSDA Padang; Permit No.: 2921/FRP/SM/XII/08).

3.4 Results

Group spread

The average maximum distance between individuals, i.e. the group spread, was 50.0m (SD: ± 56.3m; median: 33.6m), with a maximum distance of 418.5m. In 37% of the group scan observations, the group spread was larger than the average 50m. Group spread variation throughout the day (Figure 3.1) showed increased cohesion in the early morning and late afternoon. During 9:30 and 15:30 o'clock, average group spread equaled 61.6m (SD: ± 58.1m; median: 48.1m). Apart from the daily variation, group spread also varied largely per month, with the lowest average group spread of 28.9m in November 2010, and the largest average group spread of 73.6m in March 2010. Inspection of the histogram of inter-individual distances reveals no break-points in the distribution or bimodality, suggesting that the group spread out continuously without forming sub-groups (Figure 3.2).

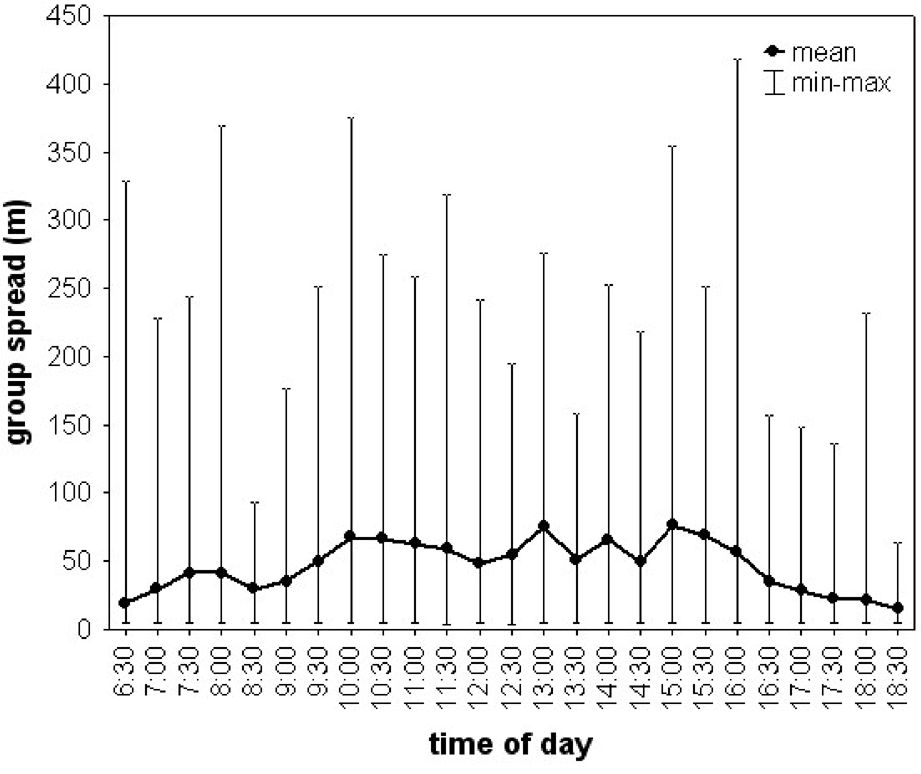

Figure 3.1 Variation of average, minimum and maximum group spread (in meters) throughout the day. Group spread was defined as the maximum distance between group members of any age-sex class, and was calculated from group scan observations between March 2010 and March 2011. Sample size for each time of the day was on average 51 scan observations (6:00 am was omitted from graph, as n = 3). Only scans where at least 5 individuals were recorded were used for group spread calculation (n = 1279 scans), with an average of 9.4 individuals recorded per scan (32.4% of total group). Only in 11 scans at least 75% of the total group was recorded.

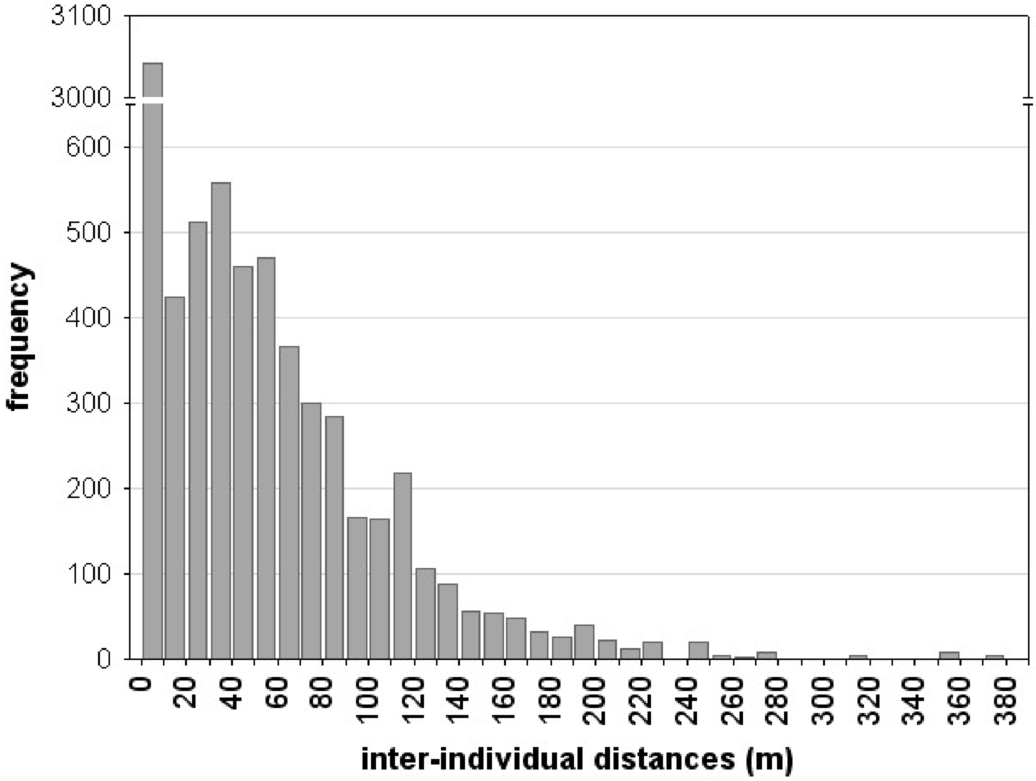

Figure 3.2 Inter-individual distances (in meters) between individuals during scan observations, calculated as distances between the individual farthest away from the group center to all other individuals at a given scan time. Only scans conducted between 9:30 and 15:30 o'clock are presented in the graph, as this was the time period with generally two observers in the field. Individuals are spread out continuously, with no formation of sub-groups.

Food characteristics: patch size, depletion, distribution, density

Here we use all focal plant observations to describe the group's resource exploitation with respect to plant species, growth form, patch size, and feeding group size. During focal plant observations the group used plants from 25 families and 60 species. The top five most frequently used species accounted for 51% of all observations. The macaques fed most often (60% of focal plant observations) on small to medium-sized food patches like rattan, lianas, stranglers, small to medium sized trees and palm trees which accounted for 70% of all the species used (Table 3.1). For all focal plant observations combined, the average number of animals feeding together simultaneously was 3.1 (SD: 3.1, range: 1-19), and varied according to the different food patch size categories (Table 3.1). The mean total number of individuals using the patch throughout the whole patch occupancy time was 5.3 (SD: 5.9, range: 1-28).

To investigate patch depletion, we compared bite rates at the beginning and end of a feeding bout and found that bite rates were slightly lower towards the end (mean first third: 3.4 bites/ 10 sec, mean last third: 3.2 bites/ 10 sec, n = 53 focal plant observations). Feeding effort, measured as the distance moved during feeding, was slightly higher at the end of the feeding bout compared to the beginning (mean first third: 0.18 m/ 10 sec, mean last third: 0.23 m/ 10 sec, n = 53). These results were in the predicted direction, although patch depletion was not statistically significant (Wilcoxon matched pairs tests n = 53: bite rates: T = 528, Z = 1.27, p = 0.206; feeding effort: T = 159, Z = 1.26, p = 0.206).

The temporal distribution of resources is illustrated in Table 3.2. From all 60 plant species the macaques fed on during focal plant observations, only 14 provided fruit for at least three months during a full year cycle. Most of these 14 species were palm trees and rattan (Family Palmae). Among the 34 (non-palm) tree species, only four provided fruit for a longer time period of at least three months (Table 3.2).

We used botanical plots of 50m x 50m size to assess food plant abundance and distribution within the area of average group spread. The spatial distribution of frequently used plant species (at least 5 focal plant observations) showed a significantly clumped distribution within botanical plots for 10 species, and a random distribution for 8 species (Table 3.3). A clumped distribution alone is not enough to provide some macaques an alternative food resource in close spatial proximity to the patch used by other group members, in order to avoid aggression from conspecifics. To become a potential alternative feeding site, resources need to occur clumped and at high densities. However, only 2 out of the 10 species with clumped distribution (the palm tree *Arenga obtusifolia* and the rattan *Korthalsia echinometra*) also had reasonable high densities (Table 3.3).

As the plant distribution within botanical plots includes all plants and not only those individuals which actually provided fruit, we also investigate the spatial distribution of the tagged plant individuals that were actually used by the group during focal plant observations across the home range. On a monthly basis, these fruit resources were distributed randomly in 8 months, and dispersed in 4 months (significant for 3 months, a trend in 1 month; Table 3.4). The fruit resources used never showed a clustered distribution (Table 3.4), which could explain the much higher daily travel distance of Siberut macaques in comparison to other macaque species. There was no correlation between the monthly distribution of resources (NN ratio) and the monthly average daily travel distance of the group (Spearman rank: r_s = -0.1, p = 0.785, n = 10 months).

Table 3.1 Overview of focal plant observations per category (rattan, lianas and strangler, small trees and palm trees, medium sized trees and large trees) with their mean diameter at breast height (dbh), mean height or length, mean and maximum of the total feeding group size (total number of different individuals using the resource throughout the whole feeding time in the patch) and mean feeding group size (average number of individuals using the resource at the same time, calculated from 5-min intervals), number of plant species and number of focal plant observations (Obs.).

	No. of plant species	Obs.	dbh (min-max)	Height* (min-max)	Total feeding group size (max)	Mean feeding group size (max)
Rattan	7	67	3 (2-4)	30 (22-42)	2 (11)	1 (4)
Lianas, strangler	12	68	11 (4-15)	43 (12-57)	5 (22)	3 (12)
Small trees/ palm trees	12	89	14 (6-17)	11 (6-13)	2 (10)	2 (6)
Medium trees	11	39	23 (17-42)	18 (12-20)	3 (13)	2 (8)
Large trees	18	176	69 (47-98)	38 (24-47)	9 (28)	5 (19)
Total	60	439			Mean ± SD: 5 ±6	Mean ± SD: 3 ±3

[1] for trees and palm trees height was measured, for rattan, lianas and strangler the length

Table 3.2 Temporal pattern of fruit resource use during focal plant observations. Species are included if they were used in at least three months between March 2010 and March 2011. The number of focal plant observations is given per species (Obs.) as well as the number of different plant individuals used per species (Ind.).

			2010									**2011**				
Fam.	**Species**	**Habit**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**Obs.**	**Ind.**
Ana	*Campnosperma auriculatum*	T			x	x					x			x		73	13
Apo	*Leuconotis eugeniifolius*	L			x	x	x	x				x				8	6
Gne	*Gnetum sp.*	L	x	x	x			x								34	12
Lau	*Litsea noronhae*	T				x	x			x						4	2
Mor	*Artocarpus rigidus*	T				x	x	x		x	x		x			40	8
Myr	*Knema sp.*	T						x	x	x						21	6
Pal	*Arenga obtusifolia*	P			x	x		x	x	x	x	x	x	x		42	19
Pal	*Calamus reinwardtii*	R		x	x	x	x	x	x	x	x	x	x	x		34	20
Pal	*Caryota mitis*	P				x		x			x					3	2
Pal	*Korthalsia echinometra*	R					x	x					x			6	5
Pal	*Korthalsia scorthechinii*	R			x			x					x			3	3
Pal	*Oncosperma horridum*	P				x		x	x	x						16	16
Pal	*Pinanga sp.*	P		x	x	x			x							16	9
Pal	*Plectocomia griffithii*	R					x	x				x	x	x		15	9

Habit: T = tree, L = liana, P = palm tree, R = rattan; Families: Ana = Anacardiaceae, Apo = Apocynaceae, Gne = Gnetaceae, Lau = Lauraceae, Mor = Moraceae, Myr = Myristicaceae, Pal = Palmae

Table 3.3 Characteristics of the most important fruit species (size, density and spatial distribution), based on botanical plot data (12 plots á 50x50 m, i.e. the area of group spread) sorted by decreasing importance (number of focal plant observations). Density is mean density per plot and density per hectare. Spatial distribution is the variance-to-mean ratio (Var./ mean ratio). Significant (*) variance-to-mean ratio >1 indicates clumped (clustered) distribution, <1 dispersed (uniform) distribution. Values ~1 and non-significant values indicate random distribution. Distribution (Distr.) abbreviations: clu = clumped, ran = random

Fam.	**Species (Habit)**	**Focal plant obs.**	**Density per plot (group spread)**	**Density per ha**	**Mean height[1] (m)**	**Mean dbh (cm)**	**Var./ mean ratio (Distr.)**
Ana	*Campnosperma auriculatum* (T)	74	0.3	1.0	26.7	56.8	3.0* (clu)
Pal	*Arenga obtusifolia* (P)	42	4.3	17.3	11.4	15.3	5.0* (clu)
Mor	*Artocarpus rigidus* (T)	40	0.2	0.7	24.5	47.1	0.9 (ran)
Pal	*Calamus reinwardtii* (R)	34	0.9	3.7	12.9	4.6	1.7 (ran)
Gne	*Gnetum sp.* (L)	34	1.6	6.3	29.1	11.8	2.5* (clu)
Myr	*Knema sp.* (T)	21	1.2	4.7	16.5	23.5	1.2 (ran)
Pal	*Pinanga sp.* (P)	16	0.8	3.3	9.2	10.3	3.0* (clu)
Pal	*Oncosperma horridum* (P)	16	13.1	52.3	15.5	16.7	1.6 (ran)
Pal	*Plectocomia griffithii* (R)	15	2.3	9.3	21.9	2.9	2.4* (clu)
Ole	*Chionanthus glomerata* (T)	13	2.3	9.0	9.4	13.5	2.6* (clu)
Sym	*Symplocos fasciculata* (T)	11	0.4	1.7	11.7	13.5	3.3* (clu)
Sap	*Harpullia arborea* (T)	8	0.4	1.7	25.1	31.3	1.1 (ran)
Apo	*Leuconotis eugeniifolius* (L)	8	0.5	2.0	25.3	6.1	1.3 (ran)
Mor	*Ficus parietalis* (L)	6	0.2	0.7	28.5	7.6	0.9 (ran)
Pal	*Korthalsia echinometra* (R)	6	13.2	52.7	14.4	1.5	8.3* (clu)
Cel	*Bhesa paniculata* (T)	5	1.9	7.7	20.1	27.2	2.3* (clu)
Dil	*Dillenia indica* (T)	5	0.6	2.3	15.4	28.9	1.1 (ran)
Sap	*Nephelium lappaceum* (T)	5	0.7	2.7	18.7	33.7	2.3* (clu)

[1] for trees and palm trees height was measured, for rattan, lianas and strangler the length; Habit: T = tree, L = liana, P = palm tree, R = rattan; Families: Ana = Anacardiaceae, Apo = Apocynaceae, Cel = Celastraceae, Dil = Dilleniaceae, Gne = Gnetaceae, Mor = Moraceae, Myr = Myristicaceae, Ole = Oleaceae, Pal = Palmae, Sap = Sapindaceae, Sym = Symplocaceae

Table 3.4 Spatial distribution (within the monthly home range) of all fruit resources visited during focal plant observations per month. Ind.: number of individual plants used. Dtd: average daily travel distance of the group. Spatial distribution was measured as nearest neighbor ratio (NN ratio). A significant NN ratio >1 indicates dispersed (uniform) distribution, <1 clumped (clustered) distribution, and ~1 and non-significant values indicate random distribution.

Month	**Dtd (m)**	**Ind.**	**NN ratio**	**Z score**	**p value**	**Distribution**
Mar-10		5	0.77	-0.98	0.328	random
Apr-10	2272.0	12	1.04	0.26	0.793	random
May-10	2321.5	21	0.93	-0.65	0.517	random
Jun-10	2283.3	28	0.95	-0.55	0.585	random
Jul-10	1877.0	17	1.69	5.44	**<0.001**	dispersed
Aug-10	1810.4	29	0.99	-0.09	0.931	random
Sep-10	1766.0	24	0.92	-0.74	0.462	random
Oct-10	2079.8	20	1.21	1.76	*0.079*	dispersed
Nov-10		12	1.00	0.02	0.981	random
Dec-10	2002.2	17	0.84	-1.28	0.200	random
Jan-11	1911.1	20	1.23	1.98	**0.048**	dispersed
Feb-11	2160.5	37	1.19	2.18	**0.030**	dispersed

Aggression

Feeding group size was usually small. From all focal plant observations, one individual was feeding alone in 27.9% of the observations without any other group member entering the patch throughout the observation. From the remaining 72.1% where at least two individuals were using the patch in total, 30.4% of the observations had an average feeding group size smaller than two, i.e. most of the time throughout the entire patch occupancy time one individual was feeding alone, and there was only little temporal overlap of individuals feeding together. Thus, the potential for aggression was either completely absent or very low in 49.8% of all recorded focal plant observations. If more than one individual used a patch, aggression occurred in 19.8% of the cases, with up to 6 aggressive conflicts per focal plant observation (95 dyadic conflicts, 3 polyadic), resulting in an aggression rate of 0.34 bouts per focal plant observation or 0.83 aggressive bouts per hour spent co-feeding with at least one other group member (all age-sex classes included). Aggression occurred more often between juveniles (36.8%) and in adult-juvenile dyads (36.8%), and less between two adults (26.3%), which can be explained solely on the basis of the opportunity for aggression between certain age classes, as observed values are not significantly different from what is predicted based on available dyads per age class (Chi² test: $\chi^2 = 2.8$, df = 2, $p = 0.24$). Most of the aggression occurred in the middle vertical layer of the crown, at the outer periphery (Table 3.5). This was also the location of most feeding events (Table 3.5).

Zero-inflated Poisson modeling suggested that the excessive number of zeros, i.e. focal plant observations where no aggression was recorded, was not caused by incomplete observations or poor observation conditions. Observation quality criteria did not significantly account for the lack of aggression in most observations (Table 3.6). The frequency of aggression was significantly influenced by three predictor variables. Feeding bout length showed the largest effect, with more aggression occurring the longer the individuals fed in a patch. The space available per individual as a measure of crowdedness had a negative effect, with less aggression occurring if there was more space per individual. Average feeding group size showed a significant positive effect, with a higher likelihood of aggression if there were more individuals feeding together on average per focal plant observation (Table 3.6). The number of adult females influenced aggression rates (statistical trend), indicating that aggression was more likely if more adult females were feeding in the same resource. Contrary to our prediction neither the abundance of fruit in the focal plant, the availability of alternative resources within the group spread, nor overall fruit availability in the forest, i.e. the number of feeding trees visited per day, influenced aggression rates. It was not possible to account for plant species as a random factor in such a zero-inflated model, but we visually confirmed that results were not driven by one or two species alone.

Table 3.5 Percentage of aggression and feeding events per crown location. Locations of aggression and general feeding did not differ significantly (Wilcoxon matched pairs test: T = 21.0, Z = 0.18, p = 0.859, n = 9). Feeding positions were recorded in 5 min intervals during focal plant observations, the position of aggression with all occurrence sampling.

Aggression		Center	Inner periphery	Outer periphery
	Crown top	2.0	5.9	15.7
	Crown middle layer	3.9	5.9	31.4
	Crown bottom	0.0	13.7	21.6
Feeding events		**Center**	**Inner periphery**	**Outer periphery**
	Crown top	2.6	5.9	17.9
	Crown middle layer	5.0	14.2	25.1
	Crown bottom	3.2	9.3	16.8

Table 3.6 Results of the zero-inflated Poisson model predicting the frequency of aggression during focal plant observations. All predictor variables in the count model were standardized.

Count model (Poisson model)	Estimate	SE	*z* value	*p* value
Intercept	-1.73	0.24	-7.22	**<0.001**
Average feeding group size	0.47	0.21	2.29	**0.022**
Number of adult females	0.39	0.22	1.81	*0.070*
Number of adult males	-0.16	0.14	-1.16	0.244
Space per individual	-0.57	0.15	-3.82	**<0.001**
Fruit abundance	-0.10	0.13	-0.81	0.420
Alternative resources	-0.11	0.20	-0.53	0.595
Visited feeding trees	-0.14	0.14	-1.01	0.313
Feeding bout length	0.74	0.18	4.14	**<0.001**
Zero-inflation model (binomial model)	**Estimate**	**SE**	***z* value**	***p* value**
Intercept	-9.72	116.25	-0.08	0.933
Complete observation	-9.21	65.02	-0.14	0.887
Visibility	18.88	133.20	0.14	0.887

3.5 Discussion

Food resource characteristics, aggression and predation risk

This study aimed to contribute to the current debate about the merit of the socioecological model by presenting critical tests of model predictions and by providing data on a species that evolved under low predation risk. Low predation risk can have impacts on two different levels, a) individuals can feed alone in a tree without running the risk of predation, and b) low-ranking individuals can feed away from the group center and use alternative food resources to avoid aggression. To clarify the influence of low predation risk on feeding competition, it is important to first assess the resource characteristics and whether they actually promote contest competition or not. Within-group contest competition is predicted when food patches are depletable, of high quality, low density, small relative to group size, i.e. not all individuals can fit in the patch, and when food occurs in monopolizable patches (van Schaik 1989; Isbell 1991; Sterck et al. 1997; Isbell and Young 2002; Koenig 2002). As Siberut macaques mainly feed on fruit (Richter et al. 2013), and fruit is generally of high nutritional quality (Schülke et al. 2006; Zuberbühler and Janmaat 2010), the high quality criteria is met. Patch depletion is important to elicit contest competition, but was not statistically significant for reasons discussed below in detail, but was at least in the predicted direction.

The density of frequently used fruit plants was very low (for 16 out of 18 species). A comparison of food tree densities in habitats of different primate species shows that only a small fraction of important feeding tree species (22%, 2 out of 9 species) reached densities of >5 individuals/ha in the habitat of Siberut macaques, compared to 33% (1 out of 3 species) for hanuman langurs (Koenig et al. 1998), 70% (7 out of 10 species) for Assamese macaques (M. Heesen pers. comm., for methods see Heesen et al (2013)), and 80% (8 out of 10 species) for chimpanzees and gorillas (Morgan and Sanz 2006). In the habitat of Siberut macaques, only one palm tree and one species of rattan had high enough densities within the average group spread to provide a potential alternative fruit resource of the same quality close by. As palm tree and rattan fruit are also temporally available over a much longer time period than tree fruit, they constitute important food resources, which confirms previous observations (Richter et al. 2013) and fits with earlier observations that Siberut macaque density was higher in areas where rattan was not collected commercially (WWF 1980; Whitten and Whitten 1982).

Most food patches used (60% of the observations) constituted small to medium-sized patches like rattan, lianas, stranglers, and small to medium sized trees and palm trees. The fruit of palm trees like *Arenga obtusifolia* and *Pinanga sp*. and fruit of all rattan species was also spatially concentrated in clumps which could be monopolized by one or a few individuals. In sum, given that the food used by Siberut macaques was of high quality, occurred in small and sometimes monopolizable patches and low densities, potential for contest competition should be high and aggression should be frequent.

Although a high contest potential existed, observed aggression rates were very low. From all observations with at least two individuals in the fruit patch, aggression only occurred in 19.8%, which is half than observed in gorillas, *Gorilla beringei* (40% of all fruit patch observations, Robbins (2008)). When comparing aggression rates in fruit patches, Siberut macaques had the lowest of all rates: adult-adult aggression rate *M. siberu*: 0.13 bouts/ h (this study), *Ateles paniscus chamek*: 0.21 bouts/ h (McFarland Symington 1988b), *Saimiri sciureus:* 0.29 bouts/ h (Mitchell et al. 1991), *Macaca assamensis*: 0.56 bouts/ h (Heesen et al. in review); female-female aggression rate *Pan troglodytes verus*: 0.22 bouts/ h (Wittig and Boesch 2003), *Cercocebus torquatus atys*: 0.59 bouts/ h (Range and Noë 2002). Unfortunately, comparative data are still sparse, as not many researchers collected overall aggression rates in food patches, but rather only during focal animal sampling in a feeding context/ food patch (Sterck and Steenbeek 1997; Korstjens et al. 2002; Hanya 2009).

The low aggression rate and partly the lack of influence of ecological factors on aggression frequencies may be a consequence of low predation risk. Without a risk of predation by carnivores, individuals can flexibly adapt their foraging behavior to the given resource characteristics, i.e. they can forage dispersed to reduce aggression over small food patches, without facing costs of increased predation. This should result in larger inter-individual distances. Group spread is of course also dependent on group size (Gillespie and Chapman 2001; Carbone et al. 2003; Smith et al. 2005). The average group spread of Siberut macaques (50m) fits well to the range of other primates (*Sanguinus fuscicollis*: 10m (4-8 individuals) (Smith et al. 2005), *Sanguinus mystax*: 12m (7-8 individuals) (Smith et al. 2005), *Colobus guereza*: 22m (7-23 individuals) (Fashing and Cords 2000; Fashing 2001), *Cercocebus albigena*: 57m (15 individuals) (Olupot et al. 1997), *Procolobus badius*: 52m (24 individuals)/ 66m (48 individuals) (Gillespie and Chapman 2001), *Macaca assamensis*: 115m (49-52 individuals), M. Heesen, pers. comm.). In 9.4% of the observations, however, group spread was larger than 100m, and in 40 group scans (0.3%) the group spread was larger than 300m, which is very large for this group size. Such a large group spread is especially remarkable because we could only record on average 32% of the group members during group scans, as individuals were often very dispersed and difficult to find. The data suggest that individuals can continuously spread out over several hundred meters, without forming sub-groups. Foraging in loose groups might also increase food encounter and intake rates, as small food patches might still provide enough food for one or a few individuals, but maybe not for the whole group. In addition, food patches might also already be partly depleted by other frugivorous primates, so that foraging alone may also partially account for this.

The dispersed foraging/feeding fashion of Siberut macaques is supported by the small observed feeding group sizes. Although the average feeding group size of 3.1 individuals in *M. siberu* is within the range for primates (Mitchell et al. 1991; Chapman et al. 1995; Phillips 1995; Koenig et al. 1998), it constitutes a relatively low percentage of the total group size (10.7%). The small feeding group sizes and the low temporal overlap of individuals feeding in the patch together at the same time might be caused by the dispersed foraging behavior, with individuals arriving and entering the food patch one after the other. Siberut macaques do not walk in straight line distances from fruit tree to fruit tree, as frugivorous neotropical primates commonly do, but rather forage as a loose group. Another reason for the small average feeding group size might be active avoidance behavior by queuing. In 7 cases, we observed that individuals were waiting for another individual to leave the food patch before they entered themselves, i.e. only one individual would use the patch at a time. As the focal plant observation method is focused on the behavior solely within the patch, we currently cannot estimate the importance of such queuing behavior. Queuing behavior was observed 4 times in palm trees of 3 different species, twice in rattan, and once in a wild banana tree, i.e. always when food patches were small to medium sized and more important, when food was spatially clumped. Queuing behavior did not only occur among juveniles or among adults, but was also observed twice where an adult female was waiting for a juvenile before entering the food patch. Such queuing behavior seems to be an effective way to avoid aggression. Although queuing might involve costs such as losing time for other activities, these costs seem negligible, as waiting time was between 0.5 and 2.5 min. This time is short as individuals can just quickly pick as many fruit possible from the fruit cluster, which does not involve movement within the patch, and then store them in their cheek pouch and leave the patch to process the fruit elsewhere. Queuing as an active behavior to avoid aggression might thus be an expression of contest competition.

The lack of felid predators might also act on another level apart from large inter-individual distances and small feeding parties, namely on juvenile behavior, and this might even be more obvious and better comparable between study sites. Juveniles are the most vulnerable to predation because of their small body size and relative inexperience, and should therefore prefer more central positions within the group (Janson and van Schaik 2002; Fichtel 2012; Cunningham et al. 2013). In Siberut macaques, juveniles and even infants were not any closer to the group center than adults, i.e. there was no significant difference from what would have been expected if all individuals space out equally (median distance to group center: infants 12.4m, juveniles

16.8m, adult males 17.1m, adult females 19.5 m; Friedman Anova $\chi^2 = 1.00$, n = 4, df = 1, p = 0.317). Thus, it is no surprise that juveniles were also frequently feeding alone in food patches without adults present close by (19.4% of focal plant observations, of which 55.4% of the cases were one juvenile feeding alone even without other juveniles). In contrast, in *Macaca fascicularis* on Sumatra, where 3 species of felids exist, individuals compete for safe spatial positions within the group (low-ranking ones in the periphery), with juveniles never being or feeding alone (van Schaik and van Noordwijk 1986; van Schaik and van Noordwijk 1988; van Noordwijk et al. 2002). In Siberut macaques, there is also likely no such spatial assortment among adults. Although dominance rank could not be determined, there was no difference in spatial position of the six adult females (when not lactating or with sexual swelling; distance to group center: median ± SD: 24.5 ± 1.4m, range: 23.1 – 26.9m; Friedman Anova $\chi^2 = 0.67$, n = 6, df = 1, p = 0.414).

Whether aerial predators constitute a threat for Siberut macaques is still unclear. The data on crown use during feeding suggest that they avoid the top layer of the crown and feed most frequently at the outer periphery of the crown middle layer, which might still get more sunlight and thus have better quality fruit than the inner periphery or center of the tree crown (Houle et al. 2007; Houle et al. 2010). During observations in windthrow areas however, which are open areas consisting of only broken trees and no protective forest canopy (Richter et al. 2013), Siberut macaques never showed any vigilance behavior while foraging or resting in these areas. Thus, either crested serpent eagles do not constitute a major risk as they mainly feed on reptiles and birds (92%) and rarely on mammals at all (Gokula 2012), and the observed avoidance behavior of the canopy top is due to other unknown reasons, or these raptors prefer to hunt animals from trees rather than from the ground. As we do not have any information on hunting behavior of *Spilornis cheela sipora,* we cannot elucidate this question so far.

Resource characteristics do not only influence feeding competition but also ranging behavior. The distribution of feeding trees which Siberut macaques used per month was either random or dispersed, suggesting that feeding trees are widely scattered, whereas feeding trees of bearded sakis, *Chiropotes sagulatus*, were clustered in 4 out of 10 months (Shaffer 2013, using same NN ratio as in this study). Although we did not find a correlation between the monthly travel distance and the spatial distribution of feeding trees, maybe because variation in distribution was too small, it might still be that the general pattern of widely distributed feeding trees, together with small patch sizes, may explain why Siberut macaques travel much more than other macaque species of similar group size (Richter et al. 2013).

Food patch depletion

Contest competition should be stronger if resources are limited, making food patch depletion a fundamental part in several models of feeding competition (van Schaik 1989; Isbell 1991). In has been demonstrated for both frugivorous and folivorous primate species that most food patches become depleted (spider monkeys, howler monkeys, chimpanzees, red colobus, Assamese macaques: (Chapman 1988; Chapman et al. 1995; Snaith and Chapman 2005; Heesen et al. in review)). However, primates may only deplete certain food patches depending on digestability, nutrient composition and presence of toxins in the food (Chapman 1988). In our study, there may be several underlying processes for our finding of only a tendency for patch depletion, but no statistical support. For large forest trees like *Campnosperma auriculatum,* which accounted for half of the observations in the analysis, food abundance is very high (usually several thousand small ripe fruit; average fruit diameter: 6.5mm, SD: 0.2mm, n = 15) so that food seems abundant enough to not get depleted during one feeding bout. This is supported by observations that the group often revisited these trees later during the day and/or on the following days. For small food patches like the palm tree *Arenga obtusifolia* (13% of observations), food abundance is much lower (usually less than 100 fruit; average fruit diameter: 34.9mm (SD: 1.5mm), average fruit height: 41.5 mm (SD: 1.5mm), n = 15), but total and average feeding group size is small as well. Also these patches can get revisited later by the same or different individuals. The main restrictions for intake rates of *Arenga* fruit may be that they are difficult to pick from the infructescence, often involving both hands, mouth and sometimes feet; they are difficult to open due to a hard woody pericarp, making handling time considerably long; and they contain oxalic acid (Whitten 1980a) which might restrict the maximum consumption by an individual at a given time. Most rattan fruit patches are also likely to not get depleted during one feeding bout. Although rattan constituted 15.3% of all focal plant observations (67 rattan focal plant observations), most of them (75%) were used for less than 10 minutes, which was our threshold for observations to be included in the patch depletion analysis. Rattan fruit were usually picked quickly, stored in the cheek pouch, and were processed at a later time by rubbing them on branches to break open the hard scales and eat the sarcotesta (flesh). Thus handling time may be the restricting factor also for these patches to not get depleted. Similar to *Arenga* and *Campnosperma* food patches, rattan patches were also sometimes observed to be revisited by group members on the same or following days. In sum, the fact that many patches do not get depleted within one feeding bout may contribute to the low aggression rates in Siberut macaques.

Predictors of aggression in food patches

Aggression frequencies, which are an expression of contest competition, were only significantly predicted by social factors, but surprisingly not by ecological factors. The strongest effect was feeding bout length, which is simply the temporal opportunity for aggression, with aggression being more likely the longer individuals feed together in a patch. The second largest effect was the space available per individual as a measure of crowdedness. The more crowded a patch becomes, the more likely aggression is to occur. The third important factor was the average feeding group size, with higher aggression frequencies if more individuals feed together, no matter to which age-sex class these individuals belong, although the number of adult females showed a statistical trend, whereas the number of males did not. This might be due to the small variations in male group size, with only 3 adult males in the group. Our results confirm findings from previous studies: in *Ateles paniscus chamek* and *Cebus capucinus* more agonism occurred when trees became crowded (McFarland Symington 1988b; Vogel and Janson 2007), in *Ateles geoffroyi* aggression rate in feeding context was higher in larger subgroups (Asensio et al. 2008), in *Macaca assamensis* aggression frequency was higher the more adults were feeding together in a food patch (Heesen et al. in review), in *Gorilla beringei* aggression rate increased with the number of individuals in a fruit tree (Robbins 2008), in *Pan troglodytes verus* aggression rate increased with the number of competitors present at a feeding site (Wittig and Boesch 2003), and in *Macaca fuscata* aggression increased with less feeding sites available (Hanya 2009). Furthermore, a recent phylogenetically controlled comparison of agonism rates in different primate taxa showed that agonistic rates are mainly influenced by group size (Wheeler et al. 2013). In a study of white-faced capuchin monkeys, *Cebus capucinus*, agonism was also significantly influenced by the time spent in a food patch and by the number of adult females (Janson and Vogel 2006; Vogel and Janson 2007).

All three ecological factors included in our model (food abundance in patch and forest, alternative resources) did not influence aggression frequencies. Whereas food abundance predicted aggression rates in Thomas langurs, *Presbytis thomasi* (Sterck and Steenbeek 1997), no effect was found for longtail macaques, *Macaca fascicularis* (Sterck and Steenbeek 1997), similar to Siberut macaques in this study. The amount of alternative resources available also did not show any influence on aggression frequencies in Siberut macaques. Thus, in order to avoid aggression, individuals could either feed on different food items rather than on the same fruit species within the distance of the average group spread (Saito 1996), or they simply might adopt the queuing strategy described above, and as most food patches do not get depleted within one feeding bout, this might be a good alternative. Such a strategy is also known from another primate on an island habitat, from *Cebus capucinus* on Barro Colorado, foraging successively in trees with limited space (Phillips 1995).

3.6 Summary and outlook

The present study contributes to the current debate about the validity and power of the socioecological model (Koenig and Borries 2006; Thierry 2008; Clutton-Brock and Janson 2012; Koenig et al. 2013) by confirming some of its predictions related to predation risk (van Schaik 1989; Koenig 2002; Koenig and Borries 2006). In support of the theory set forth by the model, we find that low predation risk allows individuals a) to flexibly increase group spread and spread out continuously to explore resources over a wider area and thus avoid aggression, b) to frequently feed alone in food patches, which was the case in 49.8% of all focal plant observations, i.e. individuals either explored the patch alone or fed in the patch with nearly no temporal overlap with other individuals, and even juveniles can feed alone without risk, and c) that these small feeding group sizes lead to very low aggression rates. Our study clearly shows that it is important to both study food resource characteristics and consider predation risk before one makes conclusions about the role and intensity of contest competition in a species. It also shows that it is not possible to predict resource distribution based on the dietary composition (Clutton-Brock and Janson 2012), nor to infer from a highly frugivorous diet alone that strong within-group contest competition exists (Ménard 2004). Furthermore, we suggest that predation risk should not only influence foraging behavior and aggression rates, but also reproductive success. We predict that if future studies can collect data dense enough to construct a dominance hierarchy for Siberut macaques, that rank will have no influence on food intake rates and female reproductive success, as individuals can forage dispersed and explore alternative food resources without costs in such a low predation risk environment. Future studies should concentrate on other species in low predation pressure environments to explore the range of impact on the competitive régime. To allow comparisons between species and better evaluate the role of predation on individuals’ spacing behavior, future studies should report group spread data more frequently, should also focus on juvenile behavior relative to predation risk, and should report overall aggression rates in food patches rather than from individual focal follows in a feeding context, to allow a better estimation of resource competition within food patches.

3.7 Acknowledgements

We would like to thank all Indonesian authorities (LIPI, DEPDAGRI, DIKTI, RISTEK, PKSDA Padang) for granting the necessary research permits (Permit No.: 2921/FRP/SM/XII/08). Thanks to the Siberut Conservation Programme (SCP) for allowance to work on their field station, and to all SCP staff for very valuable field and logistical support. Especially thanks to Marcel Quinten for his continuous and reliable help. We are grateful to all the people who made the habituation and data collection possible and successful, namely all field assistance (Adi Nugroho, Marliana Chrismiawati, Rahayu Oktaviani, Azhari Purbatrapsila, Ahmad Taufiq, Rima Lamhatul Mikrimah, Betty Millyanawati) and all field guides (P. Safrizal, P. Mathias, P. Mitchen, Bang Risel, P. Tongam, P. Teiba, P. Bitcar). We thank Pak Tarzan and Pak Nauli for sharing their knowledge about local plants, and who helped with identification of the vernacular names. Funding was provided by the Max-Planck Society and the German Initiative of Excellence to the Georg-August University Göttingen. The first author received funding by the Evangelisches Studienwerk e. V.

Chapter 4

Males matter: More males increase home range size and female reproductive success in wild Assamese macaques

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American Journal of Physical Anthropology (in revision)

4.1 Abstract

The costs and benefits of having multiple males in a group are still not fully understood. Although more males can provide certain benefits like reduced infanticide risk and resource or territory defense, they are more often associated with higher costs like increased feeding competition by increasing total group size, and increased home range overlap resulting from a collective action problem during range defense. To investigate the consequences of male group size in a primate species with male dispersal, we assessed the influence of males on home range size in Assamese macaques (*Macaca assamensis*), a species where males participate in intergroup encounters. We followed one group almost daily over more than six years to collect spatial and behavioral data (June 2006 – September 2012), and we collected climate and phenology data over five years. After controlling for food abundance, distribution, precipitation, temperature and group size, we found that male group size had a significant positive effect on both full and core home range size. Such an increase in home range area and consequently in access to food resources had a direct influence on female reproductive success, with more females conceiving when home range size before the mating season was larger. This suggests that male resource defense could be a strategy from which both sexes ultimately benefit, but which might only evolve under low contest competition which allows many males to benefit from increased female fertility.

Keywords: male resource defense, collective action problem, socioecology, daily travel distance, seasonal habitat

4.2 Introduction

The role of primate males in resource defense is still debated (Fashing 2001; Koenig et al. 2013). It is well established that in many species, males are actively participating in intergroup encounters and are often more aggressive than females (Lindburg 1971; McFarland Symington 1988a; Mehlman and Parkhill 1988; Stanford 1991; Perry 1996; Nievergelt et al. 1998; Saito et al. 1998; Fashing 2001; Cooper 2004; Cooper et al. 2004; Sicotte and Macintosh 2004; Majolo et al. 2005; Crofoot 2007; Matthews 2009; Brown 2011), but males were long thought to defend primarily mates and not resources (Trivers 1972; Rubenstein 1986; Wrangham and Rubenstein 1986; Kappeler 1999). Recently, evidence is mounting that male resource defense is more common than previously thought (Fashing 2001; Koenig et al. 2013), suggesting that females often benefit from living with many males. Co-resident males however may face a collective action problem during group defense, as all individuals in the group will benefit regardless of their contribution, which likely leads to free-riding (Nunn 2000; Willems et al. 2013). Theoretical models predict that this problem becomes larger as the number of males increases (Olson 1965; cf. Esteban and Ray 2001). A large comparative study across primates indeed could show a positive association between the number of co-resident males and the overlap of neighboring home ranges (Willems et al. 2013). Here we aim at contributing to this debate by relating the number of males to home range size in a longitudinal study.

The long-standing tenet of females being limited by access to resources and males being limited by access to mates (Trivers 1972; Emlen and Oring 1977) has guided the interpretation of male behavior during intergroup encounters as an act of mate defense. However, mate defense can be coupled with food defense by chasing off competing groups' males and thus indirectly defending food resources and protecting the females' offspring from infanticide (Wrangham and Rubenstein 1986; Fashing 2001). In this situation, males act as so called "hired guns" by serving the females' interests (Wrangham 1980; Wrangham and Rubenstein 1986). Males also have been shown to directly defend resources (Harrison 1983; Reichard and Sommer 1997; Fashing 2001; Cooper et al. 2004; Sicotte and Macintosh 2004; Korstjens et al. 2005; Crofoot 2007; Brown 2011; Wilson et al. 2012; Scarry 2013). Males may benefit from defending resources 1) if females choose selectively to mate with those males who defended resources (Steenbeek 1999; Fashing 2001; Cooper et al. 2004), or 2) if increased resource access secured by males increases female fecundity (Robinson 1988; Herrera and Macdonald 1989; Cooper et al. 2004; Williams et al. 2004; Thompson et al. 2007; Thompson and Wrangham 2008). The ability of males to increase the reproductive performance of their mates has so far received little attention among all sources of variation in male reproductive success (Alberts 2012), and will thus be discussed in the present study in more detail.

Chimpanzee males, *Pan troglodytes*, patrol and communally defend their group's territory (Williams et al. 2004; Wilson et al. 2012), and the number of males per group is positively related to territory size (Stanford 1999; Lehmann and Boesch 2003). Multimale groups of Phayre's leaf monkeys, *Trachypithecus phayrei*, defend a larger home range than similarly sized one-male groups (Carl 2009; Koenig et al. 2013). Both species are characterized by male philopatry and female dispersal where females are free to choose a target group for immigration. Yet, in tufted capuchin monkeys, *Sapajus nigritus*, a species with male dispersal and female philopatry, home range size also increases with the number of males in the group (Scarry 2013). In the latter study male group size was shown to be a good predictor of winning an intergroup-encounter, and was positively associated with per capita access to food (Scarry 2013). So far, it is unknown whether these observations are an exception or a common pattern in male dispersal species.

We collected five years of ecological and more than six years of ranging data from a wild group of Assamese macaques (*Macaca assamensis*), where females are philopatric and males disperse. As all other macaques, they live in groups of multiple males and females. Assamese macaques at our study site at Phu Khieo Wildlife Sanctuary (PKWS, northeastern Thailand) show large home range overlaps, and even sleeping trees in the core area are used by neighboring groups (Schülke, Ostner, unpublished data). No sharp territory boundaries like in chimpanzees exist. Intergroup encounters are frequent, with approximately 6 encounters with 2 habituated neighboring groups per month (Schülke, Ostner, unpublished data). This is likely to be an underestimate, as other neighboring groups are not yet habituated. Intergroup encounters can involve highly desirable food resources (fruit trees), and males take an active role in aggressive between group conflicts (Schülke, Ostner, unpublished data), suggesting that males may defend resources. We thus predicted a positive effect of male group size on home range size.

Ranging behavior of gregarious primates has been comprehensively investigated from a socioecological perspective prompting us to control for several ecological and social factors identified as affecting primate ranging behavior. One of the most important is the spatial and temporal distribution of food resources (Chapman and Chapman 2000b; Kaplin 2001; Yiming 2002; Wallace 2006). Assamese macaques at Phu Khieo spend 59% of feeding time on fruit and seeds (Heesen et al. 2013; Richter et al. 2013), suggesting that the distribution and abundance of fruiting trees and the degree of fruiting synchrony have a major effect on spatial behavior. For some primates, home range size becomes smaller when fruit is scarce, as animals restrict their ranging to reduce the energy expenditure by either broadening their diet (Kaplin 2001), or by shifting their diet from more frugivorous to more folivorous (Wallace 2006). We assumed that Assamese macaques reduce their ranging when fruit availability is low, and increase their ranging during times of high fruit availability, as they can easily find food to energetically support their travel while searching for their preferred or high quality food items (Yiming 2002). We also expected an interaction between fruit availability and distribution. We assumed that fruit patches rarely provide enough food for the whole group, so that individuals need to visit multiple patches per day, and this should be more pronounced when general fruit availability is lower. The number of fruit patches visited will also depend on group size, as larger groups deplete patches more quickly, prompting individuals to compensate by visiting more patches per day, which increases travel costs (Isbell 1991; Janson and Goldsmith 1995; Isbell et al. 1999; Chapman and Chapman 2000b; Majolo et al. 2008; ecological constraints model: Isbell 2012). We thus expected an increase in home range size with increasing group size (Isbell 1991).

Other environmental factors that influence home range size and thus need to be controlled for are precipitation, temperature, and day length. Both precipitation (Raemaekers 1980; Isbell 1983; Ganas and Robbins 2005; Matsuda et al. 2009) and lower ambient temperature (Newton 1992; Baoping et al. 2009; Carl 2009) have been shown to influence ranging negatively. Owing to thermoregulation, we assumed that home range size decreases in months with more precipitation, lower temperature, or likely an interaction of both. As daily travel distance may also influence home range size (Peres 2000), we investigated which ecological factors determine daily travel distance itself, and essentially, all predictions stated above should hold for daily travel distance as well. One additional factor, day length, may influence daily travel distance, especially given the seasonal habitat of Assamese macaques. Daylight hours will determine how much time an individual or group can spend traveling and foraging (Hill et al. 2003; Hill 2006), and should positively influence the travel distance (Yiming 2002; Baoping et al. 2009). As we focused on one group over multiple years, we did not control for habitat differences, but investigated the stability of home range boundaries over years (site fidelity: Darwin 1861; Van Moorter et al. 2009).

Our first analyses were suggestive of a positive effect of male group size on home range size. Thus, we also investigated the benefits of an increased home range size. If a larger home range is related to higher access to food resources, as it is in other species (Isbell et al. 1990; Isbell 1991), it should impact female fecundity (Williams et al. 2004). Assamese macaques at PKWS breed seasonally, with the mating season starting in October (Fürtbauer et al. 2010). Female conception is influenced by the physical condition of the female, which depends on food availability (Heesen et al. 2013). Androgen increase from August to September predicts when a female will conceive that year (Fürtbauer et al. 2013) which makes August the critical phase determining female fertility.

Specifically, we predicted that monthly home range size increases with the number of males in the group, that home range size and daily travel distance increase with increasing group size, fruit availability, a more scattered distribution of resources, and that they both decrease with more precipitation and lower temperature. Additionally we predicted a positive effect of day length on daily travel distance. Assuming that larger home ranges lead to higher access to food, we predicted home range size in August to correlate positively with the number and proportion of females conceiving in the coming mating season.

4.3 Methods

Study site, study species and study group

The present data come from a long-term field study directed by JO and OS in northeastern Thailand, at Phu Khieo Wildlife Sanctuary in Chaiyaphum Province, at the study site Huai Mai Sot Yai. The sanctuary is located between 16°5’-16°35’N and 101°20’-101°55’E, and covers a forest area of 1,573 km², which is part of the approximately 6,500 km² large Western Isaan Forest Complex (Koenig et al. 2004). Phu Khieo is home to seven diurnal primate species (*Hylobates lar*, *Macaca assamensis*, *M. arctoides*, *M. leonina*, *M. mulatta*, *Trachypithecus phayrei* and *T. cristatus*) and one nocturnal one, *Nycticebus coucang* (Borries et al. 2002). The study group (AS) of Assamese macaques, which comprised up to 64 individuals, inhabits a hill evergreen forest with some bamboo stands. This population breeds seasonally, with a mating season spanning from October to early February (dry season) and a birth season from April to July (wet season, Fürtbauer et al. 2010), which coincided with high fruit availability (Heesen et al. 2013). Female inter-birth intervals are bi-modally distributed, with females either giving birth every year or every second year (on average 13.9 or 23.2 months, Fürtbauer et al. 2010). The probability of conceptions and thus the length of the inter-birth intervals are predicted by food abundance across the first five months of lactation (Heesen et al. 2013). Male Assamese macaques disperse at all ages, and male immigration and emigration events are not limited to a certain time of the year. The study group is largely arboreal, and only spends 10% of their time on the ground (Schülke et al. 2011). The home range of the study group overlaps with at least four neighboring groups.

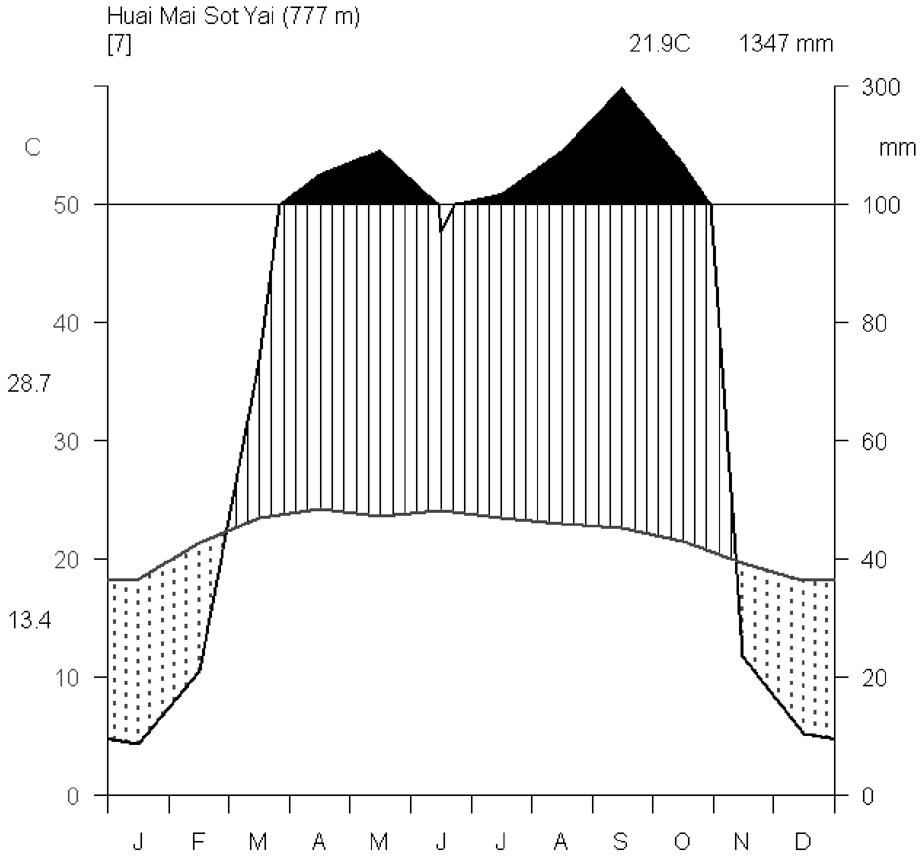

Figure 4.1 Climate at the study site Huai Mai Sot Yai during 7 years, between January 2006 and December 2012 (plotted after Walter & Lieth (1960)), with mean temperature (°C) in grey and mean precipitation (mm) in black. The filled black areas represent the perhumid period. Precipitation data for September and October 2010 were lacking. Temperature data were taken in the forest at Huai Mai Sot Yai (777m a.s.l.), precipitation data at a clearing in Salaprom (623m a.s.l.). (Courtesy: Phu Khieo Wildlife Sanctuary and A. Koenig & C. Borries, Stony Brook University). The plot was created using the R package 'climatol' (Guijarro 2012).

Climate

Climate data were recorded throughout the study period from January 2006 until December 2012. Temperature data were collected using a HOBO Pro data logger at 2h intervals directly at the study site Huai Mai Sot Yai in the forest. Precipitation data were taken using a HOBO Event data logger at the nearest clearing in Salaprom, recording every "event" of precipitation at no fixed time intervals. The climate at Phu Khieo is seasonal and influenced by the southwest monsoon, bringing warm moist air, and the northeast monsoon, bringing cold and dry air. Thus the climate can be divided into a wet season from March to October, and a dry season from November to February (Figure

4.1). The mean annual temperature during these seven years, defined as the mean of the mean daily maximum and the mean daily minimum temperature per month (Walter and Lieth 1960), was 21.9°C. The mean daily minimum of the coldest month (January) was 13.4°C, and the mean daily maximum of the warmest month (March) was 28.7°C. The mean annual precipitation equaled 1,347 mm (Figure 4.1).

Home ranges and daily travel distance

The study group was observed for more than six years (from June 2006 to September 2012) during which they were followed almost daily from sleeping tree to sleeping tree by various observers. GPS coordinates were recorded automatically and continuously every minute by Garmin GPSmap 60CSx devices. Occasionally, certain gaps in the full-day recordings occurred caused by failures of GPS devices or poor satellite reception, but this constitutes no systematic error. Coordinates were recorded in MGRS and were later transformed into UTM. The map datum used was Indian Thailand (Indian 1975 in ArcGIS). For the analysis of GPS locations a time interval of 30 minutes, i.e. every half and full hour, was used (Richter et al. 2013). This gives the group the possibility to move a few hundred meters farther if they want, but is still short enough to not lose important ranging information. In cases where multiple observers were with the group at the same time, coordinates were averaged.

Home ranges were calculated with the Home Range Tools (HRT) Add-In for ArcGIS® 9.3.1., as fixed kernel (Gaussian bivariate normal kernel) using reference bandwidth, with a raster cell size of 50m and no buffer (minimized extent of the utilization distribution). To avoid point duplicates a random error of ± 0.5m was added to the coordinates. Monthly home ranges were calculated as the full home range (95% isopleth) and core home range (50% isopleth). We chose the kernel method as this is a recommended method in the literature (Seaman and Powell 1996; Börger et al. 2006; Kie et al. 2010). However, if observations (fixes) were very unequally distributed, which happened if most observations were clumped in an area and in addition one or few “excursions” were made by the group to another area (with fixes often lying in a line rather than scattered), and/ or if certain areas were not used and fixes were distributed in a circular shape for a specific area (e.g. around a valley), then the kernel method produced results which largely overestimated the actual area used. This can be explained because the calculated reference bandwidth is overestimated if fixes are distributed very unevenly, so that the spread of the kernel that is centered over each observation point is too large, resulting in an oversmoothed utilization distribution and thus a home range area with a large band of excess area around the outermost point locations (Kie et al. 2010). Given these problems in certain months, and that an alternative bandwidth (e.g. least-squares cross-validation) also resulted in calculation failures, we applied the Minimum Convex Polygon (MCP) method as an additional measure of home range size, using a fixed mean and 95% MCP's. Annual home ranges were calculated from October (beginning of mating season) until September the following year. For annual home ranges we only used the kernel method, as the number of GPS locations over one year was large enough (average: 4,928 fixes per year, range: 4,443-5,919) and no distribution issues were present. Home range overlap (of 95% kernel estimates) between years was calculated as the percentage of an annual home range area which was also used in the previous year using ArcGIS® 9.3.1.

Daily travel distances were calculated using GPS positions of the group for every half hour (see above). Only days containing complete observations were used. Days with time gaps larger than one hour during the day were omitted from the analyses. If the time difference between the first contact with the monkeys at the sleeping tree and the first regular GPS point was larger than 30 minutes, the sleeping tree location was added to the ranging points. The same was done for the evening. Daily travel distances were calculated as the sum of distances between consecutive GPS locations on a given day. For the monthly distribution of available data on daily travel distance (n = 933 days) see Figure 4.2. Overall there was no bias of missing data points towards a certain time of year.

Figure 4.2 Log-transformed daily travel distances (in m) from June 2006 to October 2012. If data were available from consecutive days, they were connected by a line. Data quality per month is illustrated as the number of days within a month where daily travel distance could be calculated based on certain quality criteria (see methods).

Phenology

Phenological data were collected from October 2007 until October 2012 of up to 650 plants (trees and stranglers ≥10 cm dbh; climbers ≥5 cm dbh; shrubs: no dbh limit). This included 57 important food species with a median of 12 individuals per species (Heesen et al. 2013). Only 44 of these species were fruiting during the study period and were used for analysis. The abundance of different items (fruit, flowers and leaves of different ripeness and maturity) was visually assessed using binoculars and was recorded on a $\log_{10}$ scale in the middle of every month (1 = 1–9; 2 = 10–99; 3 = 100–999; 4 = 1,000–9,999; and 5 = 10,000–99,999; Janson and Chapman 1999). The percentage of food trees fruiting (shrubs and stranglers excluded) was 9.4% on average (maximum 15.8%) during most of the time (Oct. 2007 until Feb. 2012). The period from March through September 2012 however seemed to be a period of mast fruiting, as the average percentage of trees fruiting was much higher (19.8%), with a maximum of 22.8%.

Variables included in the analyses

Group size: The presence or absence of every individual was recorded every day, from which an average group size was calculated per month. We included unweaned infants in the total group size because infants should have an impact for the nutritional requirements of the group, as lactating mothers should have higher energy requirements. Group size ranged between 40 and 64 individuals between October 2007 and October 2012. If we excluded infants form the group size measure our main results were not affected.

Number of males: This includes all adult males and in addition large subadult males, which already reached the body and testes size of adults, but still appeared less muscular (Ostner et al. 2008a; Ostner et al. 2011). These large subadult males are not necessarily natal males, because males often migrate as juveniles (Ostner, Schülke, unpubl. data). Females mate with almost all males in the group (Fürtbauer et al. 2011) including large subadult males, and large subadult males are known to sire offspring (Sukmak et al. under review). The number of males ranged between 6 and 16 individuals. In the following, for simplicity, they are all referred to as adult males.

Fruit availability: An index of fruit availability was computed for every month using information from phenology trees, calculated as the sum of the mean abundance scores of species *i* multiplied by the mean density of species *i* per hectare (adapted after Koenig et al. 1997). Species densities were known from 44 botanical plots of 50m x 50m size of which 13 plots got extended to 100m x 100m size, equaling 20.75 ha in total. Botanical plots were randomly distributed throughout the home range of the study group, representing 4.8% of the annual home range (95% kernel), and 17.1% of the annual core home range (50% kernel). The variation of fruit availability over months and years is illustrated in Heesen et al (2013).

Fruit distribution: A fruit distribution index (FDI) was calculated for every fruiting species per month, calculated as the fruiting synchrony multiplied by the spatial distribution. Fruiting synchrony was based on the proportion of phenology trees bearing fruit in a given month, with an average of 12 phenology trees investigated per species and month. Fruiting synchrony often varied largely within one species across months, and also across species. The spatial distribution was defined as the proportion of the 44 botanical plots of 50m x 50m size (see above) in which this species was present. Spatial distribution also varied largely between species. FDI equals one if a species is fruiting highly synchronous and grows in every plot, and is close to zero if fruiting synchrony is low and individuals have a very clumped distribution. For each month the median was calculated from all FDI scores, ranging between 0.02 and 0.11.

Day length: The day length, or photoperiod, was calculated as the time difference between sunrise and sunset for Bangkok, from data available online (www.timeanddate.com/worldclock/astronomy.html). Bangkok was the closest place for which data were available, which is situated about 320 km SSW of the study area. June was the month with the longest days (mean day length: 12h 55min), and December had the shortest days (mean day length: 11h 20min, Figure 4.5).

Minimum temperature and precipitation: The minimum temperature (in °C) per day, the amount of precipitation (in mm) per day and their interaction were included in the day range analysis, and the amount of precipitation per month in the analysis of monthly home range size.

Diet data

To investigate whether the diet is shifted when fruit availability is low, we used a smaller data set of 24 months (Oct. 2007 – Sep. 2008, May 2010 - Apr. 2011) for which diet data were available from focal animal samples of all adult females. Diet was defined as the percentage of feeding time on different food items measured from 1-min instantaneous records. Food items were classified into the following categories: fruit, leaves, caterpillar, snails, other animal matter (including ants, termites, spiders, lizards, frogs, birds, bird eggs etc.) and other food items (e.g. flowers, roots, bark, shoots, fungi) (see Table 4 in Richter et al. 2013 for detailed percentages).

Statistical analyses

We applied multiple linear regression analysis to assess which social and ecological factors influence monthly home range size. The mean monthly minimum temperature was significantly correlated with median monthly daily travel distance and sum of monthly precipitation (Spearman rank: $r_s = 0.69$, $n = 53$, $p < 0.001$; same for both). We thus removed minimum temperature from the model, and only included group size, number of males, daily travel distance, precipitation, fruit distribution, fruit availability and the interaction of the latter two as predictor variables. Daily travel distance for a given month was only included if it was known for at least seven different days, and we preferred to use the median rather than the mean (both are correlated with $r_s = 0.97$, $n = 53$, $p < 0.001$). Skewed variables were transformed to better meet assumptions about normality. The analysis is based on standardized variables for computational reasons and for reasons of interpretability (Schielzeth 2010). We built one model for each home range estimate using the same set of predictor variables. The two methods of home range calculation (95% kernel and 95% MCP) produced similar estimates for monthly home range size ($r_s = 0.92$, $n = 53$, $p < 0.001$). Thus, we focused on the results from the model with 95% MCP here, as the estimated quantiles of the residuals better fit the sample quantiles (Q-Q-plot). Results of the models using 95% kernel estimate and the core home range (50% kernel) are given in the appendix (A1), and are overall comparable to the results for 95% MCP. For all three models, the assumptions were checked and met, including normality and homogeneity of residuals, and model validity and stability (Variance Inflation Factors (VIF's) <1.7, dffits ≤1.3, dfbetas <0.9, Cook's distance ≤0.2), showing no obvious influential cases or outliers (Quinn and Keough 2002; Field 2005).

The initial analysis of the factors influencing the daily travel distance was performed with a multiple linear regression model. The response variable follows a skewed distribution and was thus log-transformed. However, the residuals showed strong autocorrelations that could not be appropriately captured by simple autoregressive (AR) components, so that we applied an ARIMA(p,d,q) model with external regressors. The appropriate order of the ARIMA model was selected by means of smallest AIC value for a range of reasonable orders ($p,d,q = 0,1,\ldots,5$) and was selected as ($p = 3$, $d = 0$, $q = 3$). Within this modeling approach the data are considered as a time series. Thus, the observations were treated as a time series on a daily interval with missing values for the days with no observations (Figure 4.2).

As data on fruit availability and distribution were not available before October 2007, we restricted the sample to the time period from October 2007 to October 2012, resulting in a sample size of 53 months for the home range analysis and 933 days for the day range analysis.

To test whether ranging patterns were influenced by the food items consumed (diet), we conducted two multiple regression analyses, with home range size or daily travel distance being the response variable and feeding time on fruit, leaves, caterpillar, snails, other animal matter and other food items as predictor variables. Due to a strong negative correlation between feeding time on fruit and leaves (Spearman rank: $r_s = -0.63$, $n = 24$, $p < 0.001$), feeding time on leaves had to be excluded from both models (after exclusion VIF's <3 for all predictors in both models). Skewed variables were transformed and all predictor variables were standardized.

The analyses were performed with the statistical software environment R© (version 3.0.0, RCoreTeam 2013). Apart from the standard R packages, computations were performed with the R package 'car' (model diagnostics, Fox and Weisberg 2011). The figure of annual home ranges (Figure 4.3) was created in ArcGIS® 9.3.1.

4.4 Results

Home range size, stability and influential factors

The study group used an annual home range area ranging between 352 and 515 ha (95% kernel; Table 4.1, Figure 4.3). The core home range area (50% kernel) varied between 86 and 144 ha in size (Table 4.1). The area used was very stable in space and time, and no home range shift occurred during the six year observation period (Figure 4.3). The mean home range overlap between two consecutive years was 85.3% (range: 68.1-97.4%, Table 4.1). Monthly home range size varied largely, ranging between 63.4 ha and 634.1 ha (mean: 327.1 ha, n = 77 months) for the 95% kernel estimate and between 50.6 ha and 412.1 ha (mean: 221.4 ha, n = 77 months) for the 95% MCP estimate.

Overall, the monthly home range size was clearly influenced by the predictor variables ($F_{7,45} = 5.4$, $p<0.001$; Table 4.2). Monthly home range size was positively influenced by the number of adult males in the group. This was not an effect of the number of adults in general, or an artifact of the number of females, as in our data the number of adult males was not positively correlated to the number of adult females ($rs = -0.54$, $n = 53$ months, $p < 0.001$). Home range size increased in months with longer day ranges, and decreased in months with higher precipitation. Surprisingly, total group size showed no effect on home range size (Table 4.2), although it varied substantially between months, ranging from 40 to 64 individuals. Excluding unweaned infants from the group size did not change the result (data not shown). The interaction of fruit distribution and availability showed a positive influence on home range size. Thus, under the condition that overall fruit availability increased and woody plant fruit species occurred more dispersed, i.e. less clumped, the home range size became larger (Table 4.2, Figure

4.4). These results were very similar to the models where home range was estimated as 95% kernel and for the 50% kernel core home ranges (see appendix A1), indicating that they were not an artifact of the 95% MCP method.

Table 4.1 Annual home range sizes in hectare based on fixed kernel estimates for both the 95% isopleths (full home range) and 50% isopleths (core home range). In addition, the average group size and average number of adult males and females in this year are given, averaged from all monthly values of this year. The percentage of home range overlap with previous years is based on 95% kernel estimates.

	Time period	Average group size (males/ females)	95% kernel (ha)	50 % kernel (ha)	Overlap with previous year (%)
Year 1	Oct '06 - Sep '07	50.3 (12.0/ 11.2)	352.3	86.3	
Year 2	Oct '07 - Sep '08	53.5 (13.3/ 11.7)	514.6	144.3	68.1
Year 3	Oct '08 - Sep '09	50.9 (12.2/ 13.4)	451.2	122.6	89.5
Year 4	Oct '09 - Sep '10	49.3 (9.3/ 14.0)	415.5	112.8	90.1
Year 5	Oct '10 - Sep '11	53.8 (9.3/ 15.0)	474.5	140.5	81.4
Year 6	Oct '11 - Sep '12	56.6 (8.5/ 14.0)	393.3	125.3	97.4

Table 4.2 Parameter estimates of monthly home range size analysis (for 95% MCP home ranges) based on multiple linear regression and standardized (z-transformed) predictor variables. For results of the other home range measures (95% and 50% kernel estimates) see appendix A1.

Independent variable	Estimate	SE	*t* value	*p* value
Intercept	230.37	8.10	28.43	**<0.001**
Group size	4.00	9.07	0.44	0.661
Number of males	24.27	8.49	2.86	**0.006**
Daily travel distance	45.99	10.09	4.56	**<0.001**
Precipitation	-35.13	9.55	-3.68	**<0.001**
Fruit availability	1.83	8.69	0.21	0.834
Fruit distribution	-5.12	9.22	-0.56	0.581
Fruit availability x Fruit distribution	16.13	7.73	2.09	**0.043**

Values in bold indicate statistical significance ($\alpha = 0.05$). $F_{7,45} = 5.4$, $p < 0.01$, n = 53 months, adjusted $R^2 = 0.37$

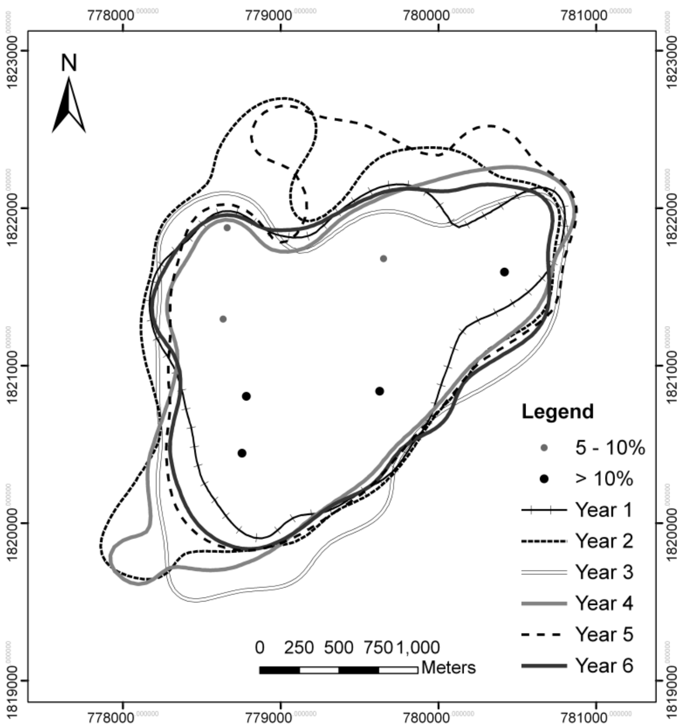

Figure 4.3 Annual overlap of home ranges (95% kernel estimates) for year 1 (2006/07) to 6 (2011/12). Dots represent the most important sleeping trees of all 18 trees used between July 2007 and October 2012, of which three were used 5-10% and four more than 10% of the time.

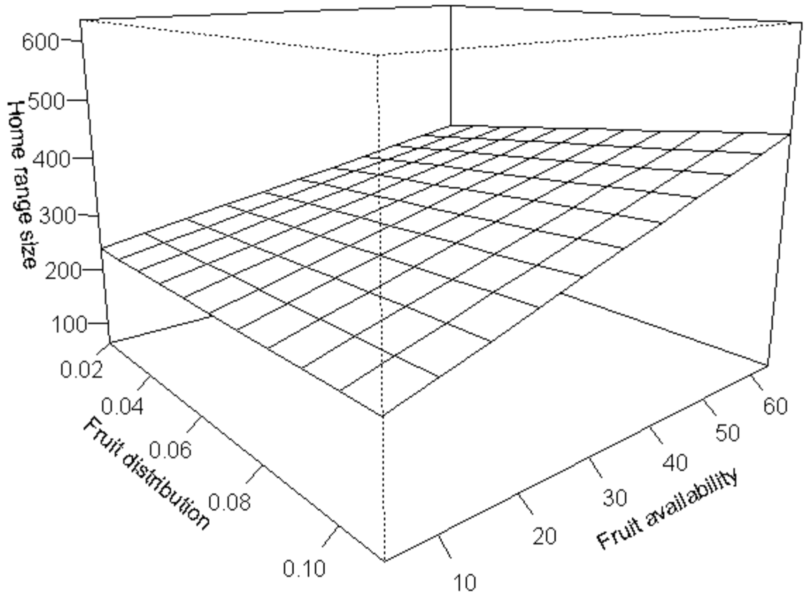

Figure 4.4 The interaction effect of fruit distribution and fruit availability on monthly home range size, as it appeared in the multiple regression model using 95% MCP home range as dependent variable. If overall fruit availability is high, and woody plants fruit synchronously and do occur more dispersed, then home range size increases.

Daily travel distance

The daily travel distance varied between 604.2 and 4980.5m (mean ± SD: 1761.8 ± 479.8m, median: 1703.7m, n = 1180 days), at an average group size of 52 individuals. The average daily travel distance was half (0.54) of the average maximum extent of the annual 95% kernel home ranges. An ARIMA analysis with external regressors showed that day length was the only factor that significantly influenced the daily travel distance of the group. Surprisingly, social factors like group size (even when unweaned infants were excluded) and environmental factors such as temperature, precipitation and the availability and distribution of fruit resources did not have significant effects (Table 4.3). Day length and minimum temperature, however, showed a positive and significant correlation (Spearman rank: $r_s = 0.84$, $n = 53$, $p < 0.001$), and both fit to the monthly variation in daily travel distance quite well (Figure 4.5).

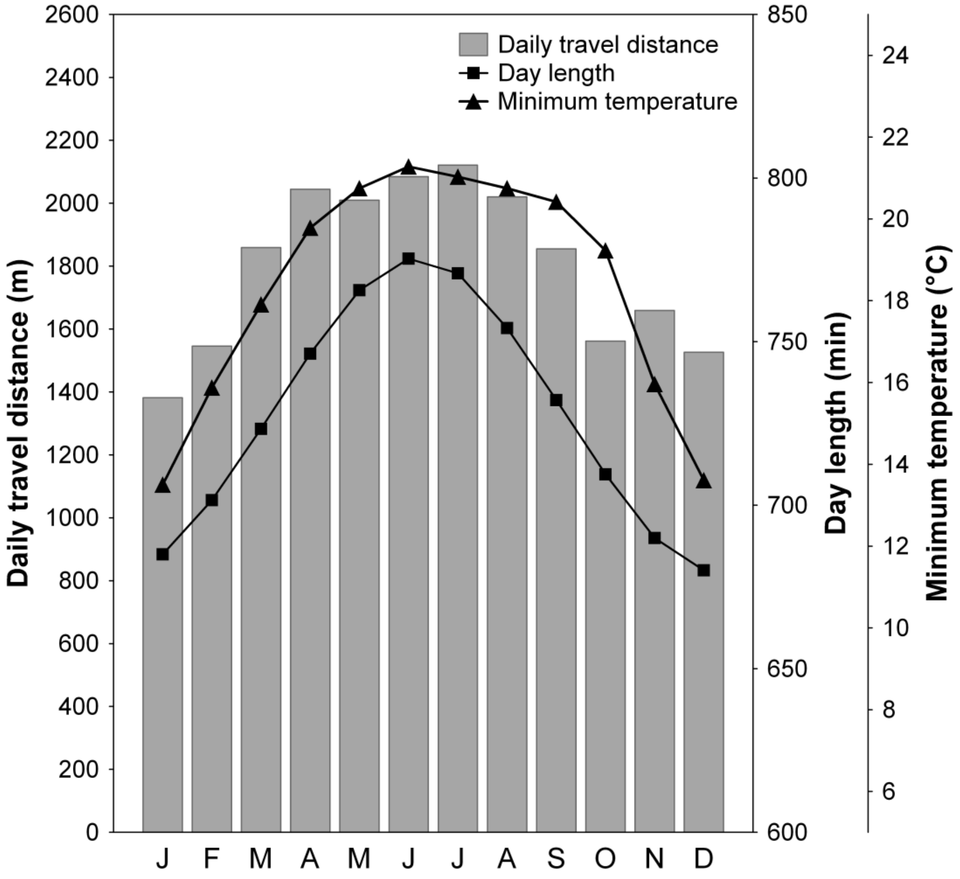

Figure 4.5 Monthly variation of the group's daily travel distance (m), day length (in minutes, for Bangkok area) and minimum temperature (°C, at the study site) calculated as the average for June 2006 – October 2012 (same period as for daily travel distance analysis on a daily level presented in Table 4.3).

Table 4.3 Estimated regression coefficients of daily travel distance analysis based on an ARIMA(3,0,3) model with external regressors. An Arima (time series) model was used to account for the temporal autocorrelation of daily travel distances (see methods). The dependent variable (daily travel distance) was log-transformed. Significant values (5%) are marked with an asterisk. For a lack of significant effects of ecological variables on daily travel distances, see explanations in the discussion section.

Independent variables	Estimate	SE	
Intercept	5.066	0.435	*
Group size	0.004	0.004	
Day length	0.003	0.001	*
Minimum temperature	0.008	0.005	
Precipitation	0.001	0.017	
Minimum temperature x Precipitation	0.000	0.001	
Fruit availability	-0.002	0.003	
Fruit distribution	-1.319	1.412	
Fruit availability x Fruit distribution	0.023	0.042	

Diet and ranging

The result above suggests that home range size increased with increasing overall fruit availability and more dispersed fruit resources, i.e. that Assamese macaques will only range over larger areas if they can energetically support their travel. At low fruit availability they could adopt less energy consuming foraging methods and switch their diet. However, only the proportion of time spent feeding on snails was significantly correlated to variation in fruit availability (Spearman rank: $r_s = -0.4$, n = 24 months, p = 0.05), whereas fruit availability was not correlated to the proportion of leaves ($r_s = 0.03$, n = 24, p = 0.885), caterpillars ($r_s = -0.13$, n = 24, p = 0.540) or other animal matter ($r_s = -0.16$, n = 24, p = 0.449) in the diet. Feeding time on different food items did not influence ranging patterns. Multiple regression models with feeding time on fruit, caterpillar, snails, other animal matter and other food items as predictors were neither significant for home range size ($F_{5,18} = 0.5$, p = 0.782, n = 24 months, adjusted $R^2 = 0.13$), nor for daily travel distance as response ($F_{5,18} = 1.2$, p = 0.341, n = 24, adjusted $R^2 = 0.05$).

Benefits of larger home ranges

To investigate whether an increase in home range size with the number of males, which is likely to be linked to increased access to food resources, is beneficial for females, we correlated the home range size (95% MCP’s) in August just before the mating season with the proportion of adult females conceiving in the following mating season (from October onwards), and found a significant positive effect (Spearman rank: $r_s = 0.90$, n = 6 years, p = 0.015; Figure 4.6). This increase in the probability for any female to conceive translated into an increase of the total number of offspring being born. Home range size (95% MCP) in August was correlated to the total number of offspring born in the following birth season (Spearman rank: $r_s = 0.88$, $n = 6$, $p = 0.020$).

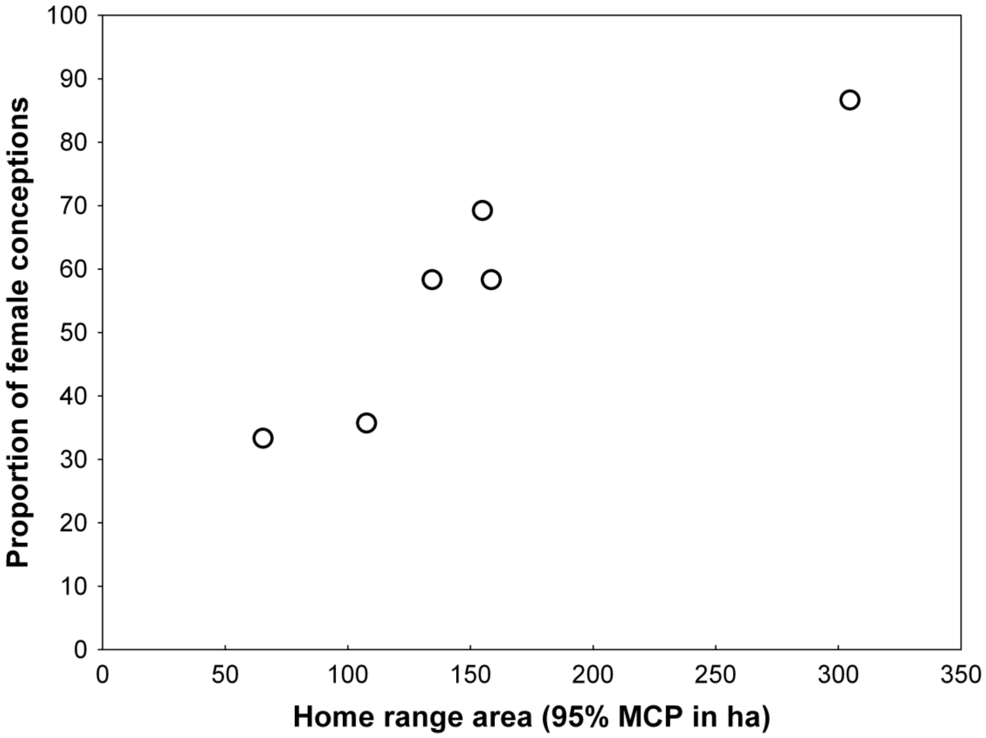

Figure 4.6 Home range size (95% MCP, ha) in August before the mating season influences the proportion of adult females conceiving during the following mating season. We chose August because hormonal data suggest that fecal androgens start to increase in August as a sign of readiness to conceive in the coming mating season from October to January (Fürtbauer et al. 2013). Data come from the mating seasons from 2006/07 until 2011/12. Conceptions are based on observations of birth events and in addition on hormonal data for two years.

4.5 Discussion

Recent studies showed that males participate more in intergroup encounters than previously thought (e.g. Fashing 2001; Cooper 2004; Cooper et al. 2004; Majolo et al. 2005), and that they frequently defend food resources (Koenig et al. 2013). Such male participation in intergroup encounters was also frequently observed in Assamese macaques, with males actively participating in the front. Especially low-ranking males participated, and dominant males always joined if aggression escalated (Schülke, Ostner, unpublished data). As a common result of these encounters, groups with more adult males (which are also the larger groups) could reside in the area, whereas smaller groups with fewer adult males had to retreat (Schülke, Ostner, unpublished data). In our present study, we could show quantitatively that having more males in a group does indeed influence the full and core home range size positively while controlling for several ecological factors. Hence, groups with more males receive the benefit to be unconstrained in their movement in overlapping areas, and they can thus use the fruiting trees in the periphery of their home range, without being displaced. Commonly, range expansion is connected to higher access to food resources (Isbell et al. 1990; Isbell 1991), and although we cannot prove this link directly in our study, it is very likely given the strong site fidelity of our group, which is similar or higher than in other primates (Easley and Kinzey 1986; Watts 1998; Lehmann and Boesch 2003; Robbins and McNeilage 2003; Janmaat et al. 2009; Asensio et al. 2012). Further indirect evidence comes from the fact that more females conceived when home range size was larger, i.e. more females had an inter-birth interval of one year instead of two years. A similar effect was found in chimpanzees, where females reproduced faster by having shorter inter-birth intervals when home range size was larger at the time they resumed cycling (Williams et al. 2004). Our results on Assamese macaques, together with data on chimpanzees, Phayre's leaf monkeys and capuchin monkeys (Lehmann and Boesch 2003; Carl 2009; Koenig et al. 2013; Scarry 2013) indicate that more males can defend larger areas in both male dispersal and female dispersal societies.

Groups with multiple males often suffer from a collective action problem, i.e. individual males fail to invest into the common good produced by home range or female defense because the benefits are not shared according to this investment. Thus, multimale groups were found to have larger home range overlap (Willems et al. 2013), less frequent loud call production, i.e. less investment in intergroup conflicts (Nunn 2000), and lower likelihoods of winning intergroup encounters (Harris 2010). We suggest that such a collective action problem partly can be overcome in Assamese macaques for two reasons. Firstly, male reproductive skew is low (29% alpha male paternity, Sukmak et al. under review) and can be influenced by home range expansion which allows many males to benefit from home range defense. Females breed seasonally and female reproductive synchrony is high. Paternity distribution over dominance ranks closely matches predictions from a Priority of Access model, i.e. rank is positively associated with paternity success, but the more females conceive the more males sire offspring (Sukmak et al. under review). Females largely conceal ovulation from males indicated by rather constant male copulation rates from the onset of the mating season through the peri-ovulatory phase until after conception when male interest fades (Fürtbauer et al. 2011). Thus, every additional female that conceives in a given mating season increases female receptive synchrony and decreases male monopolization potential so that more subordinate males get access to receptive females. Paternity analyses show that males down to rank 9, 10 and 12 may sire offspring (Sukmak et al. under review). With higher food availability, the physical condition of females improves and more females can reproduce every year. This increases female synchrony and especially low-ranking males will benefit from that, by gaining higher paternity success. Our observations that especially low-ranking males participate in intergroup encounters (Schülke, Ostner, unpublished data) do support this theory. A second explanation for how Assamese macaques overcome the collective action problem may be that females choose those males that actively participate in home range defense (Fashing 2001; Stockley and Bro-Jørgensen 2011) as their preferred mating partner, so that these males get directly rewarded for their efforts. Currently, this idea cannot be tested because the relevant data on between-male variation in range defense are not available, but we know that nearly each female has a “preferred” male with whom she mates most (Fürtbauer et al. 2011). These “preferred” males are irrespective of the males’ dominance rank (Fürtbauer et al. 2011). The costs of adding males to the group seem to be relatively low. Group size did not significantly affect either home range size or daily travel distance.

Overall, having more males in a group and thus a larger home range seems to be beneficial for many group members. With higher access to food more females can conceive, more males have a chance to sire an offspring, and even for infants it is beneficial, as they grow faster when food abundance in their first year of life is higher (Berghänel, Ostner, Schülke, unpublished data).

Socioecological influences of ranging behavior

Owing to the vast evidence on socioecological factors driving variation in ranging behavior, we investigated the effects of group size, food abundance and distribution, climate and day length on monthly home range size and daily travel distance to add to this body of research. An increase in group size is generally linked to stronger within-group feeding competition, more rapid patch depletion and thus an increase in travel distance to increase the area covered in search for food (Chapman 1990; Chapman and Chapman 2000a; Chapman and Chapman 2000b; Grove 2012; Isbell 2012). This has been shown for frugivorous and folivorous primates (Olupot et al. 1994; Di Bitetti 2001; Gillespie and Chapman 2001; Steenbeek and van Schaik 2001; Dias and Strier 2003; Izumiyama et al. 2003; Ganas and Robbins 2005; Majolo et al. 2008; Snaith and Chapman 2008; Carl 2009; Agostini et al. 2010; Shaffer 2013) and in a comparative analysis across macaque species (Richter et al. 2013). In our study, no group size effect on both home range size and daily travel distance was present although group size varied largely throughout time. There might be three possible explanations. Firstly, habitat quality at Phu Khieo is high and variations are less than in other habitats, so that the group can easily compensate for an increase in group members. This idea is confirmed by observations on sympatric Phayre’s leaf monkeys (*Trachypithecus phayrei*), where group size had no effect on daily travel distance (Carl 2009). Secondly, the group may compensate for an increasing group size by either using food patches of lower quality, resulting in a decreased energy intake but no increase in either daily travel distance or home range size (Schülke and Ostner 2012), or they may adapt their group spread to increase the encounter rate with food and decrease feeding competition (van Schaik and van Noordwijk 1986; Isbell 1991; Koenig and Borries 2006). A third explanation might be provided by the resource dispersion hypothesis, which states that group size does not influence home range size in habitats where resources are temporally very variable and spatially very heterogenous (Johnson et al. 2002). It assumes that the area covered during foraging always needs to be relatively large to find a “ripe” patch in such a highly variable environment, so that more group members do not add cost on home range size (Johnson et al. 2002). Given the seasonal habitat of Assamese macaques, a heterogenous distribution of feeding trees (68% of the feeding tree species were present in less than one third of the botanical plots), and a low average fruiting synchrony of fruit tree species used (40% over all species and months), this might me a likely explanation as well.

From all environmental factors examined, precipitation had the strongest effect on home range size. This fits our behavioral observations, with the monkeys being less active during times of rain. Such a pronounced effect of precipitation on home range size contrasts other studies (Boonratana 2000; Ganas and Robbins 2005; Minhas et al. 2013). For daily travel distance, precipitation did not show a significant effect, but this might be hampered by the autocorrelation in daily precipitation. Daily travel distances exhibit strong autocorrelations, i.e. today’s travel distance is partly influenced by yesterday’s as well as by the travel distance the day before. This dependence may partly be attributed to persistent weather conditions, like similar precipitation patterns. After accounting for these autocorrelations, the remaining effect of precipitation might be too low to become significant in the analysis, but this does not exclude an influence of precipitation on daily travel distance. Temperature, on the contrary, which influences daily ranging behavior in at least some primate groups (Kirkpatrick et al. 1998; Minhas et al. 2013), was not a significant predictor of day range. For home range size, we could not test precipitation and minimum temperature in one analysis together due to strong correlations, but another model including minimum temperature was not significant.

The second important environmental influence on home range size was fruit availability and fruit distribution as an interaction. A significant interaction indicates that home range size increased with increasing overall fruit availability and more dispersed fruit resources, due to a higher fruiting synchrony and a presence in many plots. This suggests that Assamese macaques, in line with our predictions, only range over larger areas when they can energetically support their travel. This finding is similar to black-and-gold howler monkeys, *Alouatta caraya*, which travel farther and faster in the rich season compared to the lean season (Agostini et al. 2010). It also fits well to optimal foraging theory, which predicts that animals should spend more energy searching for food during times when food-density is high (to maximize the net energy gain) and should shift to less-energy consuming but also less efficient search methods when food density is low (MacArthur and Pianka 1966; Schoener 1971; Norberg 1977; Pyke et al. 1977). Support for this theory comes from spider monkeys, *Ateles chamek*. They consume more leaves when fleshy fruit abundance is low to reduce their daily travel distance (Wallace 2005; Wallace 2006). In Assamese macaques, we observed a diet shift towards snails when fruit availability was low, but it remains unclear whether snails can be a reliable fallback food as data on snail abundance are not available. Another strategy to counterbalance low fruit availability may be to shift the monthly home range area rather than extending it, as seen in chimpanzees *(Pan troglodytes schweinfurthii,* Basabose 2005). In our study, however, home ranges in months of low fruit availability did not deviate from those in months of high fruit availability. Fruit availability and distribution only showed an effect on home range size but not on daily travel distance. This may be due to the same problem already discussed above for precipitation and remains subject for further investigation.

The only environmental influence on daily ranging behavior was day length, with longer day ranges on days with longer daylight. Such an effect is also present in Yunnan snub-nosed monkeys, *Rhinopithecus bieti* and Sichuan snub-nosed monkeys, *Pygathrix roxellana* (Yiming 2002; Baoping et al. 2009), both living in seasonal habitats. Seasonal variation in day length can also affect other behavior in primates apart from ranging, such as grooming, resting and feeding, and the minimum day length experienced by a group throughout a year can even act on the maximum possible group size (Ménard and Vallet 1997; Agetsuma and Nakagawa 1998; Hill et al. 2003; Ménard et al. 2013).

4.6 Conclusion

Our longitudinal study on Assamese macaque ranging behavior clearly shows that more males in a group can maintain a larger home range area, after controlling for key ecological and social influences. Given that a larger home range translates into more access to food resources, which is supported by the stable use of the same home range area over years, both sexes ultimately benefit from an increased home range area if female reproductive success is increased. Indeed, preliminary data over six years indicate that more females were able to conceive and that the total number of offspring born was higher when home range size was larger before the mating season. This increased female synchrony increases the chances for more males to sire offspring, from which especially low-ranking males will benefit. Thus, these low-ranking males should have higher motivation to defend the home range during intergroup encounters with neighboring groups, which fits to our observations in the field. Clearly, more data are needed to test if our observations are stable over longer time periods, and whether they are typical for different groups and populations of this species. Results of our study, together with data from chimpanzees, Phayre’s leaf monkeys and capuchin monkeys also indicate that male resource defense not only exists in female dispersal societies, but is also common in male dispersal societies.

4.7 Acknowledgements

We would like to express our sincere gratitude to the National Research Council of Thailand (NRCT) and Department of National Parks, Wildlife and Plant Conservation (DNP) for granting research permits and support (permit no.: 0004.3/3618; 0002.3/2647). We appreciate the help and support by J. Prabnasuk, K. Nitaya, M. Kumsuk and K. Kreetiyutanont from the Phu Khieo Wildlife Sanctuary. We thank A. Koenig and C. Borries (Stony Brook University) for establishing the field site at Huai Mai Sot Yai. We are grateful to all people who helped with data collection in the field, namely A. Chunchaen, D. Bootros, N. Juntuch, N. Ponganan, N. Bualeng, J.Wanart, B. Klaewkla, P. Saisawatdikul, T. Wisate, T. Kilawit, S. Jomhlotwong, W. Nuagchiyo, M.

Swagemakers, I. Fürtbauer, S. Rogahn, S. Macdonald, A. Berghänel, J. Kalbitz, C. Minge. We especially thank M. Swagemakers for establishing and maintaining the ranging database. We thank Esri Germany GmbH for granting a free 1-year ArcGIS ArcInfo license (Esri Absolventenprogramm) to the first author. We also thank 3 anonymous reviewers for providing helpful comments on the manuscript. The project was financially supported by Max Planck Society, the National Geographic Society and the German Initiative of Excellence to the Georg-August University Göttingen. The Evangelisches Studienwerk e.V. provided a scholarship for the first author.

Ethical standards

Approval and permission to conduct research was granted by the authorities of Thailand (permit no. 0004.3/3618; 0002.3/2647). This research was conducted in accordance with the laws and regulations set forth by the NRCT and DNP, and complied with the guidelines of the involved institutions.

Conflict of interest

The authors declare that they have no conflict of interest.

4.8 Appendix

A1. Results of monthly home range size analysis for 95% kernel estimates (full home range) and 50% kernel estimates (core home range) based on multiple linear regression. All predictor variables were standardized.

Dependent variable	**Independent variable**	***F* value**	**n**	**df**	**Adj. R^2**	**Estimate**	**SE**	***t* value**	***p* value**
Home range size (95% kernel)		5.3	53	7,45	0.366				
	Intercept					340.18	12.13	28.05	**<0.001**
	Group size					6.43	13.56	0.47	0.638
	Number of males					32.80	12.70	2.58	**0.013**
	Daily travel distance					70.53	15.09	4.67	**<0.001**
	Precipitation					-50.80	14.29	-3.56	**<0.001**
	Fruit availability					1.58	13.00	0.12	0.904
	Fruit distribution					-8.61	13.79	-0.62	0.536
	Fruit availability x Fruit distribution					22.26	22.26	1.92	*0.061*
Home range size (50% kernel)		5.4	53	7,45	0.375				
	Intercept					86.32	3.64	23.69	**<0.001**
	Group size					4.80	4.07	1.18	0.245
	Number of males					10.31	3.82	2.70	**0.010**
	Daily travel distance					20.63	4.53	4.55	**<0.001**
	Precipitation					-14.74	4.29	-3.43	**0.001**
	Fruit availability					-0.16	3.90	-0.04	0.967
	Fruit distribution					2.28	4.14	0.55	0.585
	Fruit availability x Fruit distribution					7.64	3.48	2.20	**0.033**

Values in bold indicate statistical significance (α=0.05), values in italic indicate a lesser level of signifi-cance (α=0.1).

Chapter 5

General Discussion

5.1 Summary of results

My thesis sheds light on two major gaps related to the feeding competition aspects of the socioecological models. Firstly, it addresses the lack of empirical data on feeding competition in low predation pressure environments, by testing model predictions for within-group competition under low predation risk, using Siberut macaques (*Macaca siberu*) as a model species. Secondly, it addresses the often neglected aspect of male resource defense by using a large data set collected on Assamese macaques (*Macaca assamensis*) to evaluate the role and consequences of male group size on between-group competition.

Socioecological theory predicts that within-group feeding competition is reduced when predation risk is low, as a) individuals can feed in the periphery of the group, alone or in small feeding groups, and b) use alternative food patches to avoid aggression, without facing increased predation risk (Terborgh and Janson 1986; Janson 1988b; van Schaik 1989; Koenig and Borries 2006; Schülke and Ostner 2012). I tested these predictions on Siberut macaques, a species endemic to the small oceanic island of Siberut in West Sumatra (Indonesia). Siberut is characterized by the absence of large carnivores (WWF 1980; Tenaza and Tilson 1985; Wilting et al. 2012). Before testing these predictions it was necessary to determine whether a contest potential over food resources exists by exploring various food resource characteristics like patch size, temporal and spatial distribution, density and patch depletion (van Schaik 1989; Isbell 1991; Sterck et al. 1997; Koenig et al. 1998; Isbell and Young 2002; Koenig 2002). Previous to my study, no quantitative ecological knowledge about Siberut macaques existed, making a comprehensive description of the ecology of this species imperative.

The studied group of Siberut macaques spent most of their time in the dense continuous forest (95.7%). They were semi-terrestrial and mainly used the ground level (25.4%) and lower-story (38.4%) during their daily activities. Their diet was largely frugivorous (75.7% of feeding time on fruit) and they spent an exceptionally large proportion of time traveling (57.3% of activity budget, Chapter 2). Compared to published data on 15 other macaque species, Siberut macaques were ecologically most similar to their sister taxa *Macaca nemestrina* on Sumatra and the Malay Peninsula (Chapter 2). Contrary to what was predicted by island biogeography theory (MacArthur et al. 1972; Yoder et al. 2010), no indication of niche expansion existed in *M. siberu* compared to *M. nemestrina* (Chapter 2). Compared to other macaques, Siberut macaques spent more time traveling (highest percentage among all macaques apart from *M. nemestrina*), and traveled farther per day relative to their group size (2,048 m/day; Chapter 2). This may be based on ecological reasons, like a lower percentage of trees bearing fruit on Siberut compared to Malay Peninsula (Whitten 1980b), low densities of food plants (including figs and rattan, Chapter 2 and 3), and food plants being well distributed and widely scattered (in all months either random or dispersed distribution, Chapter 3). Additional reasons might be the impoverished tree species richness and a lower tree basal area on Siberut island, compared to other forests in Malesia (Chapter 2).

A potential for contest competition over food is expected when food patches are of high quality, small relative to group size, and when food occurs clumped within patches so that food becomes defendable or monopolizable by one or a few individuals. Additionally, contest competition is also expected when food patch density is low, i.e. no alternative food resources exist within the area of a regular group spread (van Schaik 1989; Sterck et al. 1997; Koenig et al. 1998; Koenig 2002). Siberut macaques mainly feed on fruit, which is a high quality food item (Schülke et al. 2006). Food patches of most species used (70%) were of small to medium size, like rattan, stranglers, lianas and small to medium sized trees and palm trees (Chapter 3). Particularly for rattan, most palm trees and some other small trees, fruits occurred spatially clumped into clusters close to the stem or trunk, limiting the number of co-feeding individuals often to between one and three. Food plant densities within the average group spread of 50m were low. Taking these food resource characteristics together, a high contest potential should exist, but aggression was rare, occurring in only 19.8% of all food patches which were used by at least 2 individuals (Chapter 3). The adult-adult aggression rate in food patches (0.13 bouts/ h) was the lowest among all comparable primate rates reported (Chapter 3).

I found support for all predictions from the socioecological models given under low predation risk: Siberut macaques were able to flexibly adapt their inter-individual distances, resulting in sometimes large group spreads for their group size (larger than 100m in 9.4% of the group scan observations, with a maximum group spread of 419m, Chapter 3). Individuals were dispersed while foraging and did not form sub-groups. As a result, they were frequently feeding alone (27.9% of the focal plant observations) or in small feeding groups, with little temporal overlap between individuals (average feeding group size: 3.1 individuals, Chapter 3). These foraging and feeding strategies are likely to drive the low aggression rates observed. This is supported by the fact that aggression frequency was significantly predicted by social factors, but not by ecological factors (Chapter 3). Thus, we can assume that the spatial dispersion and loose grouping as a result of low predation risk on Siberut, causes the low aggression rates observed, as the presence of other group members in the food patch generally increased aggression frequencies. This indicates that contest competition, measured as costs of aggression, is reduced in Siberut macaques (energetic costs being unknown). Active avoidance behavior, however, also occasionally exist (e.g. queuing in small food patches), but do not seem very costly in time (see discussion in Chapter 3).

In Assamese macaques, neighboring groups show large home range overlaps so that between-group encounters with active male participation are frequent (Schülke, Ostner, unpublished data). Increasing evidence shows that male resource defense is more common than previously thought (Fashing 2001; Koenig et al. 2013), and that male group size can have a positive effect on home range size (Lehmann and Boesch 2003; Koenig et al. 2013; Scarry 2013). Although socioecological theory predicts an increased home range size for the larger group as an outcome of strong between-group competition (Isbell 1991), only female competition over food was commonly considered, as food is generally considered less important for males than access to mates (Trivers 1972; Emlen and Oring 1977). To address the often neglected aspect of male food resource defense as part of between-group feeding competition in the socioecological models, I analyzed an existing data set of over six years of ranging data on Assamese macaques (Chapter 4).

The number of males varied largely in the study group over the period of 6 years, ranging between 6 and 16 individuals. In line with my predictions, I found a positive significant effect of male group size on monthly home range size, i.e. the group’s home range increased in months with more males in the group, and this was not an effect of total group size (Chapter 4). In female Assamese macaques, conception rates are influenced by food availability (Heesen et al. 2013). Female androgen levels increase from August to September just before the mating season, reflecting a female’s readiness for conception (Fürtbauer et al. 2013). August thus seems to be a critical time period for a female’s future fertility. Indeed, I found that an increased home range size in August had a significant positive effect on the percentage of females conceiving in the following mating season, and on the total number of offspring born (Chapter 4). Therefore, a larger home range benefits both female and male reproductive success, and especially low-ranking males should gain from an increased female reproductive synchrony (see below; Chapter 4). My results also suggest that the collective action problem partly can be overcome in Assamese macaques. Surprisingly, total group size did not significantly influence home range size, with potential reasons discussed in Chapter 4. In accordance with my predictions, daily travel distance showed a significant positive influence, precipitation had a negative effect, and temperature was strongly correlated with both these factors so that it was not included in the model (Chapter 4). Fruit availability and distribution were only significant as an interaction, i.e. home range size increased when fruit availability was high, plants were fruiting more synchronously and occurred spatially more dispersed (Chapter 4). This fits to optimal foraging theory and findings of other studies, suggesting that animals only forage further if they can energetically support their travel (MacArthur and Pianka 1966; Schoener 1971; Yiming 2002; Wallace 2005; Wallace 2006). My results implicitly show that male resource defense exists in Assamese macaques, and that the role of males in between-group feeding competition was previously underestimated. If future studies can show that the role of males is equally important for feeding competition in other species, we should consider including males as a factor in future socioecological models (see below).

5.2 Predation risk and feeding competition

Predation has been a strong selective evolutionary force in shaping the ecology, behavior, morphology, cognition and social organization of animals (Lima and Dill 1990; Krause and Ruxton 2002; Caro 2005; Gursky and Nekaris 2007). Predation has been most likely one of the main factors driving the evolution of sociality, mainly through the risk dilution among group members (Krause and Ruxton 2002; Childress and Lung 2003; Caro 2005). If males are more vigilant than females (e.g. in Przewalski's gazelle, *Procapra przewalskii*: Shi et al. (2011); capuchins, *Cebus albifrons* and *C. apella*: van Schaik and van Noordwijk (1989); common marmosets, *Callithrix jacchus*: Koenig (1998), squirrel monkeys, *Saimiri oestedi*: Boinski (1988)), or more effective in predator defense (red colobus, *Colobus badius tephrosceles*: Stanford (1995)), high predation risk also selects for more males in a group (van Schaik and Hörstermann 1994; Hill and Lee 1998). In some geographic regions, predation risk influences the frequency of polyspecific associations, i.e. associations between different primate species (Struhsaker 2000). Predation risk can also influence a wide range of behavioral decisions, like where and when to feed and what to eat (reviewed in Lima and Dill (1990); risk-sensitive foraging: McNamara and Houston (1992), Bednekoff (1996)). It therefore influences the use of habitats and food patches, with for example individuals favoring taller trees to increase predator detection (patas monkeys, *Erythrocebus patas*: Enstam and Isbell (2003)). Alternatively, individuals may use poorer habitats (chacma baboons, *Papio cynocephalus ursinus*: Cowlishaw (1997)) or poorer quality food patches (impalas, *Aepyceros melampus*: Pays et al. (2012)), if predation risk in high-quality habitats or patches is too high. Thus, a trade-off exists between foraging efficiency and predator avoidance (Watson et al. 2007; Fernández-Juricic and Beauchamp 2008; Unck et al. 2009; Fichtel 2012; Cunningham et al. 2013).

Socioecological theory gives specific predictions for the strength of feeding competition under low and high predation risk. Before we can include predation risk as a factor in tests of the models' predictions, we need to quantify predation risk for a species. However, quantification of the actual predation risk remains difficult, as predation events are rare and difficult to observe. Also, the observed predation rates differ from the intrinsic risk because they only represent the events after anti-predator strategies have been implemented (Hill and Lee 1998; Nunn and van Schaik 2000; Krause and Ruxton 2002; Janson 2003; Fichtel 2012). Several categorizations of the intensity of predation risk have been put forward, such as being based on predator-prey interactions and the behavioral response of primates towards potential predators (Hill and Lee 1998). Other categorizations are based on the diversity of predators in a habitat (Anderson 1986), or on body mass, substrate use, activity patterns and geographic range (Nunn and van Schaik 2000). Medium-sized individuals might have the highest risk of predation, as they are too large to effectively hide from predators, and too small to not be caught by predators (Janson and Goldsmith 1995). Terrestrial species are usually assumed to have a higher risk of predation than arboreal species (Nunn and van Schaik 2000; Janson 2003; Shultz et al. 2004) (but see Isbell 1994).

Current theory suggests that predation risk influences the cohesion of a group, and therefore also feeding competition (Krause and Ruxton 2002). According to Hamilton (1971), predation risk is reduced by the presence of neighbors, predicting that individuals in the periphery face a higher predation risk as they have fewer neighbors, which is well supported by the literature (Di Blanco and Hirsch 2006; Hirsch 2007; Klose et al. 2009; Shi et al. 2011). As a negative side effect, closer spatial distance to neighbors, i.e. higher cohesiveness, is likely to increase competition over food, so that it is often the low-ranking individuals which have to forage in the periphery to avoid competition, at the cost of higher mortality rates (van Noordwijk and van Schaik 1987; Janson 1988b; Ron et al. 1996; Hall and Fedigan 1997). When the environmental risk of predation is low, either because of a lack of predators or because of large body size (like in great apes: Isbell 1994; van Schaik 1999), all individuals can avoid or reduce feeding competition without costs, by a) increasing inter-individual distances (i.e. decreasing cohesiveness), and b) foraging and feeding in small feeding groups or even alone (Terborgh and Janson 1986; Janson 1988b; van Schaik 1989; Koenig 2002; Koenig and Borries 2006).

Given the theory above, comparisons of species which evolved under high predation risk, and still live in a habitat with numerous carnivore predators, with species which evolved under low predation risk due to the lack of carnivores, should be highly informative. One such comparison can be drawn between long-tailed macaques, *Macaca fascicularis,* on Sumatra where a large feline predator community exists (tigers, clouded leopards, golden cats: van Schaik et al. 1983b), and Siberut macaques on Siberut island offshore of West Sumatra, where no felids are present. At first, contrary to expectations, there seems no major difference between both species. Siberut macaques show low group cohesion and feed in small groups or even alone (Chapter 4). Long-tailed macaques frequently form sub-groups when fruit is scarce (van Schaik and van Noordwijk 1986), and individuals spread out more to compensate for increased feeding competition (van Schaik and van Noordwijk 1988). However, several behavioral adjustments suggest that predation risk poses a major threat for long-tailed macaques. When foraging in small parties, they prefer to use higher forest strata which increases predator detection distance and reduces attacks by felids, and they come less often to the ground than when being in larger groups (van Schaik et al. 1983b; van Schaik and van Noordwijk 1988). Females compete for safe positions within the group, with only old and low-ranking females being in the periphery (van Schaik and van Noordwijk 1988), and high-ranking females being more frequently present in the main party, which translates into higher survival rates (van Noordwijk and van Schaik 1987). Infants and juveniles were never found alone without neighbors (van Schaik and van Noordwijk 1986; van Noordwijk et al. 2002). Younger juveniles were more often present in the main party than older ones (van Noordwijk et al. 2002), and infant mortality rate was high, which is likely due to predation (van Noordwijk et al. 2002).

In Siberut macaques, no differentiation of spatial positions among age classes existed, with infants and juveniles not being significantly closer to the group center than adult males and females (Chapter 4), which is in line with what is predicted under low predation risk. This also fits well to the behavior observed in food patches, where juveniles were feeding alone without adults in 19.4% of the focal plant observations. When they did so, one juvenile was exploring the food patch alone in more than half of the cases (55.4%), without any other group member entering the patch. When multiple juveniles used a patch, they were feeding with little temporal overlap, i.e. there were on average less than two juveniles feeding on the same time in 80.4% of the cases. Thus, Siberut macaques differ from long-tailed macaques in that even juveniles can feed alone due to the lack of feline predators, in order to reduce or avoid feeding competition. To study the behavior of juveniles relative to the risk of predation seems a promising indicator of perceived predation risk by the group, as juveniles are the most vulnerable group members, due to their smaller body size and relative inexperience, so that they should prefer more central positions whenever there is a perceived risk of predation (Janson and van Schaik 2002; Krause and Ruxton 2002; Fichtel 2012; Cunningham et al. 2013).

For Siberut macaques, I would expect no rank differences in their spatial position within the group as any spatial position is equally safe if no felids constitute a risk, as opposed to long-tailed macaques and other species (Robinson 1981; Collins 1984; Ron et al. 1996; Hall and Fedigan 1997). Unfortunately, no dominance ranks could be established for Siberut macaques, as agonistic interactions were very rare (e.g. no agonistic interactions between adults in 115 h of continuous focal animal observation of adult males and females). Still, I would expect no differences between adult females in their distance to the group center, which was indeed what I found (Chapter 4). From this I would expect that females do not differ in their energy intake rates or reproductive success, but unfortunately not enough data are available to test this prediction.

When individuals are not constrained by predation risk, all individuals should be able to adopt flexible foraging strategies. The only exception might be lactating females with dependent infants. During my field observations, lactating females seemed to stay closer to the presumed alpha and beta male than non-lactating females during their daily activities, indicating that they might be constrained in their foraging strategies by the risk of infanticide during this reproductive period. Data are too sparse, however, for analysis, so that these observations remain preliminary. An indication that infanticide constitutes a risk in Siberut macaques, however, comes from one observation that is consistent with general patterns of infanticide across primates. Two months after a new adult male immigrated into the group, I heard loud vocalizations indicating a group fight. Less than one hour later I found the only lactating female at that time with bite wounds, carrying her dead infant which had large bite wounds on the right side of the abdomen, so that the organs were exposed. By that time, the infant was about 2 months old. Although the infanticidal male emigrated from the group following the event, he did return to mate with the female when she showed a sexual swelling four months later. This suggests that infanticide might pose a threat and therefore can restrict foraging strategies of lactating females, but that all other individuals are relatively unrestricted during feeding and foraging because the risk of predation by carnivore predators is absent.

Low predation risk does not make species similar in their ecology and the extent of feeding competition they experience. Sulawesi macaques on Sulawesi island, Indonesia, also live in a low predation pressure environment where large carnivore predators and raptors are absent (Okamoto and Matsumura 2002), and are also highly frugivorous (Table 2.4 in Chapter 2). However, they still differ from Siberut macaques, especially in the role of between-group competition, which is probably less important in Siberut macaques for several reasons: Firstly, primate densities are much lower on Siberut, with an estimated density of 16.2 individuals/ km² for Siberut macaques (Waltert et al. 2008), compared to >70 individuals/ km² for *Macaca maurus* (Matsumura 1998), 67 individuals/ km² for *Macaca tonkeana* (in Riley 2010), 24-67 individuals/ km² for *Macaca nigra* (Rosenbaum et al. 1998), and 20-50 individuals/ km² for *Macaca hecki* (in Riley 2010). This high primate density on Sulawesi is probably caused by a high fruit production (five times higher than on Sumatra, Kinnaird and O’Brian (2005)), compared to Siberut, which has a very low percentage of trees bearing fruit even for its biogeographic region (Whitten (1980b), Chapter 2). Secondly, very large high-quality food patches, which should promote between-group contest competition (Wrangham 1980; Isbell 1991; Koenig 2002) are rare on Siberut (Chapter 2 and 3), whereas large fruit patches of figs (and other large fruit patches like *Dracontomelum dao*, Kinnaird and O’Brian (2000) and *Dracontomelum mangiferum* Matsumura (1991)) are common, occur at high densities and constitute large parts of the diet in Sulawesi macaques (Kohlhaas 1993; Matsumura 1998; Kinnaird and O'Brien 2005; Riley 2007). Thirdly, intergroup encounters are frequent for Sulawesi macaques (Matsumura 1991; Kinnaird and O´Brian 2000; Okamoto and Matsumura 2002), but no intergroup encounter was observed for Siberut macaques during a full year of observation time (Chapter 2). The above comparison shows that we cannot simply predict the competitive regime and ecology of a species based on categorizations of predation risk and diet. It shows that detailed measurements of food resource characteristics, behavior and other factors like population density are needed instead. The above comparison also suggests that the assumption of the socioecological model after van Schaik (1989), that between-group competition predominates among species with low risk of predation, seems not to hold for all species, but detailed investigations focused on between-group competition in species such as the Siberut macaque are needed before final conclusions can be drawn. In addition, the assumption that species experiencing low predation risk tend to live at high densities (van Schaik 1989) also does not hold for Siberut macaques. My comparison furthermore shows that the strength or role of between-group competition seems mainly influenced by resource characteristics (Kinnaird 1992; Kinnaird and O´Brian 2000; Brown 2011; Brown 2013; Scarry 2013) and population density (Harrison 1983; Sugiura et al. 2000; Brown 2011; Brown 2013). Within-group competition, instead, is mainly influenced by predation risk, as competition can be reduced through behavioral strategies when predation pressure is low, even if resource characteristics favor strong within-group contest competition (Chapter 3).

5.3 Male food resource defense

The role of males for feeding competition has been generally ignored within most socioecological models (Wrangham 1980; Isbell 1991; Sterck et al. 1997; Koenig 2002), as food is generally considered more limiting for female reproduction, whereas males mainly compete for mates (Trivers 1972; Emlen and Oring 1977; Clutton-Brock and Huchard 2013). Males, however, also bear energetic costs of reproduction (Girard-Buttoz 2013) and can be largely constrained in their reproductive success by food availability and food intake rates, not only in species with high sexual dimorphism and female defense polygyny (Lane et al. 2010). In addition to satisfy their own energetic requirements, to increase their reproductive success, males may compete over and defend food resources if this increases female reproductive output, from which males benefit. Whereas male birds and ungulates defend food resources indirectly by defending a territory (Hinde 1956; Geist 1974; Geist 1977; Hixon 1980), male primates also defend food resources more directly by defending food patches or sites during intergroup encounters (Harrison 1983; Sugiura et al. 2000; Korstjens et al. 2005; Brown 2013). Recent evidence shows that male food competition between groups is influenced by food abundance, distribution and patch size (Brown 2011; Brown 2013), the same factors predicted by socioecological theory for female competition (Chapter 1). However, so far, male resource defense only plays a minor role in studies on between-group aggression (Fashing 2001) and has only been considered in the socioecological model of van Schaik (1989). In his model, van Schaik predicts that male resource defense develops under low predation risk, as females are no longer cohesive anymore and thus cannot be easily defended by males, so that males defend resources instead to attract females (resource defense polygyny, van Schaik 1989).

Later, Fashing developed the first detailed model to predict when and in which primate species males may develop direct resource defense (Fashing 2001). Fashing's theory predicted that male resource defense is more common in single-male groups, because multi-male groups are likely to suffer from a collective action problem (Fashing 2001). For male resource defense to occur in multi-male groups, Fashing suggested that males only cooperatively defend resources if they all receive some reproductive access to the females, and if this reproductive success is higher than their share if they would not have participated in resource defense (Fashing 2001). According to his theory, general conditions for male resource defense in both single- and multi-male species are 1) food is limiting and food resources are defensible, 2) females are monopolizable, either because there are only few females in the group or because female estrous synchrony is low, and 3) females choose males which defend food resources and otherwise transfer from the group, if males only poorly defended resources (Fashing 2001).

Fashing's theory recently has been criticized in that female monopolizablility and female mate choice are contradictory, as they cannot occur at the same time (Brown 2011). Although this critique is justified to some extent, it seems that Fashing's theory originally referred to monopolizability on a group level, i.e. that no extra-group males regularly join the resident male during the mating season (Fashing 2001). The conditions under which females can choose their mating partner and thus motivate males to defend food resources was clarified by Brown: in multi-male groups, females can choose either the male which participated most intensively or frequently in resource defense, or the male which participated compared to those which refused participation; and for single-male groups, females can choose to emigrate from their natal group if the resident male performed poorly in resource defense (Brown 2011).

Building on this theory, here I try to evaluate the predicted conditions under which male resource defense might develop in primates in more detail. For this purpose, I compiled comparative data from the literature on intergroup-encounters (Table 5.1). I broadly defined male food resource defense as present in a species if males were aggressive and/ or showed displays during between-group encounters, which were either directly observed in feeding trees, in home-range quadrats frequently used during feeding, or based on close spatial proximity to feeding trees. Acoustic encounters were included for chimpanzees, *Pan troglodytes*, as direct encounters are rare and difficult to observe (Wilson et al. 2012). No criteria or threshold was used for the frequency of food-related encounters relative to the total number of encounters, or whether aggression was more frequent or intense in food-related encounters than in other contexts, or whether aggression occurred more frequently in food trees than expected by the amount of feeding on that food item. As is typical for comparative data, the quality of available data varies largely, and in order to maximize the sample size, I also included studies that did not control for other functions of male participation in intergroup encounters, such as defense of mates and infants, as is suggested for an ideal test (Harris 2007). Additionally, I collected comparative data on primate species which provide indirect evidence for male food resource defense (Table 5.2).

In total, there is direct or indirect evidence for male food resource defense for 17 species (Table 5.1 and 5.2), with the majority being multi-male groups, and in most species males participate much more frequently in aggressive intergroup-encounters than females. However, this bias towards multi-male groups may also stem from a bias of studies towards multi-male groups. Only 2 out of 17 species are characterized by male philopatry, suggesting that kinship is not a necessary prerequisite for male cooperation in food defense as was previously assumed (Perry 1996). Also, Fashing's prediction (Fashing 2001) that male resource defense is less common in multi-male groups is not supported by these data. Which males should primarily participate in resource defense depends on how much they could improve their reproductive success, or how much they have to lose. High-ranking individuals which have most to lose in terms of reproductive success are the ones commonly participating most in group defense (Kitchen and Beehner 2007). From the studies mentioned in Table 5.1 and 5.2, only few reported which males participated, but in chimpanzees it is mainly the high-rankers (Wilson et al. 2012), and in bonnet macaques, *Macaca radiata*, all males participated, but high-ranking males were more aggressive (Cooper et al. 2004). On the other hand, in species which breed seasonally and where male reproductive skew is low, so that subordinate males get at least some share of paternity, low-ranking males should participate most-frequently in resource defense. The reason for this is that higher food availability can increase the reproductive success of (lower-ranking) females, and thus the likelihood of female receptive synchrony, which increases the potential for paternity success of subordinate males. This pattern is predicted for Assamese macaques (Chapter 4). If females actively choose males as mating partners which contributed to resource defense, all males should equally attempt to engage in resource defense.

Female mate choice or preference for "good resource defenders" has been rarely investigated. In grey-cheeked mangabeys, *Lophocebus albigena,* where groups include one to five adult males, females frequently choose their mating partners, initiate about half of the matings (53%), mate with one to three males, including low-ranking males during their peak swelling and refuse 59% of mating approaches (Arlet et al. 2007). This indicates strong female mate choice (Arlet et al. 2007), but male copulation frequency was not related to aggressive participation frequency in intergroup-encounters (Brown 2011). Still, it does not necessarily rule out that males did not receive higher copulation success compared to not having participated in resource defense. Female mate choice just may depend on various factors, of which male performance in intergroup-encounters could just be one of them. In *Macaca radiata,* females mated (and groomed) more often with males with high participation in intergroup-encounters, but these were also the high-ranking males (Cooper et al. 2004). In Assamese macaques, female mate choice may occur, as females had "preferred" males, irrespective of male dominance rank, with whom they mated with most (Fürtbauer et al. 2011). These examples consider female mate choice in multi-male groups. For single-male groups, male resource defense might be more likely if females have the option to leave the group if the resident male is defending food resources poorly (Brown 2011). Indeed, in three of the five species classified as mainly single-male species, females are known to occasionally transfer between groups (Table 5.1 and 5.2). Thus, female dispersal should be studied more frequently in these species, also using genetic data (Harris et al. 2009), and female mate choice might be an important factor for male food resource defense.

The importance of female monopolizability for male resource defense has two aspects. Firstly, if the monopolization potential of females is low, reproductive skew will be less skewed towards the alpha male, therefore increasing the success of other group males, which are then more likely to cooperate in food resource defense. A second aspect may be the monopolization potential on a group level. If paternity has to be shared with extra-group males, within-group males are probably less motivated to defend resources if this does not increase their own reproductive success or survival of their offspring. Unfortunately, data on (observed) female estrous synchrony are still relatively rare, and even expected synchrony data (based on breeding season length, estrous duration and number of females in a group, see Kutsukake and Nunn (2006), Nunn (1999)) are only available for six of the multi-male species presented in Table 5.1 and 5.2. For 3 of the 6 species, expected estrous synchrony is very low (Kutsukake and Nunn 2006; Carnes et al. 2011), suggesting that a high synchrony and thus a low mating skew towards the alpha male are not a necessary prerequisite for male food resource defense to occur in multi-male groups. Data on extra-group paternity as a measure of monopolizability of matings on a group level are even rarer (Ostner et al. 2008b). For all 17 species presented in Table 5.1 and 5.2, there is data for only 3 species, with no extra-group paternities for *Cebus capucinus*, 33% for *Macaca fuscata* on Yakushima, and for *Pan troglodytes*, no data exist for Kibale, but extra-group paternity was 0% in Gombe and 20% in Taï (Ostner et al. 2008b; Muniz et al. 2010). For *Cercopithecus ascanius*, no paternity data are available, but females were observed to mate with extra-group males (Brown 2013). In addition, data on extra-group paternity or matings may not necessarily reflect the risk perceived by the within-group male(s) of whether group females can or do frequently mate with extra-group males. In sum, both female estrous synchrony and female monopolizability on a group level do not seem to explain male food resource defense, but more data are needed before we can really reject this hypothesis.

It was suggested that male food resource defense only occurs under certain ecological conditions (van Schaik 1989; Fashing 2001). The assumption that food needs to be defendable is supported by data on Tana River crested mangabeys, *Cercocebus galeritus galeritus*. When food was uniformly distributed, they were more likely to merge and engage in non-aggressive aggregations, whereas when food was mainly patchy, fights between groups were the most frequent response (Kinnaird 1992). Although most species in Table 5.1 and 5.2 defended access to fruit trees, other resources are worth defending as well. In black howler monkeys, *Alouatta pigra*, males defended ripe fruits

(56% of the encounter), unripe fruit (8%) and leaves (31%, Chaput 2001). The defense of unripe fruit patches is interesting, as this shows that they also defend access to future resources. Male resource defense was also observed in the highly folivorous population of *Colobus guereza* at Kibale, which mainly feeds on leaves (87% of feeding time), but food occurs clumped and some leaves are of high quality (Harris 2006; Harris and Chapman 2007). It is important to study multiple food characteristics before we can conclude whether a species exhibits male food resource defense or not (Brown 2011; Brown 2013). For example, in some species food defense depends on food abundance, distribution and patch size, whereas in others only on site feeding intensity (Brown 2013). This difference may be caused by different intruder pressure, i.e. population density, making it necessary to always defend food patches independently of abundance and distribution when groups are food-limited all year round because of high intruder pressure (Brown 2013). According to van Schaik's model, male resource defense should mainly occur when predation risk is low so that females are more dispersed and not monopolizable by males, making it necessary to defend food resources to attract females (van Schaik 1989). Only two studies listed Table 5.1 and 5.2 provided some information on predation pressure on the study site itself (Robinson 1988; Scarry 2013). Using the classification of predation risk by Nunn and van Schaik (2000), data are available for 13 of the species presented in Table 5.1 and 5.2 (low risk: 4 species, medium risk: 5 species, high risk: 4 species; for other classifications of predation risk see e.g. Anderson (1986)). This suggests that the occurrence of male resource defense is not limited to low predation pressure environments, as formerly predicted by the model of van Schaik (1989).

In sum and in line with socioecological theory, male food resource defense is only expected when food is defendable, i.e. spatially clumped and unevenly distributed, of high-quality, and when food is limiting female's reproductive success (i.e. populations should not be below carrying capacity, Brown 2011). Apart from these ecological factors, certain social factors might facilitate male food resource defense, especially female mate choice, and maybe a high (perceived) monopolization potential of matings on a group level. Males should engage in food defense whenever this increases their reproductive success.

Table 5.1 Primate species with direct evidence for male food resource defense (definition see text), based on observations from intergroup-encounters (IGE’s) of wild and non-provisioned groups. Where possible, I only report the number of aggressive IGE’s, i.e. peaceful encounters excluded. Species divided in single-male groups (SM) and multi-male groups (MM), and if both occur within one species, the more frequent occurrence was used for classification. The number of adult males (ADM) and adult females (ADF) is given, and number of subadult males (SAM) if they participate in aggressive IGE’s. It is indicated whether males are philopatric and whether females disperse (Y = yes, N = no). Participation in aggressive IGE’s: M = adult male; F = adult females; “=” equal participation, “>” males participate more, “>>” males participates twice as often, “<” males participate less

Species	**N groups**	**Group size**	**SM or MM**	**ADM (+SAM)**	**ADF**	**Males philo-patric**	**Females disperse**	**IGE's**	**% IGE's in food context**	**Female food defense**	**Partici-pation in aggr. IGE's**	**Source**
single-male groups												
Cercopithecus ascanius	4	10-13	SM	1	7-8	N	N	125		Y	M=F	1
Colobus guereza	6	4-9	SM, MM	1-2	1-3	N	rare	289	>26%	Y	M>>F	2
Colobus guereza	5	7-23	SM, MM	1-6	3-5	N	rare?	136		rare	M>>F	3
Colobus p. polykomos	1	12-16	SM, MM	1-2	4-6	Y	rare	62	21%	Y	M>F	4
Hylobates lar	3	5-7	SM	1 (+0-2)	1	N	rare	99	most	rare	M>>F	5
multi-male groups												
Alouatta pigra	4	9-10	MM	3-4	3-4	N	Y	14	93%	rare	M>>F	6
Cebus capucinus	6	9-25	MM	2-3	3-9	N	N	23	22%	rare	M>>F	7
Cercocebus g. galeritus	2	14-29	MM					40	63%	Y	M<F	8
Cercopithecus sabaeus	1	18-28	MM	3-6	7	N	N	27	48%		M>>F	9
Colobus vellerosus	1	15	MM	6	2	N	rare	39	87%	rare	M>>F	10
Lophocebus albigena	8	2-19	MM, SM	1-5	1-10	N	N	59		N	M>>F	1
Macaca fuscata	9	7-55	MM			N	N	213	18%	rare	M>>F	11
Macaca radiata	1	19-22	MM	2 (+3)	5	N	N	102	48%	rare	M>>F	12
Macaca silenus	3	12-18	MM	1-2 (+0-3)	5-7	N	N	31	67%	Y		13
Pan troglodytes	1	43-51	MM	10-13	12-19	Y	Y	120				14

Source: 1: Brown (2011), 2: Harris (2006), 3: Fashing (2001), 4: Korstjens et al. (2005), 5: Reichard and Sommer (1997), 6: Chaput (2001), 7: Crofoot (2007), 8: Kinnaird (1992), 9: Harrison (1983), 10: Sicotte and Macintosh (2004), 11: Saito et al. (1998), 12: Cooper et al. (2004), 13: Kumar and Kurup (1985), 14: Wilson et al. (2012)

Table 5.2 Primate species with indirect evidence for male food resource defense, based on observations of wild and non-provisioned groups. Species divided in single-male groups (SM) and multi-male groups (MM), and if both occur within one species, the more frequent occurrence was used for classification. The number of adult males (ADM) and adult females (ADF) is given, and whether males are philopatric and females disperse (Y = yes, N = no).

Species	N groups	Group size	SM or MM	ADM	ADF	Males philopatric	Females disperse	Evidence for indirect male resource defense	Source
single-male groups									
Cebus olivaceus	8	5-50	SM, MM	1-8		N	N	male group size positively influences the chances of winning an intergroup-encounter and thus determines access to fruit trees, which increases female fecundity	1
multi-male groups									
Macaca assamensis	1	40-64	MM	6-16	9-15	N	N	male group size positively influences full and core home range size and female reproductive success	2
Pan troglodytes	1		MM	5-8	9-17	Y	Y	males defend territory in IGE's, fruit availability and female reproductive success increases with territory size	3
Sapajus nigritus	4	11-23	MM, SM	1-5	4-8	N	N	male group size positively influences core home range size and per capita resource availability	4

Source: 1: Robinson (1988), 2: this study (Chapter 4), 3: Williams et al. (2004), 4: Scarry (2013)

5.4 Outlook and future directions

Socioecological theory predicts that under low predation risk, individuals can increase their inter-individual distances to avoid feeding competition without costs. My study supports this prediction, as Siberut macaques show low cohesion, can spread out widely and continuously without forming sub-groups, and feed in food patches mainly in small feeding parties or even alone. However, good comparative group spread data are still very scarce. Future studies should focus on collecting spatial data of individuals to determine group spreads during regular activities and the variation or flexibility of the group spread in relation to predation risk. Only if we obtain a large comparative data set of many species in different predation pressure environments, we can estimate the influence of predation risk on a group's cohesiveness and strength of feeding competition in more detail. Also, it is important to test for sub-grouping. A group might show a group spread comparable to another similarly sized group in a much lower predation risk environment, just because feeding competition is very intense, but might have to form sub-groups rather than being able to spread out continuously, to balance predation risk and feeding competition. For example, both long-tailed macaques on Sumatra and pigtail macaques, *Macaca nemestrina,* in Peninsular Malaysia, where predation pressure is much higher than on Siberut, form subgroups, and in pigtail macaques, individuals within a foraging party always remained close together (Caldecott 1986a; van Schaik and van Noordwijk 1986). That individuals were not able to spread out continuously as was observed for Siberut macaques, a sister taxa, might be due to predation avoidance of felids. In addition, to better address the effect of predation pressure on feeding competition and behavioral responses, it might be useful to include a measure of whether juveniles can feed alone or not. This might provide an improved indicator of predation risk perceived by the group than group spread, as group spread is difficult to compare and largely depends on group size (Carbone et al. 2003). Also, we need more detailed information on a predator's prey preference, and on the specific predator species present at each site, as this influences the response of the prey species, i.e. whether it increases or decreases cohesiveness (Treves 1999a).

During the last decades, the socioecological models have been among the most important drivers of primate ecological studies (Janson 2000; Thierry 2008). However, various model shortcomings have been identified, leading to a discussion whether to abandon or improve these models (Thierry 2008; Koenig and Borries 2009; Clutton-Brock and Janson 2012). Suggestions for improvement include better definitions and measurements of food characteristics and behavior (Isbell and Young 2002; Koenig and Borries 2006; Snaith and Chapman 2007; Vogel and Janson 2007), and the incorporation of additional factors (for overview of proposed factors see Thierry 2008). One of these additional factors, namely males, has been addressed in the present study. Males may alter female feeding competition, especially on a between-group competition level, by actively defending food resources against neighboring groups. As shown above, male participation in feeding competition occurs more frequently than previously assumed, and thus should earn more consideration in future studies and socioecological theory. The focus of socioecological models purely on female competition and social relationships is therefore not justified anymore. Whether males also intervene in female within-group competition still remains to be investigated, but is probably less important than the role of males during between-group competition. My comparative data also show that we need to adopt a broader perspective when studying the function of intergroup encounters in the future. So far, we only have a vague theory of when and in which species male food resource defense is expected, and more detailed studies on female mate choice and the role and frequency of male participation in aggressive intergroup-encounters are needed. These studies should focus on differences in participation rates between males and the consequences of low rates of participation by some males. Also, more attention should be paid on the monopolizability of matings on a group level, and the degree of extra-group matings/-paternities. Observational and genetic data should also investigate the role of occasional female dispersal in otherwise female philopatric species, as a means of female mate choice if the group male(s) perform(s) poorly as food resource defender(s).

Before we start building the next-generation of the socioecological model, however, we should first invest more effort in improving the available data set, to test current model predictions, and to investigate the relevance and relative contribution of the main factors. My present study underlines this need for more quantitative information in various ways: Firstly, without considering low predation pressure and the highly flexible and continuous group spread, we would have predicted that Siberut macaques face strong within-group contest competition. This prediction would be based on their highly frugivorous diet (commonly assumed to be a highly contestable food) and the given food resource characteristics (high quality, small patches relative to group size, low density, fruit spatially clumped within the crown in several species), but this is the opposite from what I observed. Secondly, without empirical observations, we would have predicted that closely related species in similar predation pressure environments and with similar diets show similar competitive regimes. However, the above comparison of Siberut and Sulawesi macaques, all living on islands where carnivore predators are absent, shows that this is not the case. It furthermore demonstrates that it is important to consider other factors like habitat ecology and population density as well. Thirdly, without considering the role of males in between-group aggression over food, one might wrongly infer for many species that between-group contest only plays a minor role by only considering female food-related aggression. The false generalization of assumptions based on scarce observations already has mislead socioecological theory once, with long-lasting effects, as the example of the long assumed “fruit/ leaf dichotomy” shows (i.e. stereotyping leaves as abundant, non-patchy and non-defensible, and thus not worth contesting; see Sayers (2013)). To avoid falling into a similar pitfall again, more detailed measurements for a wide range of species and populations (including non-primate social vertebrates: Clutton-Brock and Janson 2012; Blumstein 2013; Faulkes and Bennett 2013) are needed instead of turning predictions into facts for comparative tests. These studies are required before building a new version of the socioecological model by including many additional factors which lack the required empirical support. A new model without such considerations would only lead to model inflation, resulting in a highly complex model with many additional factors with only a weak increase in explanatory power.

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Curriculum Vitae

Personal Details

Name	Christin Richter
Date and Place of Birth	28th April 1983, Leipzig
Nationality	German
Email	celestina.richter@gmail.com

Education

03. 2010 – present	PhD thesis about “Within- and between-group feeding competition in Siberut macaques (*Macaca siberu*) and Assamese macaques (*Macaca assamensis*)” at Georg-August-University Göttingen, Germany
07. 2011 – present	Leibniz Graduate School “Foundations of primate social behaviour”, Göttingen, Germany
10. 2001 – 07. 2007	Graduation at University of Leipzig: Grade 1.3 (very good) Academic Degree: Diplom-Biologist (equivalent to MSc) Key Courses: • Behavioral Biology • Tropical Ecology • Zoology Non-biological subject: Ev. Theology Thesis: “Social relationships in free-ranging male stumptail macaques (*Macaca arctoides*)”, in collaboration with the Max-Planck Institute for Evolutionary Anthropology; Grade 1.1 (very good)
09. 2003	Prediploma (“Vordiplom“) in Biology

Professional Experience

11. 2008 – 03. 2011	28 months field work in Siberut, W-Sumatra, Indonesia, at the field site of the Siberut Conservation Programme (www.siberut-island.org; in collaboration with German Primate Center): Nov. 2008– Feb. 2010: field assistant of the Junior Research Group Integrative Primate Socioecology at Max-Planck Institute for Evolutionary Anthropology in Leipzig to habituate one group of Siberut macaques Mar. 2010 – Mar. 2011: behavioral and ecological data collection on Siberut macaques for PhD thesis
11. 2006 – 03. 2007	5 months field work in S-Thailand to collect data for diploma thesis

04. 2005 – 10. 2005	7 months field experience in Brazil; “Projektarbeit” about “The influence of fragmentation on frugivorous and nectarivorous bat communities in the Brazilian Atlantic Moist Forest” within the Mata Atlântica Programme (BLUMEN), funded by BMBF
04. 2004 – 04. 2005	1 year as student research assistant at the Max-Planck Institute for Evolutionary Anthropology: Several studies with chimpanzees, bonobos and gorillas at Zoo Leipzig
04. 2004 – 09. 2004	5 months field work in Germany, project about breeding biology of barn swallows (*Hirundo rustica*)
01. 2002 – 04. 2002	3 months internship at the Max-Planck Institute for Evolutionary Anthropology: Study about social cognition of domestic goats

Conference Contributions

Poster: “Ecological insights into the threatened and endemic Siberut macaques (*Macaca siberu*) with implications for conservation” at Student Conference on Conservation Science” (Cambridge, UK), 20. – 22. 03. 2012

Talk: “Siberut island under threat: First ecological insights on the endemic Siberut macaque (*Macaca siberu*)” at the conference of the Society for Tropical Ecology (GTÖ): Islands in land- and seascape - The challenges of fragmentation (Erlangen, Germany), 22. – 25. 02. 2012

Talk “Social relationships in free-ranging male stumptail macaques (*Macaca arctoides*)” at the 2nd Congress of the European Federation for Primatology (EFP) in Prague, 03. – 07. 09. 2007

Publications

C. Richter, P. Gras, K. Hodges, J. Ostner, O. Schülke (in revision). Food resource characteristics and predictors of food-related aggression in wild Siberut macaques (*Macaca siberu*), an oceanic island species with low predation risk. American Journal of Primatology

C. Richter, M. Heesen, O. Nenadić, J. Ostner, O. Schülke (in revision). Males matter: More males increase home range size and female reproductive success in wild Assamese macaques. American Journal of Physical Anthropology

C. Richter, A. Taufiq, K. Hodges, J. Ostner, O. Schülke (2013). Ecology of an endemic primate species (*Macaca siberu*) on Siberut Island, Indonesia. SpringerPlus 2: 137

C. de la O, L. Mevis, **C. Richter**, S. Malaivijitnond, J. Ostner, O. Schülke (2012). Reconciliation in male stumptailed-macaques (*Macaca arctoides*): Intolerant males care for their social relationships. Ethology 118: 1-13

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Special Skills

Languages	German	Native language
	English	Fluently, *Cambridge First Certificate in English (06/2001)*
	Portuguese	Fluently, *Certificado de Proficiência em Língua Portuguesa para Estrangeiros (08/2006)*
	Indonesian	Fluently
	Spanish	Basic
	French	Basic
Leadership Skills	Leading and management of a multicultural and multireligious team of up to 9 people during 28 months of field work in Siberut, Indonesia	
Management Skills	Occasional management of research camp in Siberut, Indonesia	
Organizational Skills	Organization of a 3-day PhD workshop (Oct. 2012) of the Courant Research Centre "Evolution of Social Behavior", held in Reinhausen, Germany	
Teaching Skills	WS 2012/13: BSc course "Practical training in anthropology": Teaching a course about "Home range analysis", University of Göttingen, Germany SS 2011: BSc course "Introduction to anthropological research methods": Practical training about "Methods of behavioral observations in primates", University of Göttingen, Germany 2009: English course for kids and adults, Siberut, Indonesia 2005: Field course about mist-netting of bats for MSc students of the Universidade Federal Rural do Rio de Janeiro (UFRRJ), Brazil	
Reviewing Skills	Ad-hoc reviewer for The Leakey Foundation	
Computer Knowledge	MS Office (including Access), Endnote, Sigma Plot, Statistical Packages (R, Statistica), GIS software (ArcGIS, OpenJUMP)	

Memberships

International Primatological Society (IPS)

Gesellschaft für Primatologie (GfP)

Gesellschaft für Tropenökologie (GTÖ)

Funding

For PhD:

10. 2011 – 07. 2013	Scholarship from Evangelisches Studienwerk e.V. Villigst
03. 2010 – 04. 2011	Scholarship from Max-Planck Society

Other funding:

06. 2012 – 07. 2012	Funding for international summer school about “Conservation biology” at Center for Marine Research, Rovinj, Croatia from Evangelisches Studienwerk e.V. Villigst
05. 2008 – 02. 2010	Scholarship from Max-Planck Society for habituating a group of Siberut macaques
11. 2006 – 03. 2007	Funding of travel expenses for field work in Thailand for Diploma thesis from Max-Planck Society

Declaration

I hereby declare that I have written this thesis entitled “Within- and between-group competition in Siberut macaques (*Macaca siberu*) and Assamese macaques (*Macaca assamensis*)” independently and with no other aids or sources than quoted.

Göttingen, 20. Feb. 2014

C. Richter

Christin Richter