Within-Group Consequences Of The Risk And Occurrence Of Between-Group Conflict In Crested Macaques (*Macaca nigra*)

James O Waterman

A thesis submitted in partial fulfilment of the requirements of Liverpool
John Moores University for the degree of Doctor of Philosophy

March 2021

Contents

Contents 1

List of Tables 4

List of Figures 6

Abbreviations and Acronyms 7

Abstract 8

Declaration 9

Acknowledgements 10

Chapter 1 13

General Introduction 13

1.1 Intergroup competition 13

1.2 Crested macaques 17

1.3 Crested macaque intergroup conflict 18

1.4 Intergroup encounter risk perception 19

1.5 Thesis aims and structure 20

Chapter 2 22

General Methods 22

2.1 Ethical statement 22

2.2 Study site 22

2.3 Study subjects 24

2.4 Data collection 24

2.5 Predators 25

2.6 Tourist encounters 25

2.7 Behavioural sampling 26

2.8 Intergroup encounters 30

2.9 Range use 31

2.10 Data processing and analysis 31

Chapter 3 38

Intergroup encounter risk in wild crested macaques (*Macaca nigra*): winner/loser effects on spatial cohesion and behavioural synchrony 38

Abstract 38

3.1 Introduction 39

3.2 Methods 47

3.3 Results 53

3.4 Discussion 61
Chapter 4 66
Potential intergroup conflict influences current intragroup behaviour in wild crested macaques (*Macaca nigra*) 66
Abstract 66
4.1 Introduction 67
4.2 Methods 73
4.3 Results 78
4.4 Discussion 87
Chapter 5 94
Impacts of intergroup conflict on intragroup social behaviour in wild crested macaques (*Macaca nigra*) 94
Abstract 94
5.1 Introduction 95
5.2 Methods 102
5.3 Results 110
5.4 Discussion 124
Chapter 6 131
General Discussion 131
6.1 Discussion 131
6.2 Limitations and future directions 137
6.3 General conclusion 140
References 141
Appendices 164
Appendix 1: Predator encounters 164
Appendix 2: Tourist encounters 165
Appendix 3: IGEs 167
Appendix 4: Home range & overlap 169
Appendix 5: Relative IGE risk 171

List of Tables

Table 2.1 Observation duration, composition and size of crested macaque study groups in TNR, Sulawesi, Indonesia. 24

Table 2.2 Definitions of focal sampling behaviours, following Thierry et al. (2000) and Duboscq et al. (2013). 27

Table 2.3 Definitions of scan sampling activities, following Thierry et al. (2000), Duboscq et al. (2013), and Allan & Hill (2018). 29

Table 2.4 Definitions of female sexual swelling states. 34

Table 3.1 Hypotheses to test the influence of perceived IGE risk on anxiety, group cohesion, and behavioural synchrony among crested macaques. 46

Table 3.2 GLMM (M1) investigating the influence of perceived IGE risk on self-scratching in crested macaques. 57

Table 3.3 GLMM (M2): Influence of perceived IGE risk and recent win/loss record on spatial cohesion in crested macaques. 58

Table 3.4 GLMM (M3): Influence of perceived IGE risk and recent win/loss record on general behavioural synchrony in crested macaques. 59

Table 3.5 GLMM (M4): Influence of perceived IGE risk and recent win/loss record on active behavioural synchrony in crested macaques. 60

Table 3.6 Summary of hypotheses, predictions, and support provided by this study. 61

Table 4.1 Hypotheses to test the function of affiliative social interactions between crested macaque dyads (F-F = female-female; F-M = female-male; M-F = male-female; M-M = male-male) in the 40 minutes prior to entering a high IGE risk location (relative to low/no IGE risk areas). 72

Table 4.2 GLMM (M1) investigating factors affecting the occurrence of PSB between mixed sex macaque dyads in response to IGE risk. 83

Table 4.3 GLMM (M2) investigating factors affecting the occurrence of PSB between female macaques in response to IGE risk. 84

Table 4.4 GLMM (M3) investigating factors affecting the number of different partners to whom macaques gave affiliative behaviour in response to IGE risk. 85

Table 4.5 GLMM (M4) investigating factors affecting the number of different partners from whom macaques received affiliative behaviour in response to IGE risk. 86

Table 4.6 Summary of hypotheses, predictions, and support provided by this study. 88

Table 5.1 Hypotheses to test the function of post-IGC social interactions relative to baseline conditions. 100

Table 5.2 Generalised variance inflation factors (GVIF) for models M1 - M7. 109

Table 5.3 Summary of hypotheses, predictions, and support provided by this study. 110

Table 5.4 GLMM (M4) investigating the influence of IGC on the probability of affiliation between crested macaque dyads. 115

Table 5.5 GLMM (M5) investigating the influence of IGC outcome, participation, and social bond strength on the probability of affiliation between crested macaque dyads. 116

Table 5.6 GLMM (M3) investigating the influence of IGC on affiliative partner numbers in crested macaques. 118

Table 5.7 GLMM (M1) investigating the influence of IGC on self-scratching rate in crested macaques. 119

Table 5.8 GLMM (M2) investigating the influence of IGC outcome on self-scratching rate in crested macaques. 120

Table 5.9 GLMM (M6) investigating the influence of IGC on aggression in crested macaques. 121

Table 5.10 GLMM (M7) investigating the influence of IGC outcome and participation on aggression in crested macaques. 122

Table A.1 Tourist-macaque encounters in TNR from March 2018 through June 2019. 165

Table A.2 Summary of IGEs between wild crested macaque groups in TNR from March 2018 through June 2019. 167

Table A.3 Utilisation Distribution Overlap Index (UDOI) values for crested macaque groups in TNR from March 2018 through June 2019. 169

List of Figures

Figure 2.1 Location of study site (panel C) within North Sulawesi (panel B), Indonesia (panel A)....23

Figure 3.1 Difference in self-scratching rate in areas of low/no and high perceived IGE risk in crested macaques (M1). 54

Figure 3.2 The effect of IGE risk and monthly win/loss record on spatial cohesion of crested macaque groups, as predicted from a GLMM (M2). 55

Figure 3.3 The effect of IGE risk and monthly win/loss record on active synchrony among crested macaques, as predicted from a GLMM (M4). 56

Figure 4.1 Predicted probability of PSB occurring between mixed sex crested macaques as a function of risk condition (M1). 80

Figure 4.2 Predicted values from a multiple logistic regression of the probability of PSB occurring between female crested macaques as a function of risk condition and receiver rank (M2)....80

Figure 4.3 Predicted values from two GLMMs of the number of different partners that crested macaques gave (A: M3) and received (B: M4) affiliative behaviour to/from as a function of risk condition and sex/reproductive state. 81

Figure 5.1 Predicted probability of PSB between crested macaques in the hours following IGC compared to baseline conditions (M4)....112

Figure 5.2 Predicted probability of PSB between crested macaques in the two hours following IGC as a function of social bond strength (DCSI) (M5). 112

Figure 5.3 Crested macaque self-scratching frequency in the hours following IGC compared to baseline conditions (M1). 113

Figure 5.4 Predicted probability of PSB between crested macaques in the two hours following IGC as a function of IGC outcome (M5). 113

Figure 5.5 Predicted probability of aggressive behaviour between crested macaques in the hours following IGC compared to baseline conditions (M6). 114

Figure A.1 Tourist-macaque encounters in TNR from March 2018 through June 2019 for groups PB1B (panel A), R1 (panel B), and R3 (panel C). 166

Figure A.2 Summary of crested macaque IGEs in TNR from March 2018 through June 2019. 168

Figure A.3 Crested macaque home range estimates (and overlaps) in TNR from March 2018 through June 2019 for all 3 study groups (panel A), PB1B (panel B), R1 (panel C), and R3 (panel D). 170

Figure A.4 Crested macaque monthly IGE relative risk maps in TNR (PB1B Jun 2018-Feb 2019)....171

Figure A.5 Crested macaque monthly IGE relative risk maps in TNR (PB1B Mar 2019-May 2019; R1 Jul 2018-Dec 2018). 172

Figure A.6 Crested macaque monthly IGE relative risk maps in TNR (R1 Jan2019-May 2019; R3 Aug 2018-Nov 2018)....173

Figure A.7 Crested macaque monthly IGE relative risk maps in TNR (R3 Dec2018-Jun 2019)....174

Abbreviations and Acronyms

BBMM: Brownian Bridge Movement Models

CAP: Collective Action Problem

DCSI: Dyadic Composite Sociality Index

F0: Female (non-swollen)

F1: Female (maximally swollen)

F-F: Female-Female dyad (behaviour directed from female to female)

F-M: Female-Male dyad (behaviour directed from female to male)

GLMM: Generalised Linear Mixed Model

GVIF: Generalised Variance Inflation Factor

IGC: Intergroup Conflict

IGE: Intergroup Encounter

LRT: Likelihood Ratio Test

M: Male

M-F: Male-Female dyad (behaviour directed from male to female)

M-M: Male-Male dyad (behaviour directed from male to male)

MNP: Macaca Nigra Project

PB1B: Pantai Batu 1B

PSB: Positive Social Behaviour

R1: Rambo 1

R3: Rambo 3

spp. Species pluralis (multiple species)

TNR: Tangkoko Nature Reserve

UD: Utilisation Distribution

UDOI: Utilisation Distribution Overlap Index

Abstract

Groups of animals often compete over resources, such as territory, food, or mates, which are critical for survival. Successful groups tend to be those in which individuals cooperate effectively, and thus intergroup competition is thought to exert a selective pressure favouring the evolution of behavioural traits that promote intragroup affiliation. However, no cohesive pattern has emerged to describe the effect of intergroup conflict (IGC) on intragroup social behaviour. Furthermore, because most studies focus on intragroup behaviour during or immediately after conflict, we know relatively little about how groups perceive and respond to the risk of encountering rivals.

Here, I investigate the function of intragroup behaviour in response to the threat and occurrence of IGC in three wild crested macaque (*Macaca nigra*) social groups. I use relative risk maps based on the timing and locations of intergroup encounters (IGEs) in conjunction with behavioural observations to test predictions that changes in intragroup behaviour function to increase social cohesion. Group spread, behavioural synchrony, and pre- and post-encounter focal observation data indicate that crested macaques remember the frequency, location, and outcome of previous IGEs: Also, that individuals in dominant and subordinate groups may perceive encounters differently. However, I found no evidence that intragroup behaviour functions to promote cohesion. Rather, my results indicate that both pre- and post-conflict behaviour functions primarily to minimise individual costs and reduce physiological anxiety.

Rather than collective action being impeded by the lack of cohesion-enhancing behaviours, I suggest that this population may not need them in the context of IGC. These findings raise the possibility that (a) when food resources are abundant and mating access is easily monopolised, not all groups that engage in IGC have something worth fighting for, and (b) that we need to find ways of incorporating this into future models of intergroup hostility.

Declaration

No portion of the work referred to in the thesis has been submitted in support of an application for another degree or qualification at this or any other university or other institute of learning.

Acknowledgements

This project was made possible by the people and organisations that provided me with financial, logistic, academic, and personal support during my graduate career; I am deeply grateful to them all. The strengths of this work I owe to their efforts, the shortcomings are mine alone.

Permission to conduct research at Tangkoko Nature Reserve was granted by the Indonesian Ministry of Research, Technology and Higher Education (RISTEKDIKTI) and Natural Resources Conservation Agency (BKSDA). Financial support was provided by a Liverpool John Moores University (LMJU) scholarship. Dr. Muhammed Agil and Ibu Uceu at the Institut Pertanian Bogor (IPB) both provided invaluable logistical support in Indonesia, for which I am very grateful.

I have been lucky enough to have benefitted from the support and guidance of three excellent supervisors. My primary supervisor, Dr. Nicola Koyama has been a generous source of inspiration, enthusiasm, and insight during my time at LJMU. I am extremely grateful to have had your guidance at every step, for pulling me out of the rabbit hole on innumerable occasions, and for the tireless feedback that has sharpened my work and my mind. Thank you for the sincerity and patience you have shown in supporting me throughout; particularly every time that I tried to start over with every chapter I had written. Your dedication, not only to me, but to the other students under your supervision is a standard to which I aspire.

Sincere thanks also to Dr. Bino Majolo. It is no exaggeration to say that you set me on this path when you employed, supported, and encouraged me to work for you many years ago in Morocco. You also recommended me to Nicola when the chance arose, without which I would never have had the chance to carry out this study. Thank you for your support then, and throughout this project; not only for reading multiple drafts, but for your incisive voice in the conversations that sparked new ideas and demanded clarity of purpose.

Thank you also to Dr. Antje Engelhardt, for allowing me to conduct research within the Macaca Nigra Project (MNP), and for guiding me through the visa, permit, and relocation processes at the start and along the way. Without your support and supervision, I would never have enjoyed the privilege of spending 15 months in the company of the inimitable yaki. Your ideas and insights helped to shape this project, and your generosity is something I hope to find in myself one day. Thank you for all your help, for lending your home to a virtual stranger, and for trusting me with Bobby and Dexter.

Many other LJMU faculty members and students have helped me with advice and support. I thank Dr. Claudia Mettke-Hofmann and Dr. Barbara Fruth for their interest and their constructive enquiries that improved my early plans. I am extremely grateful to all my erstwhile office-mates; Harriet Thatcher, Izzy Szott, Sandra Edmunds, Ed Parker, David Wells, Stamatia Galata, and Karl Busdieker, for their help and their intellects, for putting up with my pacing and my coffee spreadsheet, and for welcoming me as your friend from the moment I darkened your office door. Thank you also to my early mentors, Dr. Alison Craig and Dr. Jason Gilchrist; your passion inspired me, and your belief got me started in the first place.

In Indonesia, I would like to thank everybody at the MNP. Especially Dwi Yandhi Febriyanti and Stephan Milyosky Lentey for making any of it possible on a day-to-day basis, and Sintje Kalangi (Ibu Sin) for three square meals a day, come hell or high water, that outshone anything I made in 10 years as a cook. Thank you also to the MNP field staff: Meydi Ardi Manderos, Steven Bee, Ferdi Dalentang, Julianus Mendome, and Meldy Tamengge. Many thanks to my fellow researchers; Andre Pasetha, Risma Yanti, Gita, and Peter Clark for sharing Pos3 so graciously. Particular thanks to Dr. Kirsty Graham, with whom I shared the early challenges and triumphs. You made me a better researcher, and you made me laugh. I am extremely grateful to my Indonesian counterpart and field assistant, Eka Arisyamanti, for her incredible work ethic, fast mind, and positivity throughout: months of constant rain and not a single complaint. In all respects I could not have asked for more, thank you. From Selamatkan Yaki I must especially thank Harry Hilser and Corinne Bailey for their hospitality, and for showing me what a few dedicated people can achieve in support of something greater than themselves.

I owe special thanks to my parents, Rita and Mike Waterman, for their unwavering support throughout this process, and the maze of others that got me here. They offered encouragement, financial support, and a willing ear as the need arose. I know exactly how lucky I am, even if I don’t let on as often as I could. Finally, my deepest thanks to Corinne Bailey. You have carried my burdens for two years, patiently putting up with an alternately distracted, obsessive, and vacillating partner. Throughout, you have enlightened me with your knowledge, indulged my every rambling, and been my best friend and ally. You never gave voice to doubt. Thank goodness for laundry day at Pos3.

Chapter 1

General Introduction

1.1 Intergroup competition

Across many taxa, group-living animals compete over resources such as food (spotted hyenas (*Crocuta crocuta*): Boydston et al., 2001; banded mongooses (*Mungos mungo*): Thompson et al., 2017), shelter (honeybees (*Apis mellifera*): Rangel et al., 2010; greater ani (*Crotophaga major*): Strong et al., 2018), and mates (cichlid fish (*Neolamprologus pulcher*): Bruintjes et al., 2016; savannah baboons (*Papio cynocephalus ursinus*): Kitchen et al., 2004). These interactions can result in death or the loss of territory, significantly affecting individual fitness and group survival. Examples include territorial expansion in chimpanzees (*Pan troglodytes*) following the eradication of rival males (Mitani et al., 2010), clan wars in hyenas (Boydston et al., 2001), intergroup infanticide in white-winged trumpeters (*Psophia leucoptera*) (Sherman, 2003), and violent intergroup clashes in meerkats (*Suricata suricatta*) (Mares et al., 2012), free-ranging dogs (*Canis familiaris lupus*) (Bonanni et al., 2010), and lions (*Panthera leo*) (Mosser & Packer, 2009). The most successful groups (in the context of intergroup competition) tend to be those in which individuals cooperate effectively in pursuit of common goals (Nunn & Lewis, 2001; Willems et al., 2013); other things being more or less equal (e.g. encounter location or group size (Brown, 2013; Crofoot et al., 2008)). As such, in many animal societies the successful maintenance of home ranges or territories requires cooperation and collective resource defence against conspecifics: ants (Adams, 1990; Tanner, 2006), birds (Carlson, 1986; Woolfenden & Fitzpatrick, 1977), carnivores (Furrer et al., 2011; Mosser & Packer, 2009), and primates (Cheney, 1987; Kitchen et al., 2004; Puurtinen & Mappes, 2009).

However, cooperation in heterogenous groups, and thus competitive ability, is often hindered by collective action problems (CAPs) (Olson, 1965). A CAP occurs when non-participants (often called ‘free riders’) receive the benefit of collective action but incur none of the costs. When resources are not monopolisable within a group (e.g.

a shared home range or territory), free riders may benefit from reduced time and energy costs, and a reduced risk of injury by not participating alongside group-mates (Nunn, 2000; Nunn & Lewis, 2001; van Schaik, 1996). For example, playback studies in lions and non-human primates (hereafter primates) demonstrate that as relative group size increases, more individuals free ride in response to simulated territorial intrusion (Heinsohn & Packer, 1995; Nunn & Deaner, 2004). Collective action problems tend to occur when individuals have different levels of interest in contributing to collective behaviour. These differences arise because individuals in a group differ with respect to age, sex, dominance rank, and resource access; and therefore experience the costs and benefits of collective action differently (Majolo et al., 2020). As such, individuals must base their decision to participate on the trade-off between these potential costs and benefits, and adopt the most profitable fitness-maximising strategy.

Because reproductive investment usually differs between the sexes, males and females tend to have broadly different fitness-maximising strategies (Trivers, 1972). This is particularly evident in the context of intergroup conflict (IGC) because it may impose very different costs on males and females (e.g. Arseneau-Robar et al., 2017; Cassidy et al., 2017; Thompson et al., 2017; van Vugt, 2009). Male fitness tends to be limited by access to mates while that of females is limited by access to resources and safety (Trivers, 1972). Thus, males are expected to participate in IGC to acquire or defend sexual access to mates (directly or by protecting resources for females and themselves (Majolo et al., 2005)), whereas females should be most involved (directly or by incentivising male participation (Arseneau-Robar et al., 2017, 2016)) when access to food, water or shelter is concerned (Emlen & Oring, 1977). As a result, depending on what combination of resources are at stake, one or the other sex should participate most actively (Boydston et al., 2001; Grinnell, 2002; Koch et al., 2016; Mares et al., 2012). Importantly though, participation need not necessarily follow the pattern described above: For example, a recent study of IGC in banded mongooses that found that females tend to initiate hostilities, during which they mate with out-group males (increasing their own fitness), while in-group males bear most of the fighting costs (Johnstone et al., 2020).

Furthermore, within hierarchical groups, dominant individuals are typically able to monopolise a disproportionate share of the contested resources if their group wins

(Gavrilets & Fortunato, 2014; Willems et al., 2015). As such, in addition to sex differences, dominance asymmetries may also alter incentives to participate in IGC. For example, in species with high reproductive skew, dominant individuals (often males) should have a greater incentive than subordinates to participate; in order to defend access to mates (Cooper et al., 2004). This should be particularly evident during the mating season for both resident and prospecting dominants (e.g. Majolo et al., 2005).

There is a growing body of evidence from human and non-human animal studies that intergroup competition exerts a strong influence on intragroup social behaviour (Pisor & Surbeck, 2019; Radford et al., 2016; Robinson & Barker, 2017); and theoretical models show that over time IGC can select for genetic traits that increase both intergroup hostility and intragroup cooperation (Bowles, 2009; Choi & Bowles, 2007; Lehmann & Feldman, 2008). Related to these models is the hypothesis that groups at (imminent or future) risk of attack should also evolve on a behavioural timescale by becoming more coordinated, socially cohesive, and/or cooperative, in order to surmount the CAP and increase their odds of success in intergroup competition (Alexander & Borgia, 1978; Birch et al., 2019; Bruintjes et al., 2016; Turchin, 2018)

Indeed, there is growing evidence that exposure to rival groups increases intragroup social cohesion (represented by intragroup affiliation) in various taxa (Birch et al., 2019; Bruintjes et al., 2016; Hellmann & Hamilton, 2019; Mares et al., 2012; Morris-Drake et al., 2019; Preston et al., 2020; Radford, 2008a, 2008b; Radford & Fawcett, 2014; Thompson et al., 2020), including primates (e.g. Arseneau-Robar et al., 2016; Cords, 2002; (meta-analysis of 15 species) Majolo et al., 2016; Mirville et al., 2020; Payne, Henzi, et al., 2003; Samuni, Mielke, et al., 2019; Shaffer, 2013). However, no cohesive pattern has emerged: some studies report a decrease in intragroup affiliation (Tórrez-Herrera et al., 2020; Yi et al., 2020), an increase in intragroup aggression (Arseneau-Robar et al., 2016; Polizzi di Sorrentino, Schino, Massaro, et al., 2012), and/or no change in either (Cheney, 1992; Chism & Rogers, 2004; Grueter, 2013; Nunn & Deaner, 2004). However, Cheney's (1992) study only examined female primates, and Grueter's (2013) meta-analysis of 48 primate species used a proxy of IGC (home range overlap) that may not adequately distinguish between intergroup contest and scramble competition (Majolo et al., 2016; Sterck et al., 1997; Wrangham, 1980). In addition, most studies consider the impacts of IGC on intragroup behaviour during or immediately after the event. Therefore, we know relatively little about how social groups perceive spatial variation in the risk of encountering rival groups, and whether they exhibit pre-emptive responses to the risk of conflict (analogous to the predator-induced “landscape of fear” concept (Bleicher, 2017; Coleman & Hill, 2014; Laundré et al., 2010; Nowak et al., 2017)); although see LaBarge et al. (2020) for a recent exception. Crucially, if intragroup social behaviour changes, even in the absence of a direct out-group threat, it would highlight the importance of intergroup hostility in shaping intragroup behaviour. Currently, it is still unclear exactly how intergroup hostility and intragroup cohesion and cooperation are linked; and it appears that different social and environmental conditions may elicit/require different, or more varied behavioural responses.

Furthermore, there is considerable variety in the types of intragroup social behaviour that are assumed to represent social cohesion. For example, within the primate literature allogrooming is the most commonly used measure of cohesion (Majolo et al., 2016). There are sound reasons for this: allogrooming has several important social functions in primate societies (e.g. promoting agonistic support and feeding tolerance (Dunbar, 1991; Koyama et al., 2006; Ventura et al., 2006)). However, spatial proximity (Aureli et al., 2006; LaBarge et al., 2020; Mitani et al., 2010; Shaffer, 2013), association and relationship indices (Garber & Kowalewski, 2011; Wittig et al., 2016), party size (Samuni, Mielke, et al., 2019), and affiliative facial expressions (Micheletta et al., 2013) may all be equally relevant measures. This is problematic because although the behaviours that are used as indicators of social cohesion are generally all affiliative, they may serve different functions under different circumstances. For example, increasing spatial proximity may serve a thermoregulatory function in some contexts (Campbell et al., 2018) and a predator defence function in others (LaBarge et al., 2020; Schreier & Swedell, 2012). In the context of IGC, the function of behaviour may change depending on intrinsic factors such as individual sex, age, rank, and reproductive status, as well as extrinsic factors like season, and out-group identity etc. Many studies merely infer the social cohesion function of affiliative social behaviours without investigating competing or alternative hypotheses (although see Arseneau-Robar et al. (2016)). For example, IGC is a stressful event (Eckardt et al., 2016; Nunn & Deaner, 2004; Polizzi di Sorrentino, Schino, Massaro, et al., 2012; Wittig et al., 2016), and intragroup affiliative behaviour may function to manage stress in this context. Various studies show that the exchange of affiliative behaviour can buffer the adverse effects of stressful events by down-regulating hypothalamic-pituitary-adrenocortical (HPA) axis activity (e.g. Kikusui et al., 2006; Wittig et al., 2008; Young et al., 2014). Finally, it may also be possible that in certain IGC circumstances, individuals have no need, ability, or incentive to increase social cohesion: Either because they can free-ride on the efforts of others, because their social system impedes the emergence of cooperative behaviour, and/or because the benefits of victory/costs of defeat are too meagre to incentivise it.

1.2 Crested macaques

This study examines the functions of social behaviour before and after intergroup encounters (IGEs) in wild crested macaques (*Macaca nigra*) in Tangkoko Nature Reserve (TNR), North Sulawesi, Indonesia. Crested macaques are one of seven macaque species endemic to Sulawesi (Fooden, 1980; Riley, 2010). Notwithstanding an (estimated) introduced population of 100,000 individuals on the island of Bacan, the wild population of approximately 4,000 – 6,000 is confined to the most northern tip of Sulawesi (Johnson et al., 2020; Riley, 2010). Following sharp population declines of up to 80% in the native population over the last 40 years, crested macaques are classified as critically endangered by the International Union for Conservation of Nature (IUCN) (Supriatna & Andayani, 2008). The Bacan population is not included within the IUCN threat assessment because it exists outside the native range.

Crested macaques are semi-terrestrial primates that live in multi-male, multi-female groups of approximately 40 to 100 individuals (Marty, Hodges, Agil, et al., 2017; O’Brien & Kinnaird, 1997). They have several potential predators at this study site, such as reticulated pythons (*Python reticulatus*), dogs (*Canis familiaris*), and Sulawesi hawk-eagles (*Nisaetus lanceolatus).* However, the study site appears to be devoid of felid predators (O’Brien & Kinnaird, 1997). Females are the philopatric sex and have an unusually tolerant social style that allows for a broad range of social interactions between a large number of individuals, largely unconstrained by rank or kinship (Duboscq et al., 2013, 2017). Relations between male crested macaques more closely resemble those described for multimale groups in other macaque species:

predominantly agonistic (Hill, 1994). Males transfer out of their natal groups at or shortly after reaching their physical peak, and may continue to transfer between groups throughout their life (Marty, Hodges, Agil, et al., 2017). Male-male competition during and after emigration can be intense and reproductive skew is high (Engelhardt et al., 2017). Females signal fertility in a reliable fashion through sexual swellings and behaviour, and males appear to use this information to time their mating (and mate-guarding) effort appropriately (Higham et al., 2012), such that individual dominant males can monopolise matings with fertile females. Females give birth year-round, but more than 80% of births occur between January and May, approximately 59% of which occur between March and May (Engelhardt & Farajallah, 2008). Infant weaning starts at approximately five months and is normally complete within a year (Kerhoas et al., 2014).

1.3 Crested macaque intergroup conflict

Crested macaques, and this population in particular, are an excellent model in which to investigate the effects of IGC on intragroup behaviour because: (a) encounters with rival groups are frequent (~0.8/12h-day (Martínez-Iñigo, 2017)) and active; (b) both sexes participate to some degree, (c) home range overlap is extensive; and (d) predation risk is extremely low (which removes the possibly confounding influence of perceived predation risk on intragroup behaviour).

Compared with several other primate species (e.g. chimpanzees, capuchin monkeys (*Cebus capuchinus*), or Japanese macaques (*Macaca fuscata*)), IGC in crested macaques is not well studied. However, prior research on this population found that although encounters ranged from peaceful intermingling to violent contact aggression, most were characterised by some form of aggression (81.6% any, and 28.2% contact (Kinnaird & O'Brien, 2000; Martínez-Iñigo, 2017)). Combining back-records from 2006-2015 with 10 months of field observations across 2015-2016, Martínez-Íñigo (2017) reported that serious injuries were rare, but did occur (4 of 12 observed attacks), as did the loss of infants (4 of 12), and death (1 of 12). Notably, 11 of 13 victims (across 12 attacks) were adult females, isolated from their group and outnumbered by out-group adult females and sub-adults of both sexes. Males participated in 74.6% of encounters, behaving aggressively towards out-group males and in-group females (herding was recorded in 80% of encounters) (Martínez-Iñigo, 2017), strongly indicating a mate access defence strategy. It was unclear why females participated (50.7% of encounters): Female intergroup aggression was primarily linked to male participation, not to the value of food resources at the encounter location. Martínez-Íñigo (2017) rejected the idea that females participate to bolster male defence of food resources (because female participation was unrelated to the balance of male participants on either side), instead positing that females might defend their interests by socially incentivising male participation.

Large groups tend to win encounters (Kinnaird & O'Brien, 2000; Martínez-Iñigo, 2017), but numerical superiority does not guarantee victory: small groups are capable of displacing larger rivals if the encounter occurs in an area that the smaller group use more frequently (Martínez-Iñigo, 2017). Nevertheless, small groups appear to avoid larger groups when possible, changing travel course when they come within 100 m of dominant neighbours (Kinnaird & O'Brien, 2000). This effect seems to be transitive with respect to group dominance, i.e. of the three study groups, the smallest avoided both larger rivals, the intermediate group avoided the largest but did not alter its trajectory for the smallest, and the largest group avoided neither subordinate group (Kinnaird & O'Brien, 2000). Thus, groups seem to understand the relative risks of encountering different rivals and adjust their behaviour accordingly.

1.4 Intergroup encounter risk perception

The ability of primates to perceive and respond to varying levels of risk throughout their ranges has been well documented with respect to predation and human-wildlife conflict (Campos & Fedigan, 2014; Coleman & Hill, 2014; King & Cowlishaw, 2009; LaBarge et al., 2020; Makin et al., 2012; Nowak et al., 2014, 2017; Reisland & Lambert, 2016; Waterman et al., 2019; Willems & Hill, 2009). Common responses to perceived risk include changes in activity budget, intragroup spacing, group size, and over/underuse of risky areas; but studies of how macaques respond to spatial variation in perceived risk are notably lacking (for an exception see: Waterman et al., 2019). Furthermore, the landscape of fear (Bleicher, 2017) approach has rarely been used to examine the effects of perceived IGE risk in primates, and to my knowledge never in macaques. LaBarge et al. (2020) observed an increase in spatial cohesion among samango monkeys (*Cercopithecus albogularis schwarzi*) in reaction to actual IGC, but no pre-emptive change in areas of high perceived encounter risk. Similarly, Benadi et al. (2008) found no statistically significant increase in cohesion, or change in activity budget, among Verreaux's sifaka (*Propithecus verreauxi*) in overlapping compared to core home range areas. Phayre's leaf monkeys (*Trachypithecus phayrei crepusculus*) tended to avoid areas of their home ranges that bordered those of neighbouring groups (Gibson & Koenig, 2012), and while white-face capuchins continued to use the shared edges of their range, they socialised less in those potentially risky areas (Tórrez-Herrera et al., 2020). Taken together, the few studies that exist provide only limited support for the idea that even in the absence of a direct threat, the perceived risk of intergroup hostility may be enough to pre-emptively alter intragroup behaviour. However, by examining changing patterns (rather than rates) of behaviour at the group- and dyad-level it may be possible to clarify the effect of perceived IGE risk on intragroup behaviour.

1.5 Thesis aims and structure

The overall aim of this thesis is to develop an understanding of how the risk and occurrence of IGC influences intragroup behaviour in crested macaques. In Chapter 2, I describe the study species and site, before detailing behavioural sampling and statistical analysis methods. I refer throughout to appendices that contain figures and summary information about IGE occurrence and outcome, home range estimates, tourist pressure, predation pressure, and perceived relative inter group encounter risk. In Chapter 3, I examine the effect of perceived IGE risk on group-wide spatial cohesion and behavioural synchrony. Specifically, I investigate whether crested macaques remember the timing and location of previous IGCs, and whether they pre-emptively alter their behaviour in these high risk areas. I also ask whether the interplay between perceived encounter risk and the cumulative outcome of recent encounters (in the previous month) alters the perceived cost/benefit balance of encountering rival groups.

Having investigated two group-level responses to perceived IGE risk, in Chapter 4 I explore dyadic-level responses to a similar (though crucially different) stimulus. I compare the social behaviour of dyads in two specific risk conditions; one in which there is little to no risk of IGE, and another in which the impending probability of encountering another group is high. That is, during a 40 minute window prior to entering a high IGE risk area (where in fact an encounter did later occur). Here, I investigate whether patterns of affiliative behaviour are sensitive to the perceived risk of IGEs, and whether these responses are reactive (a response to stress), or pre-emptive (a strategic preparation for the possibility of conflict). In Chapter 5, I examine the effect of IGC on post-conflict intragroup social behaviour. Specifically, I compare levels and patterns of self-directed, affiliative, and aggressive behaviour in the three hours after IGC to those at baseline. I ask whether post-conflict behaviour functions primarily to (a) relieve tension, (b) increase group cohesion, and/or (c) incentivise future participation in intergroup aggression. Finally, in Chapter 6 I summarise the major findings, considering the social and ecological conditions that create the need (or lack thereof) for collective action. I discuss the limitations and implications of my work and consider possible future directions.

Chapter 2

General Methods

2.1 Ethical statement

All research received clearance from the Liverpool John Moores University Ethics Committee (approval number NK_JOW/2017-14), from the Indonesian Ministry of Research, Technology and Higher Education (research permit number 2C11AB0129-S), and adhered to the International Primatological Society's ethical guidelines (Riley et al., 2014).

2.2 Study site

Data collection was carried out from March 2018 through June 2019 in Tangkoko Nature Reserve (TNR) (1◦33′N, 125◦10′E); an 88.67 km2 area of lowland rainforest in North Sulawesi, Indonesia (Fig. 2.1). The study was part of the Macaca Nigra Project (MNP) (https://www.macaca-nigra.org), a long-term field project established in 2006 to study the biology and habitat of wild crested macaques. The research area (Fig. 2.1, panel C) is a mix of primary and secondary forest and regenerating former gardens. Altitude at the study site ranges from sea level to 1,351 m, and temperatures are relatively constant throughout the year, with an average range of 24-28 °C (MNP, unpublished data). Rainfall varies seasonally, with the majority falling between October and May; June through September is typically hot and dry (O'Brien & Kinnaird, 1997; Ratna Sari, 2013: MNP, unpublished data).

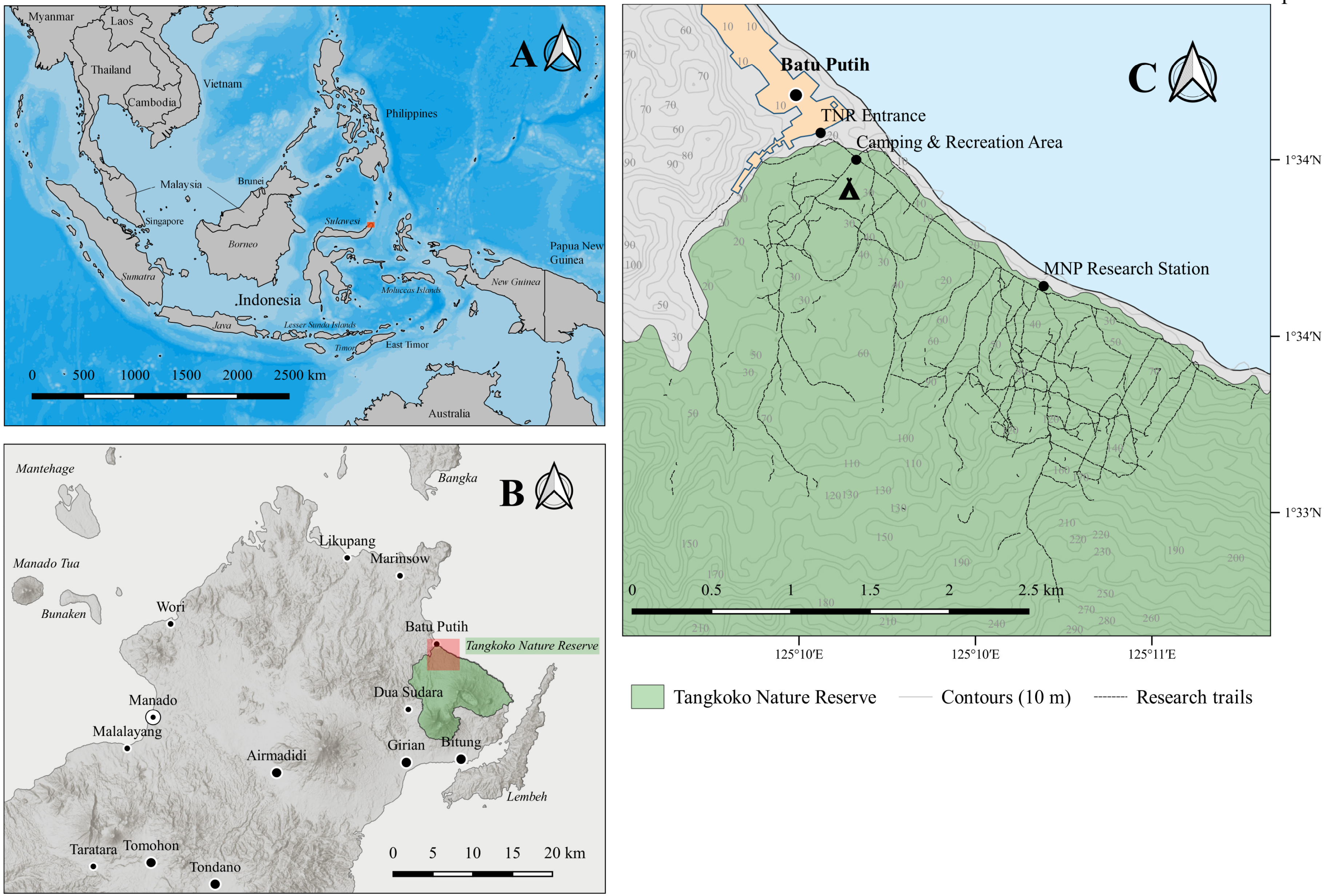

Figure 2.1 Location of study site (panel C) within North Sulawesi (panel B), Indonesia (panel A).

2.3 Study subjects

This study focused on three groups of crested macaques; Pantai Batu 1B (PB1B), Rambo 1 (R1), and Rambo 3 (R3). Group sizes varied throughout the study because of deaths and male dispersals (see Table 2.1), so I recorded the number of adults in each group daily. PB1B has been followed more or less continuously by MNP since 2008 (Marty et al., 2016); R1 was studied in the 1990s (O'Brien & Kinnaird, 1997), and again by MNP since 2006 (Marty et al., 2016); R3 has been studied intermittently by MNP since 2006. The study animals were tolerant of researchers (Bejder et al., 2009), could be observed at close range (approximately 10 m), and all adults were individually recognisable by physical characteristics such as scars, gait, and shape of the anogenital region. The study animals subsisted largely on natural food. However, in areas where their home range overlapped the edges of a nearby village, R1 occasionally ate human crops such as coconuts (*Cocos nucifera*), papayas (*Carica papaya*), sap harvested from palm trees (*Aracaceae* spp.), and processed food from human refuse.

Table 2.1 Observation duration, composition and size of crested macaque study groups in TNR, Sulawesi, Indonesia.

Group	**Observation period**	**Mean ± SD follow days per month**	**Adult group size**	**Number of adult females (F)**	**Number of adult males (M)**	**Adult Sex Ratio (F:M)**
PB1B	Mar 2018 – Jun 2019	8.83 ± 2.44	24 - 32	20 - 21	4 - 12	5:1 – 1.75:1
R1	Mar 2018 – Jun 2019	9.17 ± 3.13	47 – 49	32 - 34	15 - 17	2.13:1 – 2:1
R3	Aug 2018 – Jun 2019	6.55 ± 3.70	10	8	2	4:1

2.4 Data collection

All the behavioural data presented in this thesis were collected by me and a field assistant, Eka Arisyamanti; a biology student from Bogor Agricultural University, Java, Indonesia. I employed Eka to collect data alongside me from March 2018 to

March 2019. Additional location data for PB1B were provided by Dr. Kirsty Graham and Andre Pasetha, occasionally including the location of IGEs that occurred when neither Eka nor I were following the group.

We followed the study groups from dawn until dusk (approximately 06:00 to 18:00) each day; from sleeping tree to sleeping tree. We conducted parallel scan and focal observation trials to check for interobserver reliability (Caro et al., 1979), and a minimum agreement score of Cohen's $k = 0.80$ was achieved before data were included in the study. We recorded all behavioural data on Android smartphones using a customised Cybertracker (v3.507) data collection program (Steventon et al., 2011), and all location data using Garmin etrex-10 handheld receivers (Garmin International, Inc., Olathe, KS, USA).

2.5 Predators

For all predator encounters we recorded the following: date, time, location, predator type, predator number, and group identity. As reported elsewhere (O'Brien & Kinnaird, 2000; Riley, 2010), predator encounters and fatalities appear to be rare (see Appendix 1 for summary data).

2.6 Tourist encounters

Tangkoko Nature Reserve is a popular tourist destination for local and international visitors. Wildlife observation tours led by local guides are the main form of recreation for international visitors, and crested macaques are marketed as a key attraction (Hilser et al., 2013). The presence of tourists does not seem to affect crested macaque activity budgets, but self-scratching (indicative of physiological anxiety in primates (Maestripieri et al., 1992; Polizzi di Sorrentino, Schino, Tiddi, et al., 2012; Schino et al., 1991)) and retreat behaviours increase among all sex-age classes in their presence (Paulus, 2009). Provisioning by tourists is prohibited within TNR, but still occurrs on occasion. For all tourist encounters we recorded the following: date, time, location, number of tourists and guides, and group identity (see Appendix 2 for summary data).

2.7 Behavioural sampling

2.7.1 All-occurrences focal sampling

We collected focal animal behavioural data, using continuous all-occurrences sampling (Altmann, 1974). We collected 481.1 hours of focal animal data from 84 adult subjects, with an average of 6.3 hours of data per individual from 239 days of observation (PB1B = 211.9 hours, R1 = 169.2 hours, R3 = 99.9 hours). Focal individuals were observed for 10 minutes, during which we recorded their behaviour and the identity of all their interaction partners. We continuously recorded the subject's activity state (feeding/foraging, travelling, resting, and allogrooming), all event behaviours (affiliation, aggression, and self-scratching), and the identity of all interaction partners and neighbours (in body contact (contact-sitting) and within one body length)) (see Table 2.2 for focal sampling behavioural definitions).

To ensure that focal follows were independent, no individual was sampled twice within a two hour period and we attempted to sample all adults in the group before resampling any individual. When it was not possible to locate the appropriate individual, a pseudo-random technique for selecting focal animals was used (Boinski & Campbell, 1995; Fragaszy et al., 1992): from the animals observable at that moment, the most undersampled individual was selected.

Table 2.2 Definitions of focal sampling behaviours, following Thierry et al. (2000) and Duboscq et al. (2013).

Behaviour	**Definition**
Feeding/Foraging	An individual searching for, manipulating, and/or ingesting food.
Travelling	Rapid locomotion with no signs of searching for food.
Resting	An individual sitting, lying, or standing without engaging in any specific behaviour. Includes sleeping.
Allogrooming	An individual cleaning the skin or fur of a partner. The hair is brushed and parted using the hands; particles are picked using the hand or the mouth, teeth or tongue. A bout consisted of a continuous period of allogrooming with breaks not exceeding 10 seconds.
Affiliation	Comprised embrace, tail grasp/rub, hug, hip holding, genital grasp, body grasp/touch, pat, soft grunt; and affiliative facial expressions such as lip-smack, teeth-chatter, and silent-bared-teeth.
Aggression	Threats: aggressive vocalisations (bark, grunt, rattle, scream) and/or facial expressions (half-open mouth, open-mouth bared-teeth, stare, jaw movement). Attacks: non-contact (chase, lunge, stamp), and contact (bite, hit, missed hit, grab and push)
Displacement	An individual approaching another, without any threatening behaviour, to within five body lengths, who simultaneously moved away. Where relevant, displacement was superseded by aggression.
Self-scratching	A repetitive raking of the skin using the hands or feet.
Contact-sitting	Two individuals sitting in continuous contact for a minimum of five seconds. Allogrooming bouts were not recorded as contact-sitting.
Proximity	Two individuals remaining within one body length of each other for at least five seconds. Only non-agonistic approaches, where the approaching individual did not direct any aggressive behaviour to their partner were considered.

2.7.2 Instantaneous scan sampling

We conducted instantaneous scan samples at 30 minute intervals throughout the day, obtaining a total of 4624 scans (PB1B=1840, R1=1680, R3=1104 scans) from 239 days of observation. During each scan (10 min duration) we recorded the identity and activity of all visible individuals (see Table 2.3 for scan sampling activity definitions), as well as the number (to within five body lengths) and identity (to within one body length) of their nearest neighbours. In addition, at the end of each scan we conducted a second instantaneous scan, this time noting the number of adult individuals simultaneously in view and their activity: (1) feed/foraging, (2) travelling, (3) resting, or (4) socialising (comprised allogrooming, affiliation, aggression, play, and mating). We categorised each of the four behaviours as physically "active" or "inactive" (see Table 2.3). Feed/foraging and travelling were classified as active behaviours because they involve active physical movement during which the individual changes position and location frequently. Resting and socialising were classified as inactive behaviours because individuals tend to be lying or sitting, and remain stationary when engaged in these activities (Agetsuma, 1995; Gautrais et al., 2007). Although neither play nor aggression are likely to be stationary, inactive behaviours, they were included in the socialising category because they are clearly social activities; they comprised only 0.14% and 0.99% of all records respectively.

We also measured the distance (m) between the individuals at the front and back of the group (relative to the group's ongoing, or last direction of travel), and between the individuals on either side of the group, using an Eventek laser rangefinder (range 0.03 – 60 m, accuracy ± 2.0 mm).

Table 2.3 Definitions of scan sampling activities, following Thierry et al. (2000), Duboscq et al. (2013), and Allan & Hill (2018).

Behaviour	Active/inactive	Definition
Feeding/Foraging	Active	An individual searching for, manipulating, and/or ingesting food.
Travelling	Active	Rapid locomotion with no signs of searching for food.
Resting	Inactive	An individual sitting, lying, or standing without engaging in any specific behaviour. Includes sleeping.
Allogrooming	Inactive	An individual cleaning the skin or fur of a partner. The hair is brushed and parted using the hands; particles are picked using the hand or the mouth, teeth or tongue.
Self-grooming	Inactive	An individual cleans its own skin or fur. The hair is brushed and parted using the hands; particles are picked using the hand or the mouth, teeth or tongue.
Affiliation	Inactive	Comprised embrace, tail grasp/rub, hug, hip holding, genital grasp, body grasp/touch, pat, soft grunt; and affiliative facial expressions such as lip-smack, teeth-chatter, and silent-bared-teeth.
Aggression	Inactive	Threats: aggressive vocalisations (bark, grunt, rattle, scream) and/or facial expressions (half-open mouth, open-mouth bared-teeth, stare, jaw movement). Attacks: non-contact (chase, lunge, stamp), and contact (bite, hit, missed hit, grab and push)
Mating	Inactive	An insertion of the erect penis in the female genitals during mounting.
Play	Inactive	An individual (or individuals) engage in relaxed and exuberant behaviour patterns that include: running, swinging, dragging or throwing an object, wrestling, chasing, sparring, bouncing, or leaping over a partner.
Scanning/Looking	Inactive	An individual's eyes are open; its line of vision extends beyond its hands and the substrate, animal, or object they are in contact with.

2.7.3 Ad-libitum sampling

We collected ad-libitum data throughout the study, noting the number of group-wide aggressive events (see Table 2.2) in the 30 minutes between successive scans.

2.8 Intergroup encounters

2.8.1 Definition

Intergroup encounters were defined following a previous study at this site (Martínez-Iñigo, 2017). An encounter started when two or more groups were in visual contact, or were within 100 m of each other, and ended when these conditions were no longer met. If a single individual remained in visual contact with the out-group while the rest of the group was out of sight and/or more than 100 m away the encounter was classed as over. However, if the same two groups met again within an hour, the encounter was considered ongoing. We recorded the identity of both groups, the start and end time, the eventual outcome, and whether any intergroup aggression occurred (see Appendix 3 for summary data). We used Garmin etrex-10 handheld receivers to record the location of the focal group at the start and end of the encounter.

2.8.2 Outcome

The winning group remained at the encounter location or continued its travel path with less than a 45° deviation in trajectory. The losing group departed the encounter location and/or changed its travel path by more than 45°. A draw occurred when the travel paths of both groups deviated equally (Kinnaird & O'Brien, 2000; Martínez-Iñigo, 2017). We considered an encounter finished at the last intergroup behavioural exchange and/or when the groups were out of sight of each other.

2.8.3 Participation

Visibility permitting, we recorded the identity and behaviour of any participating individuals on an all-occurrence basis. For the purpose of analysis, individuals were later classified as combatants (threats and/or attacks given and/or received) or non-combatants (no participation and/or non-aggressive participation, e.g. scanning/looking, affiliation, or flee (travel rapidly away from out-group) (see Table 2.2).

2.9 Range use

We recorded the focal group's location every two minutes using Garmin etrex-10 handheld receivers. We began recording as soon as the first adult macaque descended from the sleeping tree in the morning and ceased when the last adult group-member ascended the sleeping tree in the evening. In addition to recording sleeping sites, we also marked any location at which a group stopped to feed continuously for more than five minutes.

2.10 Data processing and analysis

2.10.1 Home range estimation

Using location data collected across the entire study period, I estimated utilisation distributions (UDs) for the study groups using Brownian Bridge Movement Models (BBMMs) (see maps in Appendix 4). Utilisation distributions, which estimate the intensity or probability of use throughout a group/animal's range (Millspaugh et al., 2006), were created using the R (R Core Team, 2019) package 'BBMM' (Nielson et al., 2013). I created 50% and 95% density isopleths to delineate home range cores and boundaries respectively (Kernohan et al., 2001; Silverman, 1986; Worton, 1989). I chose to use BBMMs because unlike the Kernel Density Estimate approach, BBMMs (1) account for the temporal correlation of locations recorded over brief intervals, (2) assume that successive locations are non-independent, and (3) deal well with areas that are significantly over- and under-used (Fischer et al., 2013; Horne et al., 2007). The BBMM incorporates known estimates of location error to predict multiple trajectories between successive locations and quantifies the utilization distribution of a group/animal based on its path rather than on individual points (Horne et al., 2007).

The three study groups ranged widely, and there was considerable overlap in their UD estimates. I used the *kerneloverlap* command of the 'adehabitatHR' (Calenge, 2011) package in R version 3.6.1 (R Core Team, 2019) to calculate 95% UD Overlap Index values (UDOI) for each pair of groups across the entire study period (Fieberg & Kochanny, 2005). Values of UDOI < 1 indicate less overlap relative to uniform space use, whereas values of UDOI > 1 indicate higher than normal overlap relative to uniform space use (see Appendix 4 for summary data).

2.10.2 Perceived intergroup encounter risk maps

To quantify spatial variation in perceived IGE risk, I used a technique commonly used in epidemiological studies to map disease risk from case-control data (Campos & Fedigan, 2014; Davies et al., 2018; Kelsall & Diggle, 1995; Lawson & Williams, 1993). The technique estimates a relative risk function using a ratio of two kernel density estimates: one derived from "case" data, e.g. all individual occurrences of an infectious disease, and the other from "control" data, i.e. a random sample of individuals from the population at risk. By doing so it is possible to estimate spatial variation in disease risk. I calculated a "perceived IGE risk landscape" for each group as the ratio of IGEs (the "cases") to normal usage density (the "controls"). We recorded the focal group's location every two min using Garmin etrex-10 handheld receivers and extracted location data every thirty minutes (the "controls"). We also recorded the location of the start of any IGEs (the "cases").

Risk maps were made on a monthly basis for each group, producing 33 in total (see Appendix 5). The resulting maps represent the probability of the focal group encountering another given their underlying pattern of space use, and a continuous numerical value is assigned to each pixel of the map (range: 0.001 to 1). This value can be interpreted as the relative risk of experiencing an IGE in any area of a group's home range. Because each map is derived from a different number of case and control points, over a different home range area, pixel size varies by group (PB1B=17x16 m; R1=25x23 m; R3=12x18 m). Using the R (R Core Team, 2019) package 'sparr' (Davies et al., 2018), I used multiscale adaptive kernel smoothing to simultaneously smooth the density estimates at different bandwidths, depending on "case" density (Abramson, 1982; Silverman, 1986). This allows for the use of different kernel smoothing parameters (bandwidths) in areas with different amounts of data. This greatly reduces estimation bias and prevents the over- and under-smoothing that commonly results from applying the same fixed bandwidth to areas of high and low data density.

In addition, I generated P value ($\alpha = 0.05$) risk surfaces for each group using Monte-Carlo (MC) simulation of the kernel-estimated risk functions. This allowed me to identify areas of statistically significant high and low IGE risk. First, the "case" and "control" data are pooled (IGEs and normal use locations respectively); then points are randomly sampled from this pooled data, without replacement, to represent the new simulated “cases”. The remaining points are used as the estimated “controls”. The risk function is calculated as above and stored, and the procedure is repeated 1000 times. The P value surface is found as the proportion of simulated risk estimates that equal or exceed the estimated risk from the observed data at each evaluation point. Single-tailed tests produce high-risk contours around any value <= 0.05; I conducted two-tailed tests to produce both low- and high-risk contours. Low risk contours surrounded any values >= 0.95, and areas with values >0.05 and <0.95 were classified as medium risk.

2.10.3 Assignation of risk values to behavioural observations

Using the monthly risk maps described in section 2.10.2, I assigned a risk value to each focal and scan sample, based on the location at which they ended. Using the R (R Core Team, 2019) package ‘raster’ (Hijmans, 2020), I attached the risk contour value (low, medium, high) from the previous month to each sample, e.g. for each group, focal/scan samples that occurred in September 2018 were assigned risk values from the August 2018 risk map. Although using risk maps for the previous month results in a time lag between observations and risk conditions, particularly for focal/scan samples conducted late in the month, I chose to use risk maps from the previous month to avoid the possibility of assigning risk values based on IGEs that had not yet occurred. Given that I was also interested in how a group’s recent IGE win/loss record (from the previous month) influences their response to risk, using risk maps from the previous month allowed me to investigate how a group’s recent actual IGE experience might influence their current response to IGE risk. Although this approach may seem conservative, compared to constructing weekly or even daily rolling risk maps, given the frequency with which each group was followed, one month was the smallest window in which enough data were collected with which to construct accurate risk maps.

2.10.4 Food availability

Crested macaques are eclectic feeders, consuming fruit, arthropods, leaves, mushrooms, shoots, bark, and occasionally eggs, small birds (personal observation), frogs, and snakes. However, ripe fruit is the primary and preferred food item, comprising approximately 50-70% of the diet, followed by arthropods at approximately 20-35% (O’Brien & Kinnaird, 1997; Ratna Sari, 2013). Various studies have examined crested macaque dietary preferences (Kinnaird & O'Brien, 1995, 2005; Lee, 1997; O'Brien & Kinnaird, 1997; Ratna Sari, 2013) and of the 145 fruit species consumed, macaques consistently spend the most time and energy searching for and consuming *Ficus* spp., *Dracontomelum dao*, *Eugenia* spp., *Palaquium* spp., and *Canaga odorata*.

The availability of ripe fruit was derived from phenology data collected by other members of the MNP as part of a long-running ecological project. Once a month, twenty 100 x 100 m plots were sampled. The abundance of ripe fruit was measured on a logarithmic scale for 15 individual plants of the 42 most important food plant species for crested macaques (O'Brien & Kinnaird, 1997). From these data I calculated the mean ripe fruit availability per month across the study area, which estimates the relative abundance of food during the study.

2.10.5 Female reproductive state

We quantified and recorded the sexual swelling state of each adult female on each observation day using definitions adapted from the MNP working protocol (Table 2.4). We also recorded the date on which any new infant macaque was observed for the first time. We classified the new infant's mother (which was apparent either because we had witnessed the birth (or its immediate aftermath), because an umbilical cord still trailed from her genitals, and/or from her behaviour; suckling and continuously carrying the infant) as pregnant for 150 days prior to the date of birth (Thomson et al., 1992). We classified her as lactating for 155 days (average time until first observed nipple deterrence (Thierry, Iwaniuk, et al., 2000)) or until she continuously refused suckling, whichever occurred first.

Table 2.4 Definitions of female sexual swelling states.

State	**Definition**
None	No swelling.
Inflating swelling	Sexual skin starting to swell, often first on the top. Colour changing from pale pink to deep red. Visible wrinkles.
Maximally swollen	Full swelling. Sexual skin red, taught, and fully swollen. Colour is deep red. No visible wrinkles.
Deflating swelling	Sexual skin becoming less swollen. Colour changing from deep red back to pale pink. Visible wrinkles appearing.

2.10.6 Dominance rank

To determine individual dominance ranks, I used Elo-rating (Neumann & Kulik, 2014), which sequentially tracks an individual's success in agonistic interactions and updates their rating over time. As such, individual ratings can be obtained for any point in time during the study, and all ranking data used in the analyses were matched to the day of observation. I used displacements and aggressive interactions taken from all focal data, supplemented with ad libitum data to calculate ratings for all adult macaques, sub-setting by group and sex. Only interactions with a clear winner/loser were used. Following Neumann et al. (2011) I assigned a different k value to displacements (k=50) and threats/fights (k=200). Using the same k value would imply that all interaction types have equal consequences in terms of dominance rank, i.e. when calculating an individual's Elo-rating, no distinction would be made between mild and severe aggression. However, a physical fight is likely to be much more relevant in terms of determining an individual's social status than a displacement or threat (Albers & de Vries, 2001; Neumann et al., 2011). This is reflected in the use of different k values for these interaction types.

2.10.7 Dyadic composite sociality index

To estimate the strength of the social bond between individuals, I used a dyadic composite sociality index (DCSI) (Sapolsky et al., 1997; Silk et al., 2013) based on the proportion of observation time each focal subject x spent grooming, contact-sitting with, and in close proximity (sitting within one body length) to partner y. The DCSI was calculated using the following equation:

$$DCSI_{xy} = \frac{\sum_{i=1}^{d} \frac{f_{ixy}}{\bar{f_i}}}{d}$$

Here, d is the number of behaviours that contribute to the index; f_{ixy} is the proportion of observation time focal individual x spent in behaviour i for dyad xy; and $\bar{f_i}$ is the mean rate of behaviour i for individual x across all $x \ldots y_n$ dyads. Here, $\bar{f_i}$ is calculated in a different way than the DCSI presented by Silk et al. (2013): originally $\bar{f_i}$ is the mean rate or proportion of behaviour i across all dyads, such that high DCSI values represent dyads that have more frequent and/or longer lasting affiliative interactions than the average dyad in their group. However, for these analyses I was primarily interested in how individuals choose to direct their social effort when under potential threat. As such, I calculated the index so that DCSI values would instead represent the social preference of individual x for partner y_1, compared with the social preference of individual x for partner $y_2 \ldots y_n$. Therefore, a high DCSI value for dyad xy represents the high social preference of individual x for individual y, compared to the social preference of individual x for other potential partners.

2.10.8 Statistical analysis

I conducted all analyses in R version 3.6.1 (R Core Team, 2019). Data were analysed with generalised linear mixed models (GLMMs) (Bolker et al., 2009), using the 'glmmTMB' (Brooks et al., 2017) and 'lme4' (Bates et al., 2015) packages. GLMMs allow for the simultaneous analysis of multiple independent variables whilst controlling for the non-independence of repeated sampling by treating experimental units (e.g. individuals, dyads, and/or groups where relevant) as random effects (Zuur et al., 2009). Depending on the distribution of each response variable around its predicted mean, I specified a binomial, negative binominal, Poisson, zero-inflated Poisson, or Gamma response distribution, with the canonical link function in all cases (specified throughout the thesis) (Zuur et al., 2009). For all 'glmmTMB' models, I used the *Anova.glmmTMB* function from the 'glmmTMB' package (Brooks et al., 2017) to test the significance of the fixed effects using a likelihood ratio test (LRT), assuming an asymptotic chi-square distribution of the test statistic; for the 'lme4' models I used the *mixed* function from the 'afex' package (Singmann et al., 2017). These systematically drop fixed effects one at a time (Barr et al., 2013), comparing each reduced model (lacking the fixed effect of interest) with the full model. I then used the *confint* function to calculate profile likelihood confidence intervals around the fixed effect estimates (Bolker et al., 2009).

Binomial model estimates and confidence intervals were converted to odds ratios to aid in interpreting the values of the estimates, particularly for multi-level factors, and to show effect sizes (negative binomial and Poisson model estimates and confidence intervals were converted to incident rate ratios). Because it is inappropriate to evaluate interaction effects in nonlinear models simply by looking at the sign, magnitude, or statistical significance of the coefficient on the interaction term, this makes simple summary measures of these effects difficult (Ai & Norton, 2003; Brambor et al., 2006). The interaction effect may be different for different values of variables and should not be evaluated solely by reference to the p-value of the overall effect. Rather, in order to provide a substantively meaningful interpretation, based on considerations of biological significance and effect size, it is more appropriate to calculate and plot the marginal effects of the interacting variables, and the uncertainty with which they are estimated, across a representative range of their values. I used the package ‘emmeans’ (Lenth et al., 2019) to do this and where appropriate present the results of interaction effects graphically, in addition to presenting tables of coefficients. Model fit and assumptions were verified by plotting residuals versus fitted values with the package ‘DHARMa’ (Hartig, 2019). This package uses a simulation-based approach to create readily interpretable scaled (quantile) residuals for fitted GLMMs. To assess predictor collinearity I used the *collin.diag* function of the package ‘misty’ (Yanagida, 2020) to derive generalised variance inflation factors ($GVIF^{(1/(2 \times d.f.))}$) for each model. Before fitting all models, I z-transformed all continuous variables using the *scale* function.

Chapter 3

Intergroup encounter risk in wild crested macaques (*Macaca nigra*): winner/loser effects on spatial cohesion and behavioural synchrony

James O. Waterman, Muhammad Agil, Antje Engelhardt, Eka Arisyamanti,
Bonaventura Majolo, Nicola F. Koyama[1]

This chapter has been formatted for submission to
International Journal of Primatology

Abstract

The spatial distribution of perceived risk can alter behaviour and time allocation patterns in solitary and group-living animals. This "landscape of fear" concept has been well studied in the context of predation and human disturbance, but few studies have investigated whether spatial variation in perceived intergroup encounter (IGE) risk has similar effects on behaviour. We explored whether three groups of wild crested macaques (*Macaca nigra*) would pre-emptively adjust intragroup group-level spatial cohesion and behavioural synchrony in response to perceived IGE risk. First, monthly relative risk maps were created from IGE data. We then explored whether a behavioural indicator of anxiety was related to risk in order to validate the maps. We used generalised linear mixed models to compare behaviour in low and high risk areas, whilst controlling for group size, preferred resource availability, intragroup aggression, time of day, and habitat visibility. We found that groups adjusted spatial cohesion and behavioural synchrony in high risk areas. However, the nature of this response depended on the interaction between risk and IGE win/loss record for the previous month; spatial cohesion and behavioural synchrony increased among

---

[1] Author contributions: JW, NK, and BM conceived the study. JW, NK, BM, and AE designed the study. JW and EA collected data. JW analysed data and wrote the manuscript. JW, NK, and BM revised manuscript drafts. MA and AE stewarded the field project of which this study was a part.

habitual losers and decreased among habitual winners. Subordinate groups appear to adopt a defensive strategy in high risk areas, whilst dominant groups adopt a more exploratory one. This highlights the role of intergroup social dynamics in determining group-level patterns of behaviour.

3.1 Introduction

In many social species, stable groups of individuals cooperate in defence of territory, food, or mating opportunities, against other conspecific groups (Kitchen & Beehner, 2007; Krause & Ruxton, 2002; Radford et al., 2016); and there is increasing evidence that intergroup competition can drive the evolution of social behaviour (Alexander & Borgia, 1978; Choi & Bowles, 2007; Majolo et al., 2016; Puurtinen & Mappes, 2009; Thompson et al., 2017). At their most extreme, encounters with rival groups can result in the injury or death of participants, in winning as well as losing groups (Cheney & Seyfarth, 1987; Fashing, 2001; Hölldobler & Lumsden, 1980; Martínez-Iñigo, 2017; McGraw et al., 2002; Mech, 1994; Mills, 1983; Payne, Lawes, et al., 2003; Wrangham et al., 2006). Even if physical injury is avoided, defeated groups may experience increased energy expenditure (Crofoot, 2013), increased anxiety (Radford, 2008b), and reduced time for feeding or other valuable activities (Yi et al., 2020) (compared to victorious groups). Most importantly, defeated groups may lose short-term access to valuable resources, and if a pattern of group dominance is established this exclusion may become more permanent as parts of a group's home range are annexed by dominant rivals (Kitchen & Beehner, 2007; Radford, 2003; Wilson & Wrangham, 2003). Changes in home range size and/or resource access have well-established effects on lifetime reproductive fitness: individuals in groups with more productive home ranges tend to experience increased offspring survival and shorter interbirth intervals (Lemoine, Boesch, et al., 2020; Nilsen et al., 2004).

Given the significant effect that intergroup competition can have on individual fitness, researchers from various disciplines have hypothesised a link between intergroup competition and intragroup social structure (Choi & Bowles, 2007; Reeve & Holldobler, 2007; Sterck et al., 1997; Wrangham, 1980). At the group level, most investigations have focussed on the evolution of behavioural traits such as cooperation, altruism, and friendship, all of which promote intragroup social cohesion (Alexander & Borgia, 1978; Majolo et al., 2016). Increased social cohesion may facilitate future participation in intergroup conflict (IGC), overcoming the collective action problem (CAP) associated with joint territorial/resource defence (Gavrilets, 2015). That is, if collective action creates a public good that all group members can share in equally (or nearly so), natural selection favours free-riders, who partake of the benefits without sharing the costs. Their presence can inhibit collective action, resulting in the loss of the public good for all (Nunn & Lewis, 2001). However, despite the recent interest in the effect of intergroup competition on intragroup social cohesion and its role in overcoming CAPs (Bruintjes et al., 2016; Mirville et al., 2020; Preston et al., 2020; Samuni, Mielke, et al., 2019; Yi et al., 2020) (see Radford et al. (2016) for a thorough review), less attention has been payed to the possible effect of intergroup competition on intragroup spatial cohesion, i.e. the extent to which group-mates maintain interindividual proximity. To succeed in intergroup competition, individuals must not only participate, but also coordinate with group-mates the timing and intensity of action (Zhang et al., 2019). Indeed, out-group attacks frequently fail because individual participants are poorly coordinated (De Dreu et al., 2016). It seems evident then that group-mates must be in broadly the same place at the same time. Otherwise communication, information exchange, participant recruitment, and coordinated action may be compromised (Boesch et al., 2008; Grinnell, 2002; Radford, 2008b; Wrangham, 1999). In addition to the importance of spatial cohesion for coordinated action, aggregation may also reduce the individual costs of IGC. Individuals in scattered groups risk being outnumbered by the active participants of rival groups (a key determinant of encounter outcome (Majolo et al., 2020)), and/or being outmanoeuvred/isolated by the coordinated actions of rivals, with potentially lethal consequences (Boesch et al., 2008; Martínez-Iñigo, 2017; Watts et al., 2006).

One of the main factors that allows groups to remain spatially cohesive is behavioural synchrony (Agetsuma, 1995; Conradt & Roper, 2000), i.e. the extent to which individuals perform the same activity at the same time (Asher & Collins, 2012; Duranton & Gaunet, 2016). The less synchrony there is between the activities of group members, the more likely the group is to split (Conradt & Roper, 2005; Engel & Lamprecht, 1997). For example, if an individual wishes to remain with the group it cannot stay behind to sleep while the rest of the group forages in a different location (Conradt & Roper, 2000; Rook & Penning, 1991). However, the maintenance of synchrony depends less on the precise behaviour being performed and more on whether individuals are active (e.g. foraging or travelling) or inactive (e.g. resting or socialising) at the same time (Gautrais et al., 2007). Behavioural synchrony begets spatial cohesion, which promotes effective collective action in the event of an intergroup encounter (IGE). Thus, in order to remain stable (and competitive in the context of IGC), groups need to be spatially cohesive and behaviourally synchronous. As such, intergroup competition likely exerts a strong selection pressure on spatial cohesion and behavioural synchrony. Under this scenario we would expect to see adaptive changes in both group-level properties in response to temporal changes in the intensity of intergroup competition, and to spatial variation in the risk of encountering rival groups.

Spatial variation in perceived risk creates a “landscape of fear” (Bleicher, 2017) that can alter animal behaviour (changes in vigilance, foraging, spacing, and group size (Banks, 2001; Dannock et al., 2019; Laundré et al., 2001; Makin et al., 2012)) or time allocation patterns (avoiding/underusing high risk areas) (Heithaus & Dill, 2002; Kotler et al., 2016; Willems & Hill, 2009). The landscape of fear approach has largely been used to study the effects of predation risk, and to a lesser extent human-wildlife conflict (Nowak et al., 2017; Reisland & Lambert, 2016; Waterman et al., 2019), but it can also be applied to the perceived risk of aggressive encounters between conspecific groups (Gibson & Koenig, 2012; LaBarge et al., 2020; Markham et al., 2013; Tórrez-Herrera et al., 2020). Theory predicts that in response to predation risk group-living animals should clump together in order to exploit the confusion and dilution effects (Hamilton, 1971; Krause & Ruxton, 2002; van Schaik, 1983). Respectively, these make it more difficult for a predator to target any one group member and reduce the per capita risk of injury if an attack does occur. In addition, several studies indicate that individual predation risk is reduced by synchronising behaviour with others (Bode et al., 2010; May et al., 2008). Doing so allows group-mates to stay together, again making it more difficult for a predator to single-out any one individual. Given the common potential for injury or death we might anticipate similar responses to IGE risk as to the threat of predation; although these responses are likely modulated by factors specific to intergroup competition, such as group dominance (in the mid- to long-term) and winner-loser effects (in the short-term).

Of the limited studies that exist, most have focussed on non-human primates (hereafter primates). Primates are a diverse group of long-lived, socially complex animals, making them an ideal taxon in which to investigate the evolutionary and ecological processes that affect behavioural variation (Smuts et al., 2008). Most recently, LaBarge et al. (2020) explored changes in spatial cohesion in response to actual and perceived IGE risk in samango monkeys (*Cercopithecus albogularis schwarzi*). They observed an increase in cohesion in reaction to actual IGC, but no pre-emptive change in areas of high perceived encounter risk. Similarly, Benadi et al. (2008) investigated interindividual distances and activity patterns in Verreaux's sifaka (*Propithecus verreauxi*) in overlapping vs. core home range areas, but found no significant changes in spatial cohesion or time spent feeding, travelling, or resting in potentially high encounter risk areas. Both chimpanzees (*Pan troglodytes*) and spider monkeys (*Ateles geoffroyi*) stay closer together when feeding in areas where the risk of IGC is high (Aureli et al., 2006; Mitani et al., 2010), and although Tórrez-Herrera et al. (2020) did not explicitly measure spatial cohesion or behavioural synchrony they observed an increase in the number of capuchin (*Cebus capuchinus*) group members feeding together (at the same time) in contested areas of their home range. They posited that this may function to increase spatial cohesion; improving the chances of detecting rival groups, diluting individual risk of injury, and potentiating joint defence of resources in the event of an IGE.

Individuals of many group living species (including non-primate species) also act in concert to assault/repel potential predators, often in a highly coordinated, synchronous way (Crofoot, 2012). Baboons (*Papio* spp.) kill hunting leopards (*Panthera pardus*) together (Cowlishaw, 1994), and capuchin monkeys (*C. capuchinus, C. imitator*) cooperate to attack snakes (*Boa constrictor)* that have captured group mates (Chapman, 1986; Jack et al., 2020). White-lipped peccaries (*Tayassu pecari*) gather to threaten and chase jaguars (*Panthera onca*); and of particular interest in the context of spatial cohesion, the decision to do so may be driven by group size and spread (Rampim et al., 2020). A similar pattern of coordinated behaviour has been observed in response to out-group threats. After encountering rival groups of Taï chimpanzees, individuals emit loud calls, drum on buttress roots, and then wait for other group members to gather before initiating an attack (Boesch & Boesch-Achermann, 2000). During wolf (*Canis lupus*) territorial aggression the lead individual of the chasing pack will often pause or turn back mid-chase to wait for lagging members to catch up (Harrington & Mech, 1979). And, multi-female groups of eastern whipbirds (*Psophodes olivaceus*) sing highly synchronised songs to defend mating positions against rival females (Rogers et al., 2007; Rogers & Mulder, 2004).

Finally, behavioural synchrony may serve other adaptive purposes in the context of intergroup competition; to signal group cohesion to rivals, to enhance intragroup cooperation, and to stimulate an endorphin release that elevates pain thresholds. For example, it appears that the elaborate synchronous behavioural displays exhibited by allied male Indian Ocean bottlenose dolphins (*Tursiops aduncus*) are directed not only at females, but may also serve a signalling role within and between male alliances (Connor et al., 1992, 2006). And, among human subjects, synchronised physical training significantly increases pain thresholds, likely through heightened opiodergic activity (Cohen et al., 2010; Tarr et al., 2015). Clearly, in certain predatory and many IGE contexts, adaptive individual decision-making may promote the emergence of group-level spatial cohesion and behavioural synchrony. Successful intragroup cooperation requires an interplay between these factors: behavioural synchrony allows group members to remain in relatively close proximity (or allows them to reunite quickly if dispersed), which facilitates spatial cohesion, which in turn potentiates coordinated, synchronous, collective action. These strategies have been investigated for prey species (reviewed in Lima & Dill, 1990), and for animals living in human-dominated landscapes (Ciuti et al., 2012; Clinchy et al., 2016; Stillfried et al., 2017). They have also been examined in the context of actual IGC (to a limited extent). But the way in which the perceived threat of IGE influences patterns of spatial cohesion and behavioural synchrony has received very little attention.

Furthermore, because the costs and benefits of IGC are experienced very differently by winning and losing groups, it is important to consider whether risk perception is influenced by how likely individuals think they are to win/lose an encounter. Clearly, we cannot know another animal’s mind, but as a proxy we may investigate how a group’s recent IGE win/loss record influences their subsequent response to encounter risk. Groups that habitually lose encounters (hereafter subordinate groups) may perceive them as particularly costly events, whilst habitual winners (hereafter dominant groups) may perceive IGEs as opportunities to be exploited, the benefits of which may outweigh the potential costs (Crofoot, 2013; Lemoine, Boesch, et al., 2020; Sicotte et al., 2007). In addition to retaining access to any contested food resources, individuals in winning groups may gain out-group copulations, and/or the chance to assess group transfer options (Hale et al., 2003; Sommer & Reichard, 1997). Also, by repeatedly winning IGEs victorious groups may reinforce a pattern of intergroup dominance (Arseneau, 2010; Cooper et al., 2004; Crofoot & Wrangham, 2010; Harris, 2006), potentially offsetting future conflict costs by reducing rival group size (if lethal violence occurs (Langergraber et al., 2017)), expanding their home range, and/or discouraging subordinate groups from subsequent engagement (Williams et al., 2004). Evolutionary game theory predicts that animals should assess their chances of victory and avoid contests they are likely to lose (Maynard Smith, 1982). As such, we might expect subordinate groups to behave in ways that decrease the likelihood of encountering rivals, and/or minimise the potential costs if they do. However, presumably the original prediction cuts both ways: we might also expect dominant groups to behave in ways that (a) maximise the potential benefits of IGEs they are likely to win, or (b) that reflect a relatively benign attitude towards IGE risk (given that the most dominant groups may perceive little to no threat from subordinate rivals).

In this study we examine to what degree variability in perceived IGE risk explains anxiety, spatial cohesion, and behavioural synchrony among three groups of wild adult crested macaques (*Macaca nigra*) in the Tangkoko Nature Reserve (TNR), Sulawesi, Indonesia. Specifically, we hypothesise that perceived IGE risk induces anxiety among crested macaques (H1), and that groups will alter their spacing (H2) and behavioural synchrony (H3) in ways that reflect the interplay between perceived IGE risk and the perceived cost/benefit balance of engaging with rival groups. We use self-scratching as an indicator of anxiety (a well-established indicator of physiological stress in primates (Maestripieri et al., 1992; Polizzi di Sorrentino, Schino, Tiddi, et al., 2012; Schino et al., 1991), including crested macaques (Neumann et al., 2013)) to validate our approach to quantifying perceived encounter risk; the elliptical area occupied by a group as a measure of group cohesion (smaller area indicates greater cohesion (King & Cowlishaw, 2009)); a synchrony index derived from all behaviours as well as the proportion of a group simultaneously active (feeding or travelling) vs. inactive (resting or socialising) as measures of behavioural synchrony (Agetsuma, 1995; Rook & Penning, 1991); and the proportion of IGCs a group lost in the previous month (number of losses divided by number of wins) as a measure of group dominance. We test the following non-mutually exclusive predictions (Table 3.1):

Table 3.1 Hypotheses to test the influence of perceived IGE risk on anxiety, group cohesion, and behavioural synchrony among crested macaques.

Hypothesis	**Prediction**	**Rationale**
H1: Perceived IGE risk influences anxiety levels	P1.1 General increase in self-scratching in perceived high IGE risk areas.	IGEs can be stressful events and the prospect of one may induce anxiety. Self-scratching is a reliable indicator of anxiety among macaques.
	P1.2 A positive interaction between perceived IGE risk and the proportion of encounters lost in the previous month, such that individuals in subordinate groups self-scratch more in high encounter risk areas than individuals in dominant groups.	Losing an IGE causes more physiological stress than winning one, and subordinate groups are more likely to lose encounters. Therefore, the prospect of an encounter should induce more anxiety among individuals in subordinate groups than dominant groups.
H2: Perceived IGE risk influences spatial cohesion	P2.1 A spreading positive interaction between perceived IGE risk and the proportion of encounters lost in the previous month, such that subordinate groups increase spatial cohesion in high risk areas and dominant groups do not.	For individuals in subordinate groups, increasing spatial cohesion may (1) reduce the likelihood of detection by other groups, (2) potentiate the exchange of information if another group is spotted, (3) dilute the risk of injury if an encounter does occur, and (4) increase the odds of being part of a well-coordinated defensive action. This should minimise the likelihood and cost of IGEs. Individuals in dominant groups may perceive little to no threat from subordinate groups, rendering items 1-4 above unnecessary.
	P2.2 A cross-over interaction between perceived IGE risk and the proportion of encounters lost in the previous month, such that subordinate groups increase spatial cohesion in high risk areas and dominant groups spread out.	For individuals in subordinate groups, see prediction 2.1. Individuals in dominant groups may perceive IGEs as relatively cost-free opportunities to pursue out-group mating, assess group transfer options, and/or reinforce intergroup dominance. Spreading out should maximise the likelihood of encountering other groups for these purposes.
H3: Perceived IGE risk influences behavioural synchrony	P3.1 A spreading positive interaction between perceived IGE risk and the proportion of encounters lost in the previous month, such that subordinate groups increase behavioural synchrony in high risk areas and dominant groups do not.	For individuals in subordinate groups, increasing behavioural synchrony may (1) reduce the risk of being singled-out, isolated, and attacked by another group, (2) minimise the time spent in high encounter risk areas (if individuals prioritise active behaviours), (3) promote spatial cohesion, and (4) enhance intragroup cooperation. This should minimise the likelihood of detection by other groups and reduce the risk of injury if an encounter does occur. Individuals in dominant groups may perceive little to no threat from subordinate groups, and so have no need to synchronise their behaviour in high risk areas.

3.2 Methods

We studied the behaviour and ranging patterns of crested macaques living in three neighbouring groups in the TNR, Sulawesi, Indonesia (see Fig. 2.1), from March 2018 through June 2019.

3.2.1 Ethical statement

See section 2.1.

3.2.2 Study site

See section 2.2.

3.2.3 Study subjects

See section 2.3.

3.2.4 Data collection

See section 2.4.

3.2.5 Behavioural sampling

See section 2.7.2.

3.2.6 Control variables

Spatial cohesion is usually conceived of as a balancing act between the selective pressures of intragroup feeding competition and predation risk. These competing forces may be mediated by adjusting interindividual spacing (Janson, 1988), and it is important to account for this when assessing the influence of risk on spatial cohesion. The crested macaques at this study site are an ideal cohort with which to untangle the effects of perceived IGE risk from predation risk and intragroup feeding competition for two key reasons. First, predation is rare among this population: crested macaques have several potential predators, such as reticulated pythons (*Python reticulatus*), dogs (*Canis familiaris*), and Sulawesi hawk-eagles (*Nisaetus lanceolatus*), but predator encounters and fatalities are rare (O'Brien & Kinnaird, 1996, 1997; MNP, unpublished data) (see Appendix 1 for summary data). As such, no additional control variables related to predation risk were included in the analyses. Second, to control for potential effects of intragroup feeding competition on spatial cohesion (and feeding effort, which may also affect behavioural synchrony), we included a monthly measure of relative ripe fruit availability (crested macaques' primary food source (O'Brien & Kinnaird, 1997; Ratna Sari, 2013)) in all analyses.

Group size is also likely to exert a strong influence on both spatial cohesion and behavioural synchrony. Larger groups are likely to spread out more than small groups, particularly when feeding, to reduce intragroup competition (Agetsuma, 1995; Smith et al., 2005). Because this will increase the area occupied by a group and reduce opportunities for communication (and thus synchrony), we included daily adult group size as a control variable in the spatial cohesion and behavioural synchrony analyses. Crested macaques typically spend more time resting in the midday and afternoon periods of the day than the morning (O'Brien & Kinnaird, 1997); therefore time of day is likely to influence both group spread and the probability of behavioural synchrony. As such, we included hour of the day in both main analyses. It is also likely that habitat characteristics such as understory visibility will limit the ability of macaques to monitor each other (which may affect group spread and synchrony), and of observers to accurately monitor macaques (Boinski & Garber, 2000; Koda et al., 2008). Vegetation density differs greatly across the study area. Some areas are entirely clear, such as the beachfront, and others are virtually impassable, such as regenerating post-fire scrub. A categorical measure of visibility was recorded at each scan and added as a control (scan visibility) to both main analyses. Four categories were defined: open ground/forest clearing (1), light (2), medium (3), and dense (4) vegetation. For the spatial cohesion analysis, we also included the ad libitum number of group-wide aggressive events in the 30 minutes pre-scan (i.e. between successive scans), and the proportion of the group that was engaged in active behaviour (see Table 2.3). We included aggression to control for the effect of intragroup competition on social cohesion and thus group spread; selective attraction occurs between former opponents in crested macaques (Petit & Thierry, 1994). We added the proportion of the group that was active to control for the fact that 'inactive' individuals (those resting and/or socialising) tend to be in much closer proximity to each other than those foraging or travelling. Because communication deteriorates when individuals are spread over a large area, hindering the ability of individuals to synchronise their behaviour, we included group cohesion as a control in the behavioural synchrony analysis. Finally, time spent feeding is often strongly influenced by variation in individual energy requirements (Altmann, 1980; Dunbar & Dunbar, 1988). Pregnant or lactating females generally have greater (though not identically so) energy requirements than "non-reproductive" females, and males in general (reviewed in Gittleman and Thopmson, 1988). As such, high numbers of females in a single reproductive state, and/or a pregnant/lactating state may increase group-wide behavioural synchrony; because of their similar energy requirements. We controlled for this in the behavioural synchrony model by including the daily proportion of a group's females that were in the same reproductive state, and the daily proportion in a pregnant or lactating state.

3.2.7 Ripe fruit availability

The availability of ripe fruit was derived from phenology data collected by other members of the MNP as a part of a long-running ecological project (see section 2.10.4).

3.2.8 Female reproductive state

We recorded and defined the sexual swelling state of each adult female following the procedure described in section 2.10.5.

3.2.9 Dominance rank

Individual dominance ranks were determined following the procedure described in section 2.10.6.

3.2.10 Intergroup encounters

Intergroup encounters were defined as described in sections 2.8.1 and 2.8.2. Because responses to risk are likely to be subject to winner and loser effects (Arseneau, 2010; Cooper et al., 2004; Crofoot & Wrangham, 2010; Harris, 2006), we calculated a monthly IGE loss to win ratio for each group by dividing their number of losses by wins (see Appendix 3 for IGE summary data).

3.2.11 Relative intergroup encounter risk

Relative intergroup encounter risk was quantified following the procedure described in section 2.10.2.

3.2.12 Selection of scan samples for analysis

Risk values were assigned to each scan sample following the procedure described in section 2.10.3. Only low and high risk condition scans were retained for analysis, in order to compare spatial cohesion and behavioural synchrony in two contrasting risk conditions. Additionally, in order to qualify for inclusion in these analyses, scan samples had to meet three criteria: (1) the entire scan had to be undisturbed, e.g. by predators (see section 2.5) or tourists (see section 2.6) etc.; (2) at least 25% of a group's adults had to be simultaneously visible; and (3) the scan had to be independent of any IGE, i.e. scans recorded within a one hour window, before, during, or after the start/end of an IGE, were excluded from analysis. This was to ensure a focus on behaviour associated with the potential threat of IGE, and not on behavioural responses associated with an incipient or recently concluded encounter (proportion of scans removed by group due to all conditions: PB1B=0.38, R1=0.91, R3=0.29). The proportion of R1 scans that were excluded was particularly high because of criteria two (at least 25% of the group's adults had to be simultaneously visible). R1 had many more adults than either PB1B or R3 (see Table 2.1) so this condition was difficult to meet.

3.2.13 Data analysis

3.2.13.1. Relative intergroup encounter risk and self-scratching

To validate the relative risk approach, we calculated individual self-scratching rates (frequency per minute) from continuous all-occurrences ten minute focal follow data (Altmann, 1974), collected during a simultaneous data collection protocol (see all-occurrences focal sampling method in section 2.7.1). To test if self-scratching increased in line with our perceived IGE risk maps (H1: Prediction 1.1, Table 3.1), we used the package 'glmmTMB' (Brooks et al., 2017) to fit a zero-inflated Poisson generalised linear mixed model (GLMM) with log link function and an offset for *observation duration* (M1). The log link function ensures positive fitted values, and the Poisson distribution is typically used for count data (Zuur et al., 2009). We compared self-scratching rates in the low and high IGE risk conditions. Fixed effects were *risk condition* (factor with 2 levels); *proportion of IGEs lost in the previous month* (continuous); and *daily subject rank* (continuous). The interaction term *risk condition x proportion of IGEs lost in the previous month* was included to test Prediction 1.2 (Table 3.1), that win/loss record affects IGE risk perception, and the interaction *risk condition x daily subject rank* was included to account for the modulating effect of dominance rank on self-scratching among primates, including macaques (Kaburu et al., 2012; Palagi & Norscia, 2011; Troisi & Schino, 1987). To control for repeated observations of the same individuals within the same groups we used *subject* nested in *group* as a random intercept and included random slopes for the main effect of *risk condition*.

3.2.13.2 Spatial cohesion

Spatial cohesion was calculated following King & Colishaw (2009). At the end of each scan we measured the distance (m) between the individuals at the front and back of the group (relative to the group's ongoing, or last direction of travel) (*a*), and between the individuals on either side of the group (*b*), using an Eventek laser rangefinder (range 0.03 – 60 m, accuracy ± 2.0 mm). The estimated elliptical area (*e*) occupied by the visible individuals was calculated as $\pi \times \frac{1}{2}a \times \frac{1}{2}b$. From this, we calculated cohesion (*c*) as the number of individuals in view (*v*) divided by the area they occupied, that is, *v/e*.

To test if group spatial cohesion per scan changed in response to IGE risk (H2), we used the package 'glmmTMB' (Brooks et al., 2017) to fit a Gamma GLMM with a log link function (M2). The log link function ensures positive fitted values, and the Gamma distribution is typically used for continuous data with a skewed distribution (Zuur et al., 2009). Fixed effects for the cohesion model were *risk condition* (factor with 2 levels), *proportion of IGEs lost in the previous month* (continuous), *daily adult group size* (continuous), *monthly ripe fruit availability* (continuous), *hour* (continuous), *scan visibility* (factor with 4 levels), *aggressive events in previous 30 minutes* (continuous), and *proportion of group in active behaviour per scan* (continuous). The interaction term *risk condition x proportion of IGEs lost in the previous month* was included to test predictions 2.1 and 2.2 (Table 3.1), that win/loss record affects IGE risk perception. To incorporate the dependency among scans (on the occasions when two observers followed distant parts of the same group), and among observations of the same group, on the same day, we used *scan ID* nested in *day*, nested in *group* as a random intercept. When random slopes for the interaction between *risk condition* and *proportion of IGEs lost in the previous month* were included the random effects parameters and residual variance were unidentifiable, so the slopes were removed (Barr et al., 2013). This was also the case when the simple main effects were included as random slopes, so these were also removed.

3.2.13.3 Behavioural synchrony

General behavioural synchrony was also calculated following King & Colishaw (2009). We quantified group-wide general behavioural synchrony using Simpson's Diversity Index (Krebs, 1989; Peet, 1974), a simple index that measures diversity in categorical data. Behavioural synchrony (*Bs*) at each scan was calculated as $Bs = \sum_{i=4}^{S} \frac{n_i(n_i-1)}{N(N-1)}$ where n_i is the number of individuals engaged in a specific activity and N is the total number of individuals in view, for i=4 categories (feed/foraging, travelling, resting, socialising; Table 2.3). *Bs* values can range from zero to one, with values near zero indicating that group behaviour is heterogeneous, and thus asynchronous. Values near one indicate that group behaviour is homogeneous, and thus synchronous. For the second measure of behavioural synchrony we compared the number of individuals per scan in an active vs. inactive state (Table 2.3).

To test if behavioural synchrony per scan increased in response to IGE risk (H3), we used the 'glmmTMB' package (Brooks et al., 2017) to fit two models. The first model (M3) examined general behavioural synchrony (*Bs*). We fit a Beta GLMM with log link function. The log link function ensures positive fitted values, and the Beta distribution is typically used for continuous data on the interval from zero to one (Zuur et al., 2009). The second model (M4) examined what proportion of the group was engaged in active vs. inactive behaviour per scan. We used a binomial GLMM with logit link function. The logit link function ensures fitted values within the 0 -1 range, and the binomial distribution is typically used to model proportion data (Zuur et al., 2009).

Fixed effects for both models were *risk condition* (factor with 2 levels), *proportion of IGEs lost in the previous month* (continuous), *daily adult group size* (continuous), *monthly ripe fruit availability* (continuous), *hour* (continuous), *scan visibility* (factor with 4 levels), *group cohesion per scan* (continuous), *daily female reproductive synchrony* (continuous), and *daily proportion of females pregnant or lactating* (continuous). The interaction terms *risk condition x proportion of IGEs lost in the previous month* were included in both models to test the prediction that win/loss record affects IGE risk perception. To incorporate the dependency among scans, and among observations of the same group, on the same day, we used *scan ID* nested in *day*, nested in *group* as a random intercept for both models. As with the spatial cohesion model, when random slopes were included the models failed to converge, so these were removed.

3.2.13.4 Hypothesis testing and model validation

We conducted all analyses in R version 3.6.1 (R Core Team, 2019) following the general procedure described in section 2.10.8. For these analyses we used the *Anova.glmmTMB* function from the 'glmmTMB' package (Brooks et al., 2017) to test the significance of the fixed effects, and the *confint* function to calculate profile likelihood confidence intervals around the fixed effect estimates (Bolker et al., 2009). Where appropriate, model estimates and profile likelihood based confidence intervals were converted to odds/rate ratios to aid in interpreting the values of the estimates (particularly for multi-level factors) and to show effect sizes (see section 2.10.8 for further details). Where appropriate we present the results of interaction effects graphically, in addition to presenting tables of coefficients.

Model fit and assumptions were verified following the procedure described in section 2.10.8. We used the *collin.diag* function of the package 'misty' (Yanagida, 2020) to derive generalised variance inflation factors ($\mathrm{GVIF}^{(1/(2 \times \mathrm{d.f.}))}$) for each model, which did not reveal any predictor collinearity problems (Zuur et al., 2009) (largest GVIF: self-scratching model = 1.56; cohesion model = 1.74; general synchrony model = 1.82; active vs. inactive model = 1.82). Before fitting the models, we z-transformed all continuous variables using the *scale* function.

3.3 Results

3.3.1 Self-scratching rates and intergroup encounter risk

As predicted (P1.1), self-scratching increased significantly in high risk areas compared to low risk areas (M1: Fig.3.1 and Table 3.2). However, contrary to Prediction 1.2, there was no modulating effect of recent win/loss record (M1: Table 3.2). These results indicate that the relative risk maps accurately reflect perceived levels of IGE risk for these study groups (H1).

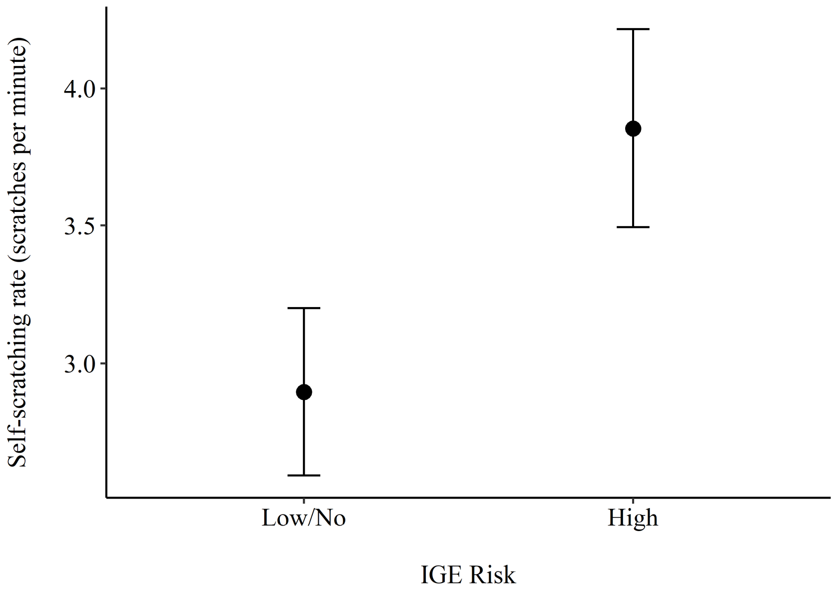

Figure 3.1 Difference in self-scratching rate in areas of low/no and high perceived IGE risk in crested macaques (M1). Points and error bars represent estimated marginal means and their standard errors.

3.3.2 Spatial cohesion

Consistent with hypothesis H2, we found evidence that perceived IGE risk significantly influenced the spatial cohesion of crested macaque groups. As predicted, this effect differed depending on recent win/loss record (M2: Fig. 3.2 and Table 3.3): In high risk areas spatial cohesion per scan increased for groups with poor win/loss records (individuals clumped together) and decreased for groups with strong win/loss records (individuals spread out) (prediction 2.2). However, this effect was only evident at the edges of the win/loss scale, i.e. for groups that had lost or won more than 70% of their IGEs in the previous month (see areas to the right and left of the dotted red lines in Fig. 3.6). As anticipated, several control variables also had statistically significant effects on spatial cohesion: Group spread increased when more ripe fruit was available (M2: Table 3.3), when more of the group were engaged in active behaviours (feeding or travelling) (M2: Table 3.3), and in medium and dense vegetation, compared to open areas (M2: Table 3.3).

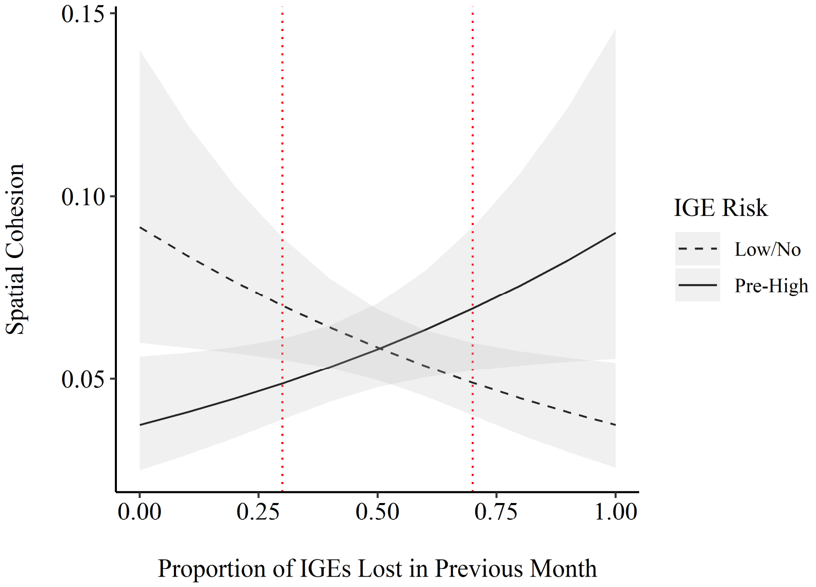

Figure 3.2 The effect of IGE risk and monthly win/loss record on spatial cohesion of crested macaque groups, as predicted from a GLMM (M2). Shaded grey areas represent 95% confidence intervals around estimates. Red dotted lines indicate the range of x-axis values (to the outer left and right respectively) for which the relationship between IGE risk and spatial cohesion is statistically significant at α=0.05.

3.3.3 Behavioural synchrony

We found partial evidence in support of hypothesis H3, that perceived IGE risk influences behavioural synchrony in crested macaques. No statistically significant effect of IGE risk was indicated by the general behavioural synchrony model (M3: Table 3.4); although synchrony decreased as the proportion of females in a pregnant or lactating state increased (M3: Table 3.4). However, we found that the probability of being observed in an active vs. inactive state (i.e., feeding or travelling vs. resting or socialising) increased significantly in high encounter risk areas compared to low/no risk areas (M4: Fig. 3.3 and Table 3.5). As predicted (P3.1), this effect was modulated by recent win/loss record (M4: Fig. 3.3 and Table 3.5), but, as with the spatial cohesion results, the effect was not significant across the entire range of win/loss values: Active synchrony was significantly greater in high IGE risk areas than low/no risk areas, but only among groups that had lost 70% or more of their IGEs in the previous month. On the other hand, dominant groups (i.e. those that had lost 10% or less of their previous month’s encounters) were significantly less synchronous in high risk areas (see areas to the right and left of the dotted red lines in Fig. 3.3, respectively).

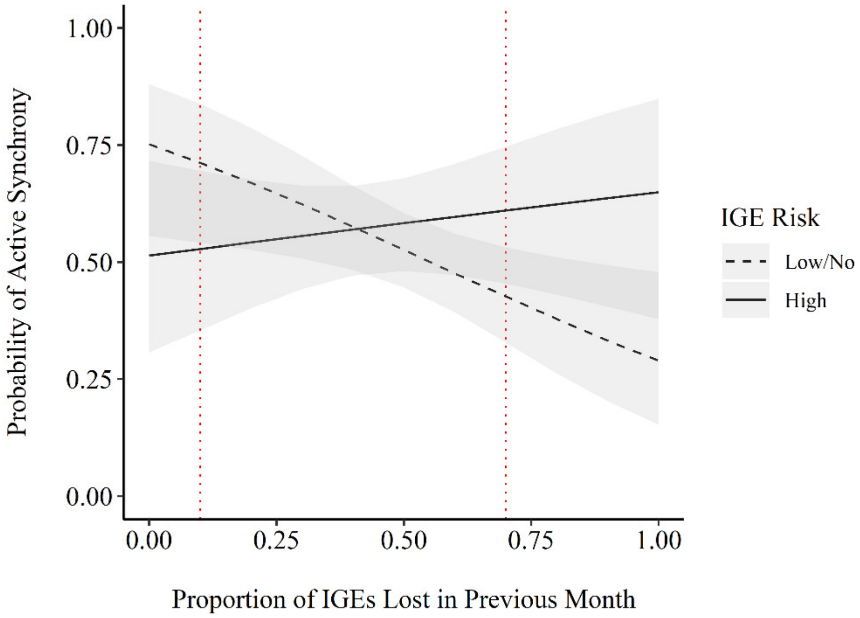

Figure 3.3 The effect of IGE risk and monthly win/loss record on active synchrony among crested macaques, as predicted from a GLMM (M4). Shaded grey areas represent 95% confidence intervals around estimates. Red dotted lines indicate the range of x-axis values (to the outer left and right respectively) for which the relationship between IGE risk and the probability of being observed in an active state is statistically significant at α=0.05.

Table 3.2 GLMM (M1) investigating the influence of perceived IGE risk on self-scratching in crested macaques.

Term	**Levels**	**Est**	**SE**	**RR**	**RR 95% CI**	**LRT**	**df**	***P* value**
Test fixed effects								
Intercept		-1.24	0.11	[a]	[a]	[a]	[a]	[a]
IGE risk	**High**	**0.29**	**0.13**	**1.33**	**[0.97; 1.76]**	**4.86**	**1**	**0.027**
Subject rank[b]		0.05	0.09	1.05	[0.92; 1.33]	0.08	1	0.777
Proportion of IGE losses in previous month[b]		-0.01	0.08	0.99	[0.82; 1.12]	0.41	1	0.523
IGE risk x Subject rank[b]		-0.12	0.12	0.89	[0.64; 1.09]	1.05	1	0.306
IGE risk x Proportion of IGE losses in previous month[b]		-0.05	0.11	0.95	[0.82; 1.26]	0.20	1	0.656
Zero-inflation model								
Intercept		-1.66	0.27	[a]	[a]	[a]	[a]	[a]
IGE risk		-0.08	0.43			0.03	1	0.855
Random intercepts	**Variance**		**SD**					
Subject within group	0.34		0.58					
Random slopes								
IGE risk	0.36		0.60					

The model was run with a Poisson error structure and log link function, controlling for repeated observations within subjects nested in groups. Random slopes for the main effect of IGE risk were included, as was a zero-inflation component to model the main effect of IGE risk. The table shows fixed effects parameter estimates and standard errors (Est; SE); rate ratios and their 95% profile likelihood confidence intervals (RR; RR 95% CI); and LRT statistics, degrees of freedom, and p values (LRT; df; *P* value). Also shown are random effects variance and standard deviation (Variance; SD). [a] Not shown because of having no meaningful interpretation. [b] z-transformed; mean ± SD of the original value. Statistically significant (α = 0.05) P values are in bold.

Table 3.3 GLMM (M2): Influence of perceived IGE risk and recent win/loss record on spatial cohesion in crested macaques.

Term	**Levels**	**Est**	**SE**	**95% CI**	**LRT**	**df**	***P* value**
Test fixed effects							
Intercept		-2.05	0.18	[a]	[a]	[a]	[a]
IGE risk	High	-0.06	0.12	[c]	[c]	[c]	[c]
Proportion of IGE losses in previous month[b]		-0.23	0.09	[c]	[c]	[c]	[c]
IGE risk x Proportion of IGE losses in previous month[b]		**0.45**	**0.12**	**[0.22; 0.68]**	**15.13**	**1**	**<0.001**
Control fixed effects							
Adult group size[b]		-0.02	0.07	[-0.16; 0.12]	0.08	1	0.777
Ripe fruit availability[b]		**-0.19**	**0.05**	**[-0.30; -0.08]**	**12.24**	**1**	**<0.001**
Aggressive events in previous 30 mins[b]		-0.001	0.06	[-0.12; 0.11]	0.0003	1	0.986
Hour[b]		0.03	0.06	[-0.09; 0.14]	0.25	1	0.617
Proportion of group in active behavioural state[b]		**-0.54**	**0.17**	**[-0.88; -0.20]**	**9.91**	**1**	**0.002**
Visibility	2	-0.41	0.21	[-0.82; 0.01]	**20.59**	**3**	**<0.001**
	3	-0.71	0.18	[-1.05; -0.36]			
	4	-0.76	0.18	[-1.12; -0.40]			
Random effects		**Variance**	**SD**				
Scan within day within group		0.28	0.53				

The model was run with a Gamma error structure and log link function, controlling for repeated observations within scans, days, and study groups (entered as random effects). The table shows fixed effects parameter estimates and standard errors (Est; SE); their 95% profile likelihood confidence intervals (95% CI); and LRT statistics, degrees of freedom, and p values (LRT; df; *P* value). Also shown are random effects variance and standard deviation (Variance; SD). [a] Not shown because of having no meaningful interpretation. [b] z-transformed; mean ± SD of the original value. [c] Not shown because of having no meaningful interpretation in the presence of a significant interaction. Statistically significant (α = 0.05) P values are in bold.

Table 3.4 GLMM (M3): Influence of perceived IGE risk and recent win/loss record on general behavioural synchrony in crested macaques.

Term	**Levels**	**Est**	**SE**	**95% CI**	**LRT**	**df**	***P* value**
Test fixed effects							
Intercept		-0.18	0.25	[a]	[a]	[a]	[a]
IGE risk	High	-0.04	0.18	[-0.40; 0.32]	0.04	1	0.848
Proportion of IGE losses in previous month[b]		-0.30	0.15	[-0.61; -0.0005]	2.02	1	0.155
IGE risk x Proportion of IGE losses in previous month[b]		0.28	0.18	[-0.08; 0.65]	2.34	1	0.126
Control fixed effects							
Adult group size[b]		-0.26	0.16	[-0.57; 0.06]	2.60	1	0.107
Ripe fruit availability[b]		0.03	0.09	[-0.15; 0.21]	0.11	1	0.745
Hour[b]		0.05	0.09	[-0.13; 0.23]	0.33	1	0.568
Group cohesion[b]		0.03	0.09	[-0.15; 0.20]	0.09	1	0.759
Overall synchrony in female reproductive state[b]		0.03	0.15	[-0.27; 0.34]	0.05	1	0.821
Proportion pregnant or lactating females[b]		**-0.32**	**0.11**	**[-0.54; -0.10]**	**8.39**	**1**	**0.004**
Visibility	2	0.42	0.33	[-0.23; 1.08]	6.50	3	0.090
	3	-0.05	0.28	[-0.60; 0.51]			
	4	-0.33	0.28	[-0.90; 0.23]			
Random effects	**Variance**		**SD**				
Scan within day within group	0.10		0.10				

The model was run with a beta error structure and log link function, controlling for repeated observations within scans, days, and study groups (entered as random effects). The table shows fixed effects parameter estimates and standard errors (Est; SE); their 95% profile likelihood confidence intervals (95% CI); and LRT statistics, degrees of freedom, and p values (LRT; df; *P* value). Also shown are random effects variance and standard deviation (Variance; SD). [a] Not shown because of having no meaningful interpretation. [b] z-transformed; mean ± SD of the original value. Statistically significant ($\alpha = 0.05$) P values are in bold.

Table 3.5 GLMM (M4): Influence of perceived IGE risk and recent win/loss record on active behavioural synchrony in crested macaques.

Term	**Levels**	**Est**	**SE**	**OR**	**OR 95% CI**	**LRT**	**df**	***P* value**
Test fixed effects								
Intercept		-0.06	0.33	[a]	[a]	[a]	[a]	[a]
IGE risk	High	[c]	[c]	[c]	[c]	[c]	[c]	[c]
Proportion of IGE losses in previous month[b]		[c]	[c]	[c]	[c]	[c]	[c]	[c]
IGE risk x Proportion of IGE losses in previous month[b]		**0.65**	**0.24**	**1.92**	**[1.19; 3.12]**	**7.10**	**1**	**0.008**
Control fixed effects								
Adult group size[b]		-0.22	0.20	0.8	[0.54; 1.19]	1.26	1	0.262
Ripe fruit availability[b]		-0.16	0.12	0.85	[0.67; 1.07]	1.87	1	0.172
Hour[b]		0.11	0.12	1.12	[0.88; 1.42]	0.81	1	0.369
Group cohesion[b]		-0.20	0.12	0.82	[0.65; 1.02]	3.09	1	0.079
Overall synchrony in female reproductive state[b]		-0.07	0.20	0.93	[0.62; 1.38]	0.13	1	0.717
Proportion pregnant or lactating females[b]		-0.03	0.14	0.97	[0.74; 1.29]	0.03	1	0.857
Visibility	2	0.18	0.47	1.2	[0.48; 3.03]	3.80	3	0.284
	3	0.13	0.38	1.14	[0.54; 2.42]			
	4	0.54	0.37	1.72	[0.82; 3.59]			
Random effects	**Variance**	**SD**						
Scan within day within group	2.14	1.46						

The model was run with a binomial error structure and logit link function, controlling for repeated observations within scans, days, and study groups (entered as random effects). The table shows fixed effects parameter estimates and standard errors (Est; SE); odds ratios and their 95% profile likelihood confidence intervals (OR; OR 95% CI); and LRT statistics, degrees of freedom, and p values (LRT; df; *P* value). Also shown are random effects variance and standard deviation (Variance; SD). [a] Not shown because of having no meaningful interpretation. [b] z-transformed; mean ± SD of the original value. [c] Not shown because of having no meaningful interpretation in the presence of a significant interaction. Statistically significant ($\alpha = 0.05$) P values are in bold.

3.4 Discussion

These results show that the risk of encountering rival groups influences spatial cohesion and behavioural synchrony among wild crested macaques, and that group dominance modulates this effect (Table 3.6). Where the likelihood of IGE is high, the most subordinate groups (those with poor win/loss records in the previous month) increase spatial cohesion. However, the most dominant groups (those with strong win/loss records) do the opposite and spread out. Furthermore, although it is unclear from these analyses whether behavioural synchrony is a driver or consequence of spatial cohesion (likely both), the same pattern is observed: in high risk areas, active behavioural synchrony (but not general behavioural synchrony) increases among subordinate groups and decreases among dominant groups. Notably, the evidence for this effect is only statistically significant among groups at the extreme ends of the dominance spectrum, i.e. groups with particularly skewed win/loss records in the previous month.

Table 3.6 Summary of hypotheses, predictions, and support provided by this study.

Hypothesis	Predictions	Supported?
1. Perceived IGE risk influences anxiety levels	1.1 General increase in self-scratching.	Yes
	1.2 Increase in self-scratching greater among subordinate groups.	No
2. Perceived IGE risk influences spatial cohesion	2.1 Spatial cohesion increases among subordinate groups; no change among dominant groups.	No
	2.2 Spatial cohesion increases among subordinate groups and decreases among dominant groups.	Yes
3. Perceived IGE risk influences behavioural synchrony	3.1 Behavioural synchrony increases among subordinate groups; no change among dominant groups.	Partially

For subordinate groups, there are clear benefits to increasing spatial cohesion and behavioural synchrony in response to IGE risk. First, individuals in spatially cohesive, well-coordinated groups are less likely to be targeted, isolated, or injured if an encounter does occur (Hamilton, 1971; van Schaik, 1983; Wilson & Wrangham, 2003). Lone individuals are at greater risk of being injured or killed by out-group rivals in many group-living, spatially cohesive species (Boesch et al., 2008; Gros-Louis et al., 2003; Mech, 1994; Shimada et al., 2009; Stanford, 1995; Watts et al., 2006). Indeed, twelve of the thirteen recorded instances of intergroup coalitionary aggression in this crested macaque population (i.e. simultaneous attacks by two or more members of one group against another, lasting more than one minute and involving contact aggression (Martínez-Iñigo, 2017)) occurred when a lone female was separated from her group and outnumbered by attackers (MNP; Martínez-Iñigo, 2017). Second, macaques in spatially cohesive, synchronous groups may detect and flee from rival groups more quickly in high encounter risk areas because there are more individuals to keep watch (Braune et al., 2005). Early detection followed by efficient information transfer can create an escape-wave, whereby the behavioural changes of a small proportion of the group initiates a rapid, group-wide flight response (Herbert-Read et al., 2015). Finally, increased spatial cohesion may relieve anxiety in high encounter risk areas via 'social buffering' (Kikusui et al., 2006; Sanchez et al., 2015), and increased behavioural synchrony may function likewise via endorphin release (Cohen et al., 2010; Tarr et al., 2015). Both serve an adaptive function: at the individual-level by buffering the negative physiological effects of heightened stress, and at the group-level by promoting cooperative behaviour (Dunbar et al., 2012; Wiltermuth & Heath, 2009).

Increased spatial cohesion and behavioural synchrony among subordinate groups can be understood within the landscape of fear framework as a defensive strategy, i.e. in high IGE risk areas, individuals alter their behaviour to minimise their risk of detection and/or injury; and in doing so they form a more cohesive counter-attacking unit (Stanford, 1995). In contrast, there are several possible, non-mutually exclusive, explanations for the observed decrease in spatial cohesion and behavioural synchrony among the most dominant groups that may suggest a more exploratory/aggressive strategy. First, in high encounter risk areas dominant groups may spread out to increase the likelihood of encountering rivals. By consistently seeking out and winning IGEs, the strongest groups may reinforce a pattern of intergroup dominance that increases lifetime reproductive fitness at an individual and group level ('Intergroup Dominance' hypothesis: Crofoot & Wrangham, 2010; Sugiura et al., 2000). Second, because large groups must spread out to reduce intragroup feeding competition (Agetsuma, 1995; Smith et al., 2005), group size could potentially explain the decrease in spatial cohesion and behavioural synchrony among dominant groups. However, by including adult group size as a control variable (i.e. holding group size at its mean) we were able to isolate and confirm the effects of encounter risk and win/loss record. Furthermore, group size was not a significant predictor of spatial cohesion or behavioural synchrony in any of the model outputs. As such, we may consider alternative explanations.

Finally, spatial cohesion and behavioural synchrony may decrease among dominant groups in high risk areas because males in those groups perceive IGEs differently from those in subordinate groups. Encounters provide opportunities to assess the composition of neighbouring groups in advance of immigration attempts, which can be costly due to resistance from resident males in this and other species (Cheney & Seyfarth, 1983; Marty et al., 2016; van Noordwijk & van Schaik, 1985). However, because males in dominant groups can be relatively certain of victory if an encounter does occur, they may be able to take advantage of this in a way that males in subordinate groups cannot by roaming more widely. If this is the case, the decrease in spatial cohesion and behavioural synchrony observed among dominant groups in high encounter risk areas could be the result of young adult males leaving the main body of the group to investigate transfer opportunities (Saito et al., 1998). This contrasts with resident males from subordinate groups who are likely to be more focussed on avoiding or repelling interloping out-group males, and guarding in-group females than investigating transfer opportunities. These males are, at least temporarily, better served by increasing spatial cohesion and synchrony. It would be worth investigating this possibility by comparing interindividual distances of different age-sex classes in dominant and subordinate groups in high risk areas, while considering the fact that large (likely dominant) groups tend to have proportionally more young adult males than small (likely subordinate) groups (Suzuki et al., 1998).

Taken together, these results indicate that crested macaques remember the frequency, location, and outcome of previous IGEs, and use this information to respond pre-emptively to varying levels of perceived encounter risk across their home ranges. Indeed, the fact that the active vs. inactive measure of behavioural synchrony changed in response to risk when the general measure did not, suggests that individuals do not synchronise their behaviour per se, but rather their patterns of locomotion, presumably (in the case of subordinate groups at least) to maintain spatial cohesion. Crucially, these results also demonstrate that the way in which groups responds to this variation in risk is significantly influenced by how likely they are to win or lose an encounter; perhaps reflecting the considerable difference in cost to habitual losers and winners of IGEs. Few landscape of fear (Laundré et al., 2001) studies have focussed on the role of intergroup competition in shaping animal behaviour (Bleicher, 2017), and with only one exception of which we are aware (Kurihara & Hanya, 2018), none have considered group dominance as we have here. Doing so raises interesting questions about how self-assessed resource holding potential, or fighting ability (Maynard Smith, 1982), affects IGE risk perception and home range use. For example, it is important to note that the changes in spatial cohesion observed in high encounter risk areas only occurred when groups had won or lost >= 70% of their IGEs in the previous month. The same was true of subordinate groups with respect to active behavioural synchrony, whilst it only decreased among dominant groups that had won >= 90% of their encounters in the previous month. This suggests that the costs associated with altering spatial cohesion and behavioural synchrony in response to IGE risk (e.g. increased feeding competition in groups that clump together and reduced likelihood of support in groups that spread out) may only be acceptable for individuals in groups at either end of the intergroup dominance spectrum. For groups in the middle it is perhaps more efficient to continue as normal in high risk areas and meet the costs/benefits of conflict on a case-by-case basis.

In summary, these findings support our understanding of the important role that intergroup competition plays in shaping social evolution. They also further our understanding by highlighting the influence of group dominance on both intergroup and intragroup processes, even at times when neighbouring groups do not interact directly. More research effort is required (ideally with a greater number of study groups) to clarify two key points. First, the extent to which behavioural synchrony drives spatial cohesion. It is unclear whether individuals synchronise their behaviour in order to increase spatial cohesion, or whether spatial cohesion increases their ability to synchronise. Conducting multiple simultaneous focal observations within a group may shed light on this question. Second, and most crucially, whether the cohesion and synchrony strategies posited here for subordinate and dominant groups pay off. It should be possible to investigate this by simultaneously tracking the positions of all the groups in the study area. By tracking group spread and degree of behavioural synchrony in 'real-time' and aligning these with the occurrence of actual IGEs it may be possible to identify instances when subordinate groups avoided detection and/or dominant groups searched for and found rivals. Although these data were collected during this study, due to personnel limitations, there were too few days on which all groups were followed simultaneously to conduct a thorough analysis. Even with these limitations, this study provides insights into the importance of intergroup competition as a driving force of animal behaviour.

Chapter 4

Potential intergroup conflict influences current intragroup behaviour in wild crested macaques (*Macaca nigra*)

James O. Waterman, Muhammad Agil, Antje Engelhardt, Eka Arisyamanti, Bonaventura Majolo, Nicola F. Koyama[2]

This chapter has been formatted for submission to Animal Behaviour

Abstract

In many social species, groups of individuals cooperate to defend resources and territory, often at great individual cost. Conflict participants risk injury or death, and experience costs like reduced feeding efficiency or reduced access to high-energy food sources. The effects of recent and incipient intergroup conflict (IGC) on intragroup social behaviour have been examined in numerous species, however we know relatively little about if and how the anticipation of IGC influences intragroup social behaviour in non-human animals. The previous chapter of this thesis used monthly intergroup encounter (IGE) risk maps to assess group-level responses to risk; this chapter uses the same maps to investigate the function of dyadic-level responses. Here, we investigated whether patterns of affiliative behaviour in three groups of wild crested macaques (*Macaca nigra*) were sensitive to the perceived risk of IGEs, and whether these responses were reactive (a response to stress), or pre-emptive (a strategic preparation for the possibility of conflict). We hypothesised that the function of pre-conflict affiliative behaviour would be to (a) reduce the anxiety associated with IGEs, (b) minimise the potential costs of conflict, or (c) increase group cohesion prior to encounters. Using generalised linear mixed models, we

---

[2] Author contributions: JW, NK, and BM conceived the study. JW, NK, BM, and AE designed the study. JW and EA collected data. JW analysed data and wrote the manuscript. JW, NK, and BM revised manuscript drafts. MA and AE stewarded the field project of which this study was a part.

compared the affiliative behaviour of dyads in two risk conditions; one in which there was little to no risk of IGE, and another in which the impending probability of encountering another group (within 40 minutes) was high. All models controlled for the effects of preferred resource availability, available social time, dyad reproductive state, and encounter win/loss record in the previous month. We found that affiliative interactions between female and male macaques decreased almost to zero in the pre-high-risk condition, male-male interactions were entirely absent, and the usual pattern of female-female affiliation reversed such that high-ranking females were the most preferred partners. These behavioural changes show that even in the absence of a direct threat, the risk of encountering rival groups influences patterns of social behaviour among wild crested macaques. Evidence for the function of male behaviour was scarce, but for females these patterns appear to have a clear purpose: to minimise the occurrence/cost of intragroup sexual coercion and out-group aggression. These findings indicate that crested macaque pre-conflict affiliative behaviour functions to minimise potential individual costs rather than to increase group cohesion or incentivise the future participation of group-mates.

4.1 Introduction

Intergroup competition has important consequences for individual fitness and the social structure of animal groups in both the long- and short-term. Losing an encounter with another group may constrain a group's home range, alter travel behaviour, and restrict access to high quality resources, negatively affecting lifetime reproductive fitness in a wide range of taxa that include Hymenopterans (Batchelor & Briffa, 2010; Hölldobler & Lumsden, 1980; Rangel et al., 2010), Passeriformes (Langen & Vehrencamp, 1998; Strong et al., 2018), Carnivores (Christensen et al., 2016; Dyble et al., 2019; Mosser & Packer, 2009), and non-human Primates (hereafter primates) (Cooksey et al., 2020; Crofoot, 2013; Lemoine, Preis, et al., 2020). Other potential costs associated with intergroup competition include physical injury or death (Mech, 1977; Rosenbaum et al., 2016), the death of offspring (Cords & Fuller, 2010; Sherman, 2003), increased energy expenditure (Schoof & Jack, 2013), increased anxiety (Radford, 2008b), and disruptive changes in social structure, e.g. loss of rank, and/or changes in reproductive access following the immigration of out-group individuals (Marty, Hodges, Agil, et al., 2017).

Numerous recent studies highlight the effects of intergroup competition on intragroup social behaviour (see Radford et al., 2016 for a review). However, most of these studies focus on the immediate aftermath of intergroup encounters (IGEs). Among green woodhoopoes (*Phoeniculus purpureus*) allopreening increased after intergroup conflict (IGC) (Radford, 2008a; Radford & Fawcett, 2014), whilst Javan gibbon (*Hylobates moloch*) pairs groomed less (Yi et al., 2020). Following simulated threats from rival groups, dwarf mongooses (*Helogale parvula*) invested more time in grooming, foraged closer together, and more regularly acted as sentinels (Morris-Drake et al., 2019). Similarly, affiliation between cichlid fish (*Neolamprologus pulcher*) increased following simulated out-group intrusions (Bruintjes et al., 2016).

A smaller number of studies have examined the effects of IGC on intragroup social behaviour during the encounter itself. Intragroup affiliation and aggression increased among vervet monkeys (*Chlorocebus pygerythrus*) in-between bouts of intergroup aggression (Arseneau-Robar et al., 2018, 2016), and intragroup aggression increased among tufted capuchins (*Cebus apella*) during, but not after IGEs (Polizzi di Sorrentino, Schino, Massaro, et al., 2012). Thus, there is mounting evidence that the intragroup behaviour of numerous species is affected by recent and/or incipient IGEs. However, we know relatively little about how group-living animals respond to the perceived risk of IGEs.

There is considerable evidence that many species remember where, and how recently they have encountered danger and use this information to alter their behaviour (Fagan et al., 2013; Laundré et al., 2010; Willems & Hill, 2009). For example, in response to the threat of predation many animals alter space use, how they travel, and how they behave in perceived risky areas. Predation risk prompts sexual segregation in Dall's sheep (*Ovis dalli dalli*) (Corti & Shackleton, 2002); numerous primate species show signs of heightened anxiety in risky habitats, moving through them at great speed (Gebo et al., 1994), or choosing travel routes that minimise risk exposure (see review in Boinski & Garber, 2000); and kangaroos (*Macropus rufous* and *M. fuliginosus*) and wallabies (*M. agilis*) persistently avoid particular feeding areas after detecting predator scent cues (Parsons & Blumstein, 2010). Given the potentially high costs of IGC, the risk of encountering rival groups might also be expected to prompt behavioural changes (LaBarge et al., 2020; Tórrez-Herrera et al., 2020).

Several studies have investigated this possibility, but they tend to focus on broad (activity budget) responses to simulated encounters and/or proxies of risk, such as areas of home range overlap (Benadi et al., 2008; Morris-Drake et al., 2019; Radford, 2011; Tórrez-Herrera et al., 2020). Very few studies have examined the influence of IGE risk on fine-scale patterns of social behaviour in groups of wild animals. Furthermore, we understand little about whether these responses are best characterised as reactive (a response to the stress of potential aggression), or pre-emptive (a strategic preparation for the possibility of conflict) (LaBarge et al., 2020). It is well established that IGC causes stress in wild primates (Eckardt et al., 2016; Nunn & Deaner, 2004; Wittig et al., 2016). As such it is possible that any changes in affiliative behaviour observed in association with IGE risk function primarily to reduce, relieve, or re-direct this anxiety. In this scenario, individuals may increase affiliative interactions with group-mates to relieve the physiological stress caused by the prospect of IGEs ('social buffering' as defined by Kikusui et al., 2006). Alternatively, the function of affiliative behaviour in the face of IGE risk may be strategic: to maximise individual reproductive fitness and/or to minimise individual costs (Radford, 2011).

Primates are an ideal order in which to test theories about the effects of intergroup competition on intragroup social behaviour because many species live in large social groups and form complex, long-lasting relationships (Smuts et al., 2008). This presents an opportunity to examine individual decision-making in a group context; specifically, how different classes of individuals in heterogenous groups respond to the threat of IGEs, and how existing relationships between individuals influence these responses (Cheney, 1987; Kitchen & Beehner, 2007). In this study, we examine the influence of perceived IGE risk on patterns of affiliative social behaviour (specifically partner choice and number) in three wild groups of crested macaques (*Macaca nigra*) in Tangkoko Nature Reserve (TNR) in Sulawesi, Indonesia. This species, and this population is an excellent model in which to investigate the effects of IGE risk on intragroup social behaviour because: (a) encounters with rival groups are frequent (~0.8/12h-day (Martínez-Iñigo, 2017)) and active; (b) home range overlap is extensive; (c) predation risk is extremely low (which removes the possibly confounding influence of perceived predation risk on intragroup behaviour); and (d) both sexes participate to some degree.

To investigate the possibility that individuals alter their social behaviour in anticipation of contact with rival groups, we test two contrasting hypotheses, the tension-reduction hypothesis (H1) and the preparing-for-conflict hypothesis (H2), within which we focus on two possible, non-mutually exclusive, preparatory strategies: (H2A) in which individuals try to maximise their own reproductive interests, and (H2B) in which individuals try to minimise their risk of injury. We compare patterns of social behaviour in two contrasting risk conditions, one in which the likelihood of encountering a rival group is very low, and another in which the impending probability of encountering another group is high (see sections 4.2.12 and 4.2.13 for details). A range of predictions (summarised in Table 4.1) are generated from these hypotheses.

According to the tension-reduction hypothesis (H1), individuals may increase affiliative interactions with group-mates to relieve physiological stress caused by the prospect of IGEs. Thus, the primary function of these interactions is to reduce tension by maximising the effects of social buffering (Kikusui et al., 2006; Rincon et al., 2019). If this is the case, we predict that patterns of affiliative behaviour in high IGE risk areas will largely resemble those observed in low/no IGE risk areas. That is, individuals will continue to interact with the partners with whom they are most familiar; those with whom they most frequently affiliate in low/no IGE risk areas, but at a higher rate (see Table 4.1 for specific predictions and rationales). Thus, there should be no change in the number of different partners with whom an individual exchanges affiliative interactions, and males and females will likely behave in similar ways.

Whilst the tension-reduction hypothesis (H1) essentially predicts no change in partner quality or quantity, according to the preparing-for-conflict hypothesis (H2) the function of affiliative behaviour in the face of IGE risk is strategic: to maximise the benefits and minimise the costs that individuals may face in the event of conflict (Radford, 2011). If this is the case, we predict that patterns of social behaviour in high IGE risk areas will change (relative to low/no IGE risk areas) in a way that maximises individual reproductive interests and/or minimises risk of injury (Table 4.1). In terms of partner numbers the preparing-for-conflict hypothesis (H2) predicts a range of responses: Depending on which strategy a male or female adopts it may best serve their interests to either focus their social effort on a specific subset of partners, or to spread their social effort among a greater number of partners. If individuals focus on a strategic subset this may be evidenced by a decrease in affiliative partner numbers. However, because other factors (such as feeding requirements) may impose an upper limit on the time that individuals can allocate to social behaviour, they may purposefully direct their effort towards different, rather than more individuals, predicting no change in partner numbers. Finally, strategies intended to incentivise the participation of group-mates in IGEs, and/or that rely on safety in numbers, predict an increase in partner numbers (see Table 4.1 for specific predictions and rationales).

Table 4.1 Hypotheses to test the function of affiliative social interactions between crested macaque dyads (F-F = female-female; F-M = female-male; M-F = male-female; M-M = male-male) in the 40 minutes prior to entering a high IGE risk location (relative to low/no IGE risk areas).

Hypothesis		**Sex**	**Strategy**	**Predictions:** **Pre-High IGE risk areas vs. low/no IGE risk areas**	**Rationale**
H1: Tension-reduction		♀	Social buffering	1.1 General increase in affiliative behaviour.	Affiliation relieves the physiological stress associated with potential IGEs, and the anxiolytic effects of affiliation are maximised with closely bonded social partners.
				1.2 No change in partner choice: Prefer closely bonded social partners.	
				1.3 No change in number of different partners.	
		♂	Social buffering	1.4 General increase in affiliative behaviour.	
				1.5 No change in partner choice: Prefer closely bonded social partners.	
				1.6 No change in number of different partners.	
H2: Preparing-for-conflict	A: Maximise individual reproductive interests	♀	Incentivise male participation	2A.1 Increase in F-M affiliative behaviour.	If males act as ‘hired-guns’, females may benefit by incentivising the most frequent, aggressive, and influential IGE participants (high ranking males).
				2A.2 Prefer high-ranking male partners to mid/low-ranking male partners.	
				2A.3 Increase in number of male vs female partners.	
		♂	Sexual coercion of females	2A.4 Decrease in M-F and F-M affiliative behaviour.	To deter out-group copulations males may aggressively herd females before and during IGEs. This may be evidenced by a decrease in affiliative behaviour between the sexes.
				2A.5 Decrease in number of female partners.	
	B: Minimise risk of injury	♀	Avoid male sexual coercion	2B.1 Decrease in F-M affiliative behaviour.	By avoiding males, females may avoid costs associated with aggressive sexual coercion.
				2B.2 Decrease in number of male partners.	
			Safety in numbers	2B.3 Increase in F-F affiliative behaviour.	Because recent affiliation may increase the likelihood of agonistic support and cooperation, F-F affiliation may increase, whilst avoiding potentially aggressive males. Preferred partners may be high-ranking females.
				2B.4 Decrease in F-M affiliative behaviour.	
				2B.5 Prefer high-ranking female partners to mid/low-ranking female partners.	
				2B.5 Increase in female partner numbers.	
		♂	Safety in numbers	2B.6 Increase in M-M affiliative behaviour.	Because recent affiliation may increase the likelihood of agonistic support and cooperation, M-M affiliation may increase. Preferred partners may be high-ranking males, who are likely to be the strongest fighters.
				2B.7 Increase in male partner numbers.	

4.2 Methods

From March 2018 through June 2019 we studied the behaviour and ranging patterns of three crested macaque social groups in TNR, Sulawesi, Indonesia (see Fig. 2.1. in section 2.2).

4.2.1 Ethical statement

See section 2.1.

4.2.2 Study site

See section 2.2.

4.2.3 Study subjects

See section 2.3.

4.2.4 Data collection

See section 2.4.

4.2.5 Behavioural sampling

See section 2.7.1.

4.2.6 Control variables

To properly investigate the effect of IGE risk on crested macaque social behaviour, additional variables had to be accounted for. First, feeding competition can alter rates of affiliation, aggression, and reconciliation between group-mates (Janson & van Schaik, 1988; Koenig, 2002). We controlled for variation in food abundance by including a monthly measure of ripe fruit availability in all models (the primary and preferred food item for crested macaques (O'Brien & Kinnaird, 1997; Ratna Sari, 2013). We initially included the rate of aggression given/received by the focal individual in each dyad as a control variable, but this rate was zero in all but two qualifying focal observations, so this variable was dropped to avoid model convergence problems associated with over-fitting. Second, female reproductive state can influence crested macaque social behaviour; females exhibit conspicuous sexual swellings and maximally swollen females receive less social attention (including grooming) from other females, but are groomed more by males (Clark & Melfi, 2005). They are also more likely to be herded by males, often aggressively, during IGC (Martínez-Iñigo, 2017). We controlled for this by including a variable in the dyadic social behaviour models that describes the reproductive state of the dyad as donor maximally swollen, receiver maximally swollen, or neither partner swollen. There were so few instances of both donor and receiver maximally swollen that it caused problems with model convergence, so this level was excluded. Third, a group's recent IGE win-loss record may affect how individuals in that group perceive the possibility of contact with other groups (Crofoot & Wrangham, 2010; Dugatkin, 1997). As demonstrated in Chapter 3, individuals in groups that habitually lose encounters tend to clump together in high risk areas, while those in groups that habitually win tend to spread out. To control for this, in all models we included a variable that quantified the proportion of IGEs that each group lost in the previous month. Finally, we included in all models a control variable that quantified the proportion of each observation that was available for social interaction, i.e. the proportion of time spent resting and socialising ('inactive' behaviours) as opposed to feeding and travelling ('active' behaviours). This was to account for the possibility that individuals may spend less time resting and socialising in high risk areas than safer, low risk areas (Cowlishaw, 1997), and the fact that crested macaques spend more time socialising in the morning and midday periods than the afternoon (O'Brien & Kinnaird, 1997).

4.2.7 Dyadic composite sociality index

To estimate the strength of the social bond between individuals, we used a dyadic composite sociality index (DCSI) (Sapolsky et al., 1997; Silk et al., 2013), calculated as described in section 2.10.7.

4.2.8 Dominance rank

Individual dominance ranks were determined following the procedure described in section 2.10.6.

4.2.9 Ripe fruit availability

The availability of ripe fruit was determined following the procedure described in section 2.10.4.

4.2.10 Female reproductive state

The sexual swelling state of each adult female was defined following the procedure described in section 2.10.5.

4.2.11 Intergroup encounters

Intergroup encounters were defined as described in sections 2.8.1 and 2.8.2. Because risk perception is likely to be subject to winner and loser effects (Arseneau, 2010; Cooper et al., 2004; Crofoot & Wrangham, 2010; Harris, 2006), we calculated a monthly IGE loss to win ratio for each group by dividing their number of losses by wins (see Appendix 3 for IGE summary data).

4.2.12 Relative intergroup encounter risk

Relative intergroup encounter risk was quantified following the procedure described in section 2.10.2.

4.2.13 Selection of focal observations for analysis

Risk values were assigned to each focal observation, based on the location at which that focal ended, following the procedure described in section 2.10.3.

Because the focus of our investigation was how individuals might respond to IGE risk it was crucial to compare behaviour in two contrasting risk conditions; one in which there was little to no risk of IGE, against another in which the impending probability of encountering another group was high. Observations were assigned to the low/no risk condition only when the following four criteria were met: (1) the focal individual was in a low risk area for the entire observation, (2) the entire observation occurred within at least a continuous one hour stay in the low risk area, (3) no part of the observation occurred within the final 30 minutes prior to leaving that low risk area, and (4) at no point during that day did the group experience an IGE.

Observations were assigned to the pre-high IGE risk condition only when the following four criteria were met: (1) the focal individual was in a medium risk area for the entire observation, (2) the entire observation occurred within at least a continuous 30 minute stay in the medium risk area, (3) the observation ended a maximum of 40 minutes prior to entering a high risk area, and (4) the group experienced an IGE that day, at some time after the focal observation ended. The final condition was included to ensure that these observations represented macaque behaviour prior to entering an area of genuinely high IGE risk, as evidenced by the subsequent occurrence of an actual encounter. Only focal follows in which the subject was in view for five minutes or more were included in analyses.

4.2.14 Data analysis

4.2.14.1 Probability of positive social behaviour

To test if behavioural changes in pre-high IGE risk areas supported the tension-reduction (H1) or preparing-for-conflict (H2) hypotheses, we first created a dyadic matrix of positive social behaviour (PSB) from all allogrooming, affiliation, and contact-sitting interactions between every paired combination of adult macaques. We then collapsed this into a single dyadic matrix indicating the presence or absence of any PSB between dyads. We chose this outcome measure instead of rates or proportions of individual PSBs because the three separate dyadic matrices were too sparse to compare specific behaviours in pre-high IGE risk areas to low/no risk areas. Even after this process there were no PSBs observed between male-male dyads in either risk condition. Thus, these dyads were dropped from all analyses and predictions 2B.6 and 2B.7 (see Table 4.1 above) could not be tested. However, the total absence of PSB between males strongly suggests that these predictions would not be supported.

The first full PSB model contained a three-way interaction between risk condition, dyad sex, and actor/receiver rank, however its inclusion resulted in over-fitting, which is associated with a loss of power (Bates et al., 2015). As such, to test the remaining predictions we fitted two simpler binomial generalised linear mixed models (GLMMs) (Bolker et al., 2009) with logit link functions and offsets for *observation duration*, using the ‘lme4’ package (Bates et al., 2015) in R (R Core Team, 2019). The logit link function ensures fitted values between 0 and 1, and the binomial distribution is typically used for 0/1 responses (Zuur et al., 2009). The first model (M1) examined how rank and social bond strength affected the probability of PSB between mixed sex dyads (F-M and M-F), addressing the following predictions (and strategies): 1.1, 1.2, 1.4, 1.5 (social buffering); 2A.1, 2A.2 (female incentivisation of males); 2A.4 (male sexual coercion of females); 2B.1 (female avoidance of male sexual coercion); and 2B.4 (female safety in numbers) (see Table 4.1 above). Fixed effect predictor variables in this model were: *risk condition* (factor with 2 levels); *dyad sex* (factor with 2 levels); *DCSI* (continuous); *daily actor rank* (continuous), *daily receiver rank* (continuous); and as controls: *monthly ripe fruit availability* (continuous); *daily dyad reproductive state* (factor with 3 levels); *proportion of IGEs lost in the previous month* (continuous); and *available social time per focal observation* (continuous). The interaction terms were: *risk condition x dyad sex*; *risk condition x DCSI*; *risk condition x daily actor rank*; and *risk condition x daily receiver rank*. To incorporate the dependency among observations of the same individuals within the same groups, we used *actor* nested in *group*, and *receiver* nested in *group* as crossed random intercepts. When random slopes for *risk condition* were included the models failed to converge, so these were removed. The second model (M2) examined how rank and social bond strength affected the probability of PSB between female only dyads (F-F), directly addressing predictions 2B.3 and 2B.5 (female safety in numbers strategy) (see Table 4.1 above). M2 used the same link function, offset, and random effects structure as the first, the fixed effects differed only by the exclusion of *dyad sex*.

4.2.14.2 Number of positive social behaviour partners

To test if the number of different PSB partners differed between low/no IGE risk and pre-high IGE risk conditions, we fitted two Poisson GLMMs with log link functions and offsets for *observation duration*, using the ‘lme4’ package (Bates et al., 2015) in R (R Core Team, 2019). The log link function ensures positive fitted values, and the Poisson distribution is typically used for count data (Zuur et al., 2009). The first (M3) modelled the number of different partners to whom the focal individual gave PSB, and the second (M4) how many different partners the focal individual received PSB from (M4), addressing the following predictions (and strategies): 1.3, 1.6 (social buffering); 2A.3 (female incentivisation of males); 2A.5 (male sexual coercion of females); 2B.2 (female avoidance of male sexual coercion); and 2B.6 (female safety in numbers) (see Table 4.1 above). Fixed effect predictor variables in both models were: *risk condition* (factor with 2 levels); *subject sex* (factor with 2 levels) and *daily subject rank* (continuous); and as controls: *monthly ripe fruit availability* (continuous); *daily donor/recipient reproductive state* (factor with 3 levels); *proportion of IGEs lost in the previous month* (continuous); and *available social time* *per focal observation* (continuous). The interaction terms were: *risk condition x subject sex* and *risk condition x daily subject rank.* To incorporate the dependency among observations of the same individuals within the same groups, we used *subject* nested in *group* as crossed random intercepts for both models. When random slopes for *risk condition* were included the models failed to converge so the slopes were removed (Barr et al., 2013).

4.2.14.3 Hypothesis testing and model validation

We conducted all analyses in R version 3.6.1 (R Core Team, 2019) following the general procedure described in section 2.10.8. For these analyses we used the *mixed* function from the 'afex' package (Singmann et al., 2017) to test the significance of the fixed effects, and the *confint* function to calculate profile likelihood confidence intervals around the fixed effect estimates (Bolker et al., 2009).

Model estimates and profile likelihood based confidence intervals were converted to odds ratios to aid in interpreting the values of the estimates (particularly for multi-level factors) and to show effect sizes (see section 2.10.8). Where appropriate we present the results of interaction effects graphically, in addition to presenting tables of coefficients.

Model fit and assumptions were verified following the procedure described in section 2.10.8. To assess predictor collinearity we used the *collin.diag* function of the package 'misty' (Yanagida, 2020) to derive generalised variance inflation factors ($GVIF^{(1/(2 \times d.f.))}$) for each model, which did not reveal any serious collinearity problems (Zuur et al., 2009): (largest $GVIF^{(1/(2 \times d.f.))}$: probability of PSB model (M1) = 2.74; probability of PSB model (M2) = 1.39; PSB partner number (given) model (M3) = 1.42; PSB partner number (received) model (M4) = 1.46). Before fitting the models, we z-transformed all continuous variables using the *scale* function.

4.3 Results

4.3.1 H1. Tension-Reduction Hypothesis

Considered together, the results of models M1 through M4 fail to support the tension-reduction hypothesis (H1). Contrary to Predictions 1.1 and 1.4 there was no general increase in affiliative behaviour in pre-high IGE risk areas. Rather, we found a significant decrease in the exchange of affiliative behaviour between mixed sex dyads in the pre-high IGE risk condition (M1: Fig. 4.1 and Table 4.2). Although affiliative behaviour increased between female only dyads in the pre-high IGE risk condition, the significant interaction between risk condition and receiver rank (M2: Fig. 4.2 and Table 4.3) indicates that female macaques chose partners from outside their usual cohort, contrary to Predictions 1.2 and 1.5 of the tension-reduction hypothesis (H1). We found no significant change in the number of different partners to whom macaques gave affiliative behaviour (M3: Table 4.4), however, contrary to Prediction 1.6 we observed a significant decrease in the number of different partners that male macaques received affiliative behaviour from in the pre-high IGE risk condition, compared to the low/no risk condition (M4: Fig. 4.3B and Table 4.5). Because no male-male affiliative interactions were included in these analyses it is safe to assume that fewer females gave affiliative behaviour to males in the pre-high IGE risk condition. However, as indicated by the estimated marginal means and associated confidence intervals plotted in figures 4.3A and 4.3B, we found no statistically significant evidence of a change in female partner numbers, lending partial support to Prediction 1.3.

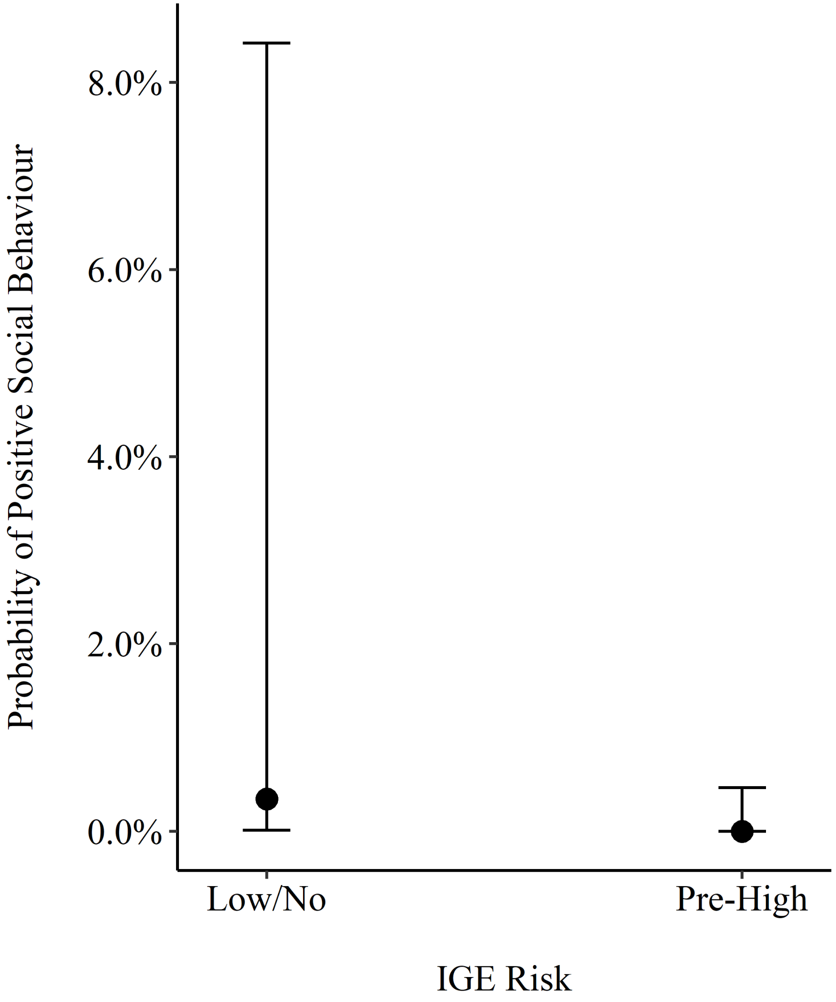

Figure 4.1 Predicted probability of PSB occurring between mixed sex crested macaques as a function of risk condition (M1). Points and error bars represent estimated marginal means and their standard errors.

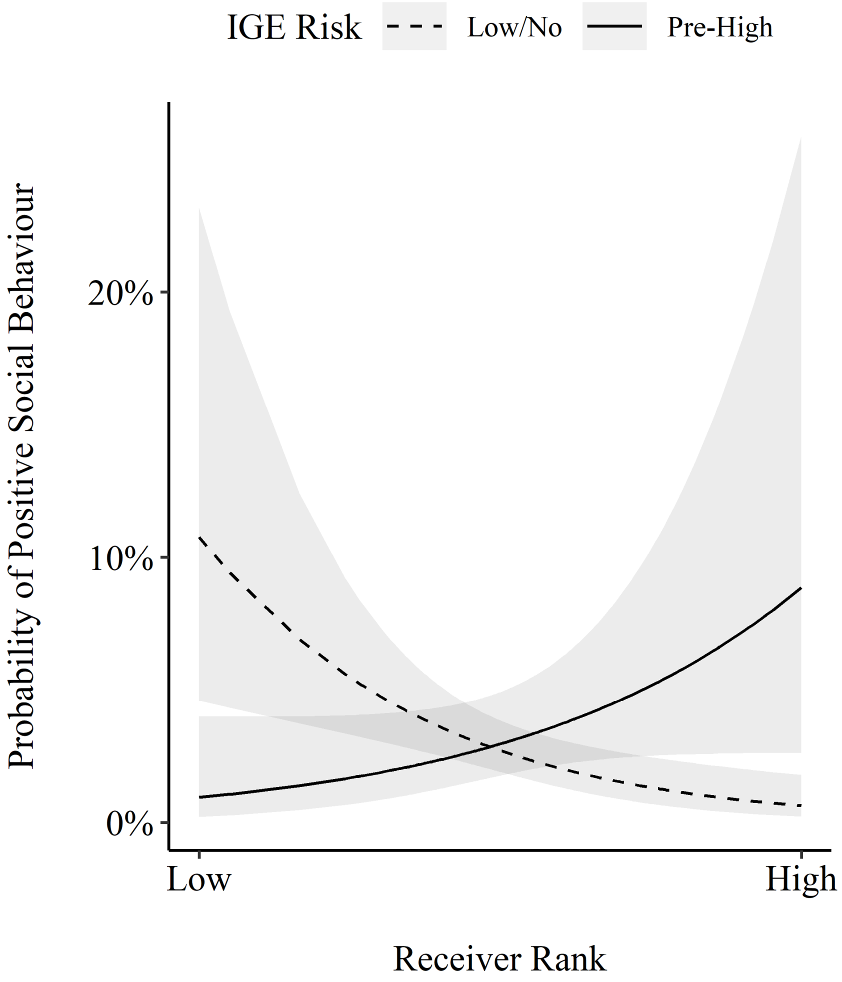

Figure 4.2 Predicted values from a multiple logistic regression of the probability of PSB occurring between female crested macaques as a function of risk condition and receiver rank (M2). Shaded grey areas represent 95% confidence intervals around estimates.

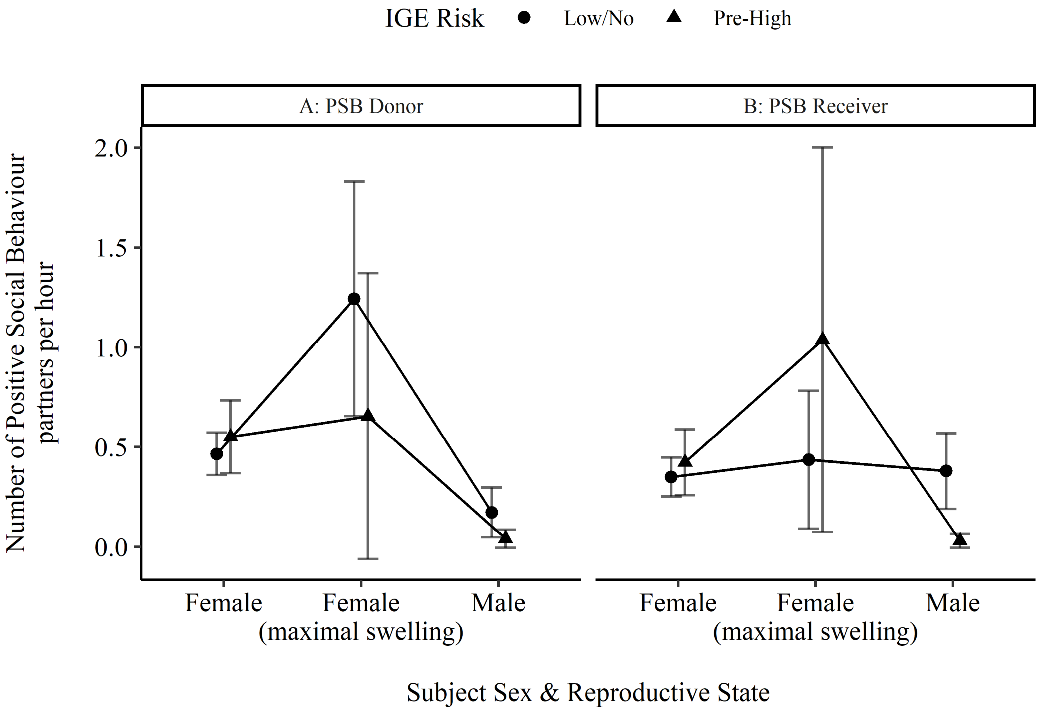

Figure 4.3 Predicted values from two GLMMs of the number of different partners that crested macaques gave (A: M3) and received (B: M4) affiliative behaviour to/from as a function of risk condition and sex/reproductive state. Shapes and error bars represent estimated marginal means and their standard errors.

4.3.2 H2. Preparing-For-Conflict Hypothesis

We found no evidence that females use affiliative behaviour to incentivise male IGE participation prior to entering high IGE risk areas (Predictions 2A.1, 2A.2, and 2A.3). This strategy predicted an increase in female-male affiliative behaviour, that females would prefer high-ranking male partners, and that females would increase the number of different males they exchanged affiliative behaviour with, at the expense of female partners. However, we found that in pre-high IGE risk areas female-male affiliative behaviour decreased (M1: Fig. 4.1 and Table 4.2), that affiliation was unaffected by receiver rank (M1: Table 4.2), and that males received affiliative behaviour from significantly fewer different female partners (M4: Fig. 4.3B and Table 4.5).

However, we did find evidence indicating that sexual coercion may play a major role in shaping patterns of affiliative behaviour among crested macaques prior to entering high IGE risk areas. This was true of both sexes. In response to aggressive male herding of females, we predicted a decrease in affiliative behaviour between the sexes (Predictions 2A.4 and 2B.1), and a decrease in the number of different mixed sex affiliative partners (Predictions 2A.5 and 2B.2). All four predictions were supported: We observed a decrease in affiliative behaviour between mixed sex dyads (M1: Fig. 4.1 and Table 4.2), and a decrease in the number of female partners from whom males received affiliative behaviour (M4: Fig. 4.3B and Table 4.5).

Finally, we found partial evidence that females seek safety in numbers prior to entering high IGE risk areas (Predictions 2B.3, 2B.4, 2B.5, and 2B.6). This strategy predicted an increase in affiliative behaviour between female dyads, that high ranking females would be preferred partners, that affiliative behaviour between the sexes would decrease, and that females would exchange affiliative behaviour with a greater number of different female partners. The first three of these predictions were supported: We found an increase in affiliation between female dyads in the pre-high IGE risk condition, specifically that high ranking females were significantly more likely to receive affiliative behaviour prior to entering high IGE risk areas than mid or low ranking females (M2: Fig. 4.2 and Table 4.3). As previously stated, this was accompanied by a decrease in affiliative behaviour between the sexes (M1: Fig. 4.1 and Table 4.2). However, we found no support for the final prediction; there was no significant increase in female affiliative partner numbers in the pre-high IGE risk condition (see estimated marginal means and confidence intervals in Fig. 4.3A and Fig. 4.3B).

Table 4.2 GLMM (M1) investigating factors affecting the occurrence of PSB between mixed sex macaque dyads in response to IGE risk.

Term	**Levels**	**Est**	**SE**	**OR**	**OR 95% CI**	**LRT**	**df**	***P* value**
Test fixed effects								
Intercept		-6.02	1.14	[a]	[a]	[a]	[a]	[a]
IGE risk	**Pre-High**	**-5.58**	**2.42**	**0.004**	**[0.00; 0.24]**	**5.07**	**1**	**0.024**
Dyad sex (F-M)	M-F	-1.37	1.29	0.25	[0.01; 2.62]	0.02	1	0.885
Dyad DCSI[b]		-3.16	2.65	0.04	[0.00; 0.66]	2.15	1	0.142
Actor rank[b]		0.81	0.62	2.25	[0.66; 8.24]	0.27	1	0.602
Receiver rank[b]		0.37	0.63	1.45	[0.41; 5.31]	0.76	1	0.384
IGE risk x Dyad sex	Pre-High x M-F	3.06	2.11	21.33	[0.41; 2285.81]	2.30	1	0.129
IGE risk x Dyad DCSI[b]		1.02	3.61	2.77	[0.00; 1664.21]	0.08	1	0.778
IGE risk x Actor rank[b]		-2.41	1.54	0.09	[0.00; 1.25]	3.06	1	0.080
IGE risk x Receiver rank[b]		-1.99	1.57	0.14	[0.00; 2.16]	1.97	1	0.778
Control fixed effects								
Proportion of IGE losses in previous month[b]		**-2.54**	**1.24**	**0.08**	**[0.01; 0.72]**	**5.19**	**1**	**0.023**
Ripe fruit availability[b]		-0.70	0.47	0.50	[0.16; 1.14]	2.95	1	0.086
Available social time[b]		**2.64**	**0.87**	**14.01**	**[3.22; 104.72]**	**16.27**	**1**	**<0.001**
Dyad reproductive state	Actor max swollen	0.88	1.43	2.41	[0.13; 45.66]	0.90	2	0.636
	Receiver max swollen	1.26	1.76	3.53	[0.08; 139.71]			
Random effects	**Variance**		**SD**					
Actor within group	2.49 x 10-15		4.99 x 10-8					
Receiver within group	0		0					

The model was run with a binomial error structure and logit link function, controlling for repeated observations within actors nested in groups, and receivers nested in groups. The table shows fixed effects parameter estimates and standard errors (Est; SE); odds ratios and their 95% profile likelihood confidence intervals (OR; OR 95% CI); and LRT statistics, degrees of freedom, and p values (LRT; df; *P* value). Also shown are random effects variance and standard deviation (Variance; SD). [a] Not shown because of having no meaningful interpretation. [b] z-transformed; mean ± SD of the original value. Statistically significant ($\alpha = 0.05$) P values are in bold. Dyad sex (F=Female, M=Male).

Table 4.3 GLMM (M2) investigating factors affecting the occurrence of PSB between female macaques in response to IGE risk.

Term	Levels	Est	SE	OR	OR 95% CI	LRT	df	*P* value
Test fixed effects								
Intercept		-4.49	0.20	[a]	[a]	[a]	[a]	[a]
IGE risk	Pre-High	[c]	[c]	[c]	[c]	[c]	[c]	[c]
Dyad DCSI[b]		0.05	0.84	1.05	[0.16; 4.81]	0.12	1	0.732
Actor rank[b]		-0.39	0.16	0.68	[0.49; 0.91]	1.15	1	0.285
Receiver rank[b]		[c]	[c]	[c]	[c]	[c]	[c]	[c]
IGE risk x Dyad DCSI[b]		-0.65	1.67	0.52	[0.01; 10.09]	0.18	1	0.675
IGE risk x Actor rank[b]		0.49	0.27	1.63	[0.97; 2.80]	3.36	1	0.067
IGE risk x Receiver rank[b]		**0.90**	**0.27**	**2.46**	**[1.45; 4.33]**	**11.28**	**1**	**<0.001**
Control fixed effects								
Proportion of IGE losses in previous month[b]		**-0.29**	**0.14**	**0.75**	**[0.57; 0.98]**	**4.58**	**1**	**0.032**
Ripe fruit availability[b]		-0.02	0.12	0.98	[0.77; 1.25]	0.02	1	0.891
Available social time[b]		**0.73**	**0.14**	**2.08**	**[1.59; 2.74]**	**32.17**	**1**	**<0.001**
Dyad reproductive state	Actor max swollen	-0.57	0.56	0.57	[0.16; 1.56]	1.14	2	0.565
	Receiver max swollen	-0.12	0.49	0.89	[0.31; 2.17]			
Random effects	**Variance**		**SD**					
Actor within group	0		0					
Receiver within group	0		0					

The model was run with a binomial error structure and logit link function, controlling for repeated observations within actors nested in groups, and receivers nested in groups. The table shows fixed effects parameter estimates and standard errors (Est; SE); odds ratios and their 95% profile likelihood confidence intervals (OR; OR 95% CI); and LRT statistics, degrees of freedom, and p values (LRT; df; *P* value). Also shown are random effects variance and standard deviation (Variance; SD). [a] Not shown because of having no meaningful interpretation. [b] z-transformed; mean ± SD of the original value. [c] Not shown because of having no meaningful interpretation in the presence of a significant interaction. Statistically significant ($\alpha = 0.05$) P values are in bold.

Table 4.4 GLMM (M3) investigating factors affecting the number of different partners to whom macaques gave affiliative behaviour in response to IGE risk.

Term	Levels	Est	SE	OR	95% CI	LRT	df	*P* value
Test fixed effects								
Intercept		-3.07	0.23	[a]	[a]	[a]	[a]	[a]
IGE risk	Pre-High	0.17	0.39	1.18	[0.55; 2.54]	1.36	1	0.243
Subject rank[b]		-0.51	0.18	0.60	[0.41; 0.85]	3.73	1	0.053
Subject sex & reproductive status	F1	0.98	0.53	2.67	[0.80; 7.07]	**12.94**	**2**	**0.002**
	M	-0.99	0.74	0.37	[0.06; 1.28]			
IGE risk x Subject rank[b]		0.20	0.40	1.22	[0.56; 2.73]	0.27	1	0.606
IGE risk x Subject sex & reproductive status	Pre-High x F1	-0.81	1.30	0.45	[0.02; 4.60]	2.24	2	0.327
	Pre-High x M	-1.60	1.28	0.20	[0.01; 2.35]			
Control fixed effects								
Proportion of IGE losses in previous month[b]		**-0.35**	**0.15**	**0.70**	**[0.52; 0.94]**	**5.70**	**1**	**0.017**
Ripe fruit availability[b]		-0.02	0.15	0.98	[0.71; 1.32]	0.02	1	0.896
Available social time[b]		**0.78**	**0.16**	**2.19**	**[1.61; 3.04]**	**27.34**	**1**	**<0.001**
Random effects	**Variance**		**SD**					
Subject within group	0		0					

The model was run with a Poisson error structure and log link function, controlling for repeated observations within subjects nested in groups. The table shows fixed effects parameter estimates and standard errors (Est; SE); odds ratios and their 95% profile likelihood confidence intervals (OR; OR 95% CI); and LRT statistics, degrees of freedom, and p values (LRT; df; *P* value). Also shown are random effects variance and standard deviation (Variance; SD). [a] Not shown because of having no meaningful interpretation. [b] z-transformed; mean ± SD of the original value. Statistically significant ($\alpha = 0.05$) P values are in bold. Subject sex & reproductive status (F0=Female, F1=Female max swelling, M=Male).

Table 4.5 GLMM (M4) investigating factors affecting the number of different partners from whom macaques received affiliative behaviour in response to IGE risk.

Term	**Levels**	**Est**	**SE**	**OR**	**OR 95% CI**	**LRT**	**df**	***P* value**
Test fixed effects								
Intercept		-3.35	0.28	[a]	[a]	[a]	[a]	[a]
IGE risk	Pre-High	[c]	[c]	[c]	[c]	[c]	[c]	[c]
Subject rank[b]		-0.62	0.21	0.54	[0.35; 0.80]	2.66	1	0.103
Subject sex & reproductive status	F1	[c]	[c]	[c]	[c]	[c]	[c]	[c]
	M	[c]	[c]	[c]	[c]			
IGE risk x Subject rank[b]		0.45	0.45	1.57	[0.66; 3.92]	1.07	1	0.30
IGE risk x Subject sex & reproductive status	Pre-High x F1	0.68	1.29	1.97	[0.14; 27.75]	**7.49**	**2**	**0.024**
	Pre-High x M	-2.71	1.19	0.07	[0.00; 3.92]			
Control fixed effects								
Proportion of IGE losses in previous month[b]		-0.35	0.17	0.71	[0.50; 1.00]	3.86	1	0.050
Ripe fruit availability[b]		0.02	0.16	1.02	[0.73; 1.40]	0.01	1	0.905
Available social time[b]		**0.96**	**0.18**	**2.61**	**[1.84; 3.83]**	**31.49**	**1**	**<0.001**
Random effects	**Variance**		**SD**					
Subject within group	0.09		0.30					

The model was run with a Poisson error structure and log link function, controlling for repeated observations within subjects nested in groups. The table shows fixed effects parameter estimates and standard errors (Est; SE); odds ratios and their 95% profile likelihood confidence intervals (OR; OR 95% CI); and LRT statistics, degrees of freedom, and p values (LRT; df; *P* value). Also shown are random effects variance and standard deviation (Variance; SD). [a] Not shown because of having no meaningful interpretation. [b] z-transformed; mean ± SD of the original value. [c] Not shown because of having no meaningful interpretation in the presence of a significant interaction. Statistically significant ($\alpha = 0.05$) P values are in bold. Subject sex & reproductive status (F0=Female, F1=Female max swelling, M=Male).

4.4 Discussion

These results show that the risk of encountering neighbouring groups influences patterns of social behaviour among wild crested macaques, and that these patterns appear to serve a strategic purpose, that cannot be explained by the tension-reduction hypothesis (H1). When faced with the risk of an IGE, macaques apportioned their social effort outside the usual cohort of partners. Had individuals continued to associate with their usual partners, even at a higher rate, this would indicate that the primary purpose of affiliative behaviour in response to the risk of IGE is to reduce physiological tension by maximising the effects of social buffering (Cheney & Seyfarth, 2009; Kikusui et al., 2006). However, both partner choice and number changed, in support of several predictions of the preparing-for-conflict hypothesis (H2) (Table 4.6). Specifically, we found evidence indicating that prior to entering high IGE risk areas, female macaques alter their social behaviour in order to minimise the occurrence/cost of male sexual coercion, and/or out-group aggression.

Sexual coercion and aggressive herding are common in primate societies (Smuts & Smuts, 1993), particularly in the context of IGEs (Arseneau-Robar et al., 2018; Cheney & Seyfarth, 1977; Sicotte, 1993). The costs can be high for females, and may include physical wounding, increased physiological stress, heightened energetic demands, and lost opportunity costs (Palombit, 2014). Injuries resulting from sexual coercion or mating have been described in a wide range of primates, including other macaques (*Macaca* spp.) (Carpenter, 1942; Enomoto, 1981; Lindburg, 1971; Teas, 1984), baboons (*Papio* spp.) (Baniel et al., 2017; Smuts, 1985), chimpanzees (*Pan troglodytes*) (Goodall, 1986; Muller et al., 2009), and atelines (*Atelidae* spp.) (Gibson et al., 2008). Several non-mutually exclusive female counterstrategies have been observed, including but not limited to: convenience polyandry (Engelhardt et al., 2006; Huchard et al., 2012), post-copulatory manipulation of reproduction/cryptic female choice (Dixson, 2002), and individual defence by sexual segregation or evasion (Brockman, 1999; Mackinnon, 1974). The results of this study strongly suggest that female crested macaques employ the latter when faced with the prospect of IGEs.

Table 4.6 Summary of hypotheses, predictions, and support provided by this study.

Hypothesis	Strategy	Predictions	Supported?
H1: Tension-reduction	Female: Social buffering	1.1 General increase in affiliative behaviour.	No
		1.2 No change in partner choice: Prefer closely bonded social partners.	No
		1.3 No change in number of different partners.	Partially
	Male: Social buffering	1.4 General increase in affiliative behaviour.	No
		1.5 No change in partner choice: Prefer closely bonded social partners.	No
		1.6 No change in number of different partners.	No
H2A: Preparing-for-conflict: Maximise individual reproductive interests	Female: Incentivise male participation	2A.1 Increase in F-M affiliative behaviour.	No
		2A.2 Prefer high-ranking male partners to mid/low-ranking male partners.	No
		2A.3 Increase in number of male partners vs female partners.	No
	Male: Sexual coercion of females	2A.4 Decrease in M-F and F-M affiliative behaviour.	Yes
		2A.5 Decrease in number of female partners.	Yes
H2B: Preparing-for-conflict: Minimise risk of injury	Female: Avoid male sexual coercion	2B.1 Decrease in F-M affiliative behaviour.	Yes
		2B.2 Decrease in number of male partners.	Yes
	Female: Safety in numbers	2B.3 Increase in F-F affiliative behaviour.	Yes
		2B.4 Decrease in F-M affiliative behaviour.	Yes
		2B.5 Prefer high-ranking female partners to mid/low-ranking female partners.	Yes
		2B.5 Increase in female partner numbers.	No

Prior to entering high IGE risk areas, affiliative behaviour between the sexes decreased. The odds of affiliative behaviour occurring between male and female macaques were approximately 100% lower in the pre-high IGE risk condition than the low/no risk condition (Fig. 4.1). Furthermore, males received affiliative behaviour from significantly fewer (female) partners. The predicted number of different partners from whom males received affiliative behaviour (per hour) in the pre-high-risk condition was 93% lower than in the low/no risk condition, dropping almost to zero (Fig. 4.3B). In common with most female-philopatric primate species, male crested macaques receive a great deal more social attention from females than other males (Gumert, 2007; Reed et al., 1997). Indeed, we observed no affiliative behaviour between males in the focal observations that were eligible for inclusion in this study. As such, the significant decrease in the number of partners from whom males received affiliative behaviour is necessarily attributable to a reduction in the number of adult females directing affiliative behaviour towards them, rather than from any change in male-male social relations. Both findings support the predictions of the preparing-for-conflict hypothesis (H2) that relate to sexual coercion.

Furthermore, we found that female macaques also altered their choice of (female) partner in pre-high IGE risk areas. As predicted by the preparing-for-conflict hypothesis (H2), individuals in the lower half of the dominance hierarchy tended to receive less affiliative behaviour in response to the risk of IGE, while high-ranking females received more (Fig. 4.2). The odds of receiving affiliative behaviour were 628% (approximately 7 times) higher for the highest ranked individual compared to the lowest in the pre-high-risk condition, and 121% higher than that of an average ranked individual, suggesting that high-ranking females are much more attractive social partners in the face of IGE risk. It is not unusual for high ranking individuals to be attractive social partners in primate societies (Schino, 2001), however, because of their highly tolerant social style, interactions between female crested macaques are largely unconstrained by rank, or even kinship (Duboscq et al., 2013, 2017). Combined with the clear preference for lower ranking females in the low/no risk condition, this suggests that females may have a specific purpose for directing PSB up the hierarchy so strongly in response to IGE risk, given that partner choice is theoretically free.

Three non-mutually exclusive strategies are predicted by the preparing-for-conflict hypothesis (H2), all of which reduce a female macaque's risk of injury prior to/during IGEs. First, because recent affiliation may increase the likelihood of agonistic support and cooperation between partners (Koyama et al., 2006; Schino, 2007)), females may choose to associate with the strongest fighters in their group. In many primate species these are likely to be high-ranking males (Franz et al., 2015; Marty et al., 2016; Marty, Hodges, Heistermann, et al., 2017), however we have shown that females tend to avoid males in the pre-high IGE risk condition. Consequently, females may choose to affiliate with the most socially powerful/attractive female partners, who are likely to be high-ranking. Second, because isolated and out-numbered adult females are the most frequent recipients of intergroup coalitionary aggression during crested macaque IGEs (Martínez-Iñigo, 2017; personal observation), the prospect of encounter risk may prompt females to seek out the most socially attractive partners to (a) reduce the likelihood of being isolated, and (b) take advantage of the dilution effect (Hamilton, 1971). Indeed, among female crested macaques, recent affiliative partners tend to be found in close proximity even after the interaction has ended (Aureli & Yates, 2010). Finally, females in many primate species direct affiliative behaviour preferentially towards high-ranking males (Reed et al., 1997; Schino, 2001; Seyfarth, 1978), however because females avoid males in the pre-high IGE risk condition (as predicted by the preparing-for-conflict hypothesis (H2)) it is possible that high-ranking females become available as social partners, which could also account for the observed increase in affiliative behaviour directed towards them.

Taken together the results of the PSB probability and partner number models suggest (a) a strategic change in patterns of social behaviour between crested macaques in response to IGE risk, and (b) that the change in female affiliative behaviour functions to minimise risk of injury; from in-group males and/or out-group aggressors. Resident females appear to avoid males to reduce the risk of aggressive herding, whilst preferentially associating with high-ranking females for social/agonistic/numerical support; when they become available as partners.

Following recent work by LaBarge et al. (2020), this study is one of the first to investigate pre-emptive social responses to the threat of IGE in a wild primate species; notably, one belonging to a genus (*Macaca*) in which the capacity for future planning is generally thought to be limited (Beran et al., 2004; Bourjade et al., 2012; Dekleva et al., 2012; Scarf et al., 2011). Although complex planning may not be required to explain these results, they do indicate that crested macaques remember where they previously encountered rivals and adjust their behaviour accordingly. It would be adaptive for animals to remember locations where they recently experienced danger, and to alter their behaviour when next in or around that area.

Evidence from a limited few other primate species demonstrates this with respect to predator encounters: After captive marmosets (*Callithrix geoffroyi*) were presented with a snake model in the evening, the next day they were significantly more vigilant in the area where the model was seen (Hankerson & Caine, 2004). Similarly, presentation of a stuffed python at a favoured sleeping site deterred long-tailed macaques (*Macaca fascicularis*) from using that site for at least 12 days, whilst periodically "checking" it while travelling to another tree (van Schaik & Mitrasetia, 1990); And moustached tamarins (*Sanguinus mystax*) avoided the site of a snake attack for two days before returning to feed there on every observation day for the following three months (Tello et al., 2002). However, examples of primates altering their social behaviour in response to IGE risk on the same fine temporal scale are very rare.

Although several studies provide evidence of changes in activity budget, space-use, and/or social behaviour (Benadi et al., 2008; Lewis, 2006; Mirville et al., 2020; Tórrez-Herrera et al., 2020; Wrangham et al., 2007; Yi et al., 2020), these generally focus on behaviour along territorial borders, or in areas of home range overlap. Primate home ranges are usually relatively static, and although dramatic shifts can occur, they tend to be infrequent (Mitani et al., 2010; Scarry & Tujague, 2012). As such, it is possible that animals alter their behaviour because these areas are less familiar to them and/or their older conspecifics do so (Clarke et al., 1993; Isbell, 1990), rather than as a pre-emptive response to IGE risk. However, by using the timing and locations of actual IGEs to create monthly relative IGE risk maps, we were able to assess (a) whether crested macaques remembered the locations of recent IGEs anywhere within their home range, (b) whether they altered their social behaviour in these areas, and crucially (c) whether those changes could be characterised as reactive (intended to reduce the stress of being in a potentially risky area), or pre-emptive (intended to maximise individual benefits and/or minimise individual costs of potential encounters). In doing so these results provide novel evidence in support of the hypothesis that between group contest competition has an important role in shaping primate social behaviour (Alexander & Borgia, 1978; Choi & Bowles, 2007; Hamilton, 1975; Puurtinen & Mappes, 2009).

Further studies could attempt to collect more data on two key dyad combinations. Specifically, male-male dyads and female-female dyads in which both partners were maximally swollen. We only had a limited amount of data for these dyads, primarily because they interacted so infrequently, but even these had to be excluded from analysis to meet the rigorous data selection criteria; the purpose of which was to compare social behaviour in two greatly contrasting risk contexts. Although social interaction between male crested macaques is rare, it is possible that by allowing more focal observations into the analyses, the responses of these two dyad types could be more closely examined and the role of males in shaping the group-wide response to IGE risk could be more clearly understood. This is particularly relevant given the importance of considering the different fitness-maximising strategies of females and males in IGE studies (Arseneau-Robar et al., 2017; Kitchen & Beehner, 2007; Majolo et al., 2005; Trivers, 1972). Without a complete picture of how male crested macaques behave under these circumstances it is difficult to be certain whether the female response (avoid males in favour of high-ranking females) is actually a consequence of the fact that (some) adult males are often absent during and immediately prior to IGEs (because they are engaged with the other group in some way) (Martínez-Iñigo, 2017; personal observation), or whether the female response is part of a strategy to minimise potential injury as proposed here. Future studies would benefit from a larger number of observers to more precisely record which males participate, which stay with the group, and which of those aggressively herd females during IGEs. With this information it might be possible to understand whether the female pre-emptive strategies observed here are a response to the general threat of male sexual coercion prior to/during IGEs, or a response to the specific social milieu that results from differential male participation in IGEs.

In sum, this study demonstrates that crested macaques remember the timing and locations of recent encounters with rival groups, and that in response to the threat of IGEs they alter their social behaviour in ways that minimise the potential costs associated with these events. The evidence for this is relatively unambiguous for female macaques, however, the forces that motivate male preparatory behaviour are still unclear. These data are most consistent with the preparing-for-conflict hypothesis (H2), in which individuals make strategic changes in the allocation of their social effort, rather than the tension-reduction hypothesis (H1) in which individuals focus on their usual cohort of preferred partners. Comparisons with other female-philopatric primates suggest that the unusually tolerant social style of female crested macaques may be a key component in the realisation of their pre-emptive strategy; allowing them a relatively unconstrained choice of partner with whom to aggregate in response to the dual threat (internal and external) posed by IGEs.

Chapter 5

Impacts of intergroup conflict on intragroup social behaviour in wild crested macaques (*Macaca nigra*)

James O. Waterman, Muhammad Agil, Antje Engelhardt, Eka Arismayanti, Bonaventura Majolo, Nicola F. Koyama[3]

This chapter has been formatted for submission to Behavioural Ecology

Abstract

Group-living animals face a variety of threats from rival groups and recent work indicates that intergroup conflict (IGC) can affect subsequent intragroup behaviour in a range of species, even after conflict has ended. Because intergroup hostility is often associated with the evolution of cooperative behaviour many studies have focused on behaviours that promote cohesion and cooperation within groups. However, the function of post-conflict social behaviour remains unclear because results differ considerably by species, social system, and competitive regime. Here, we studied the intragroup social behaviour of three wild groups of crested macaques (*Macaca nigra*) following IGC to test the hypotheses that post-conflict behaviour functions to (a) relieve tension, (b) increase group cohesion, and/or (c) incentivise future participation. The previous chapters of this thesis used risk maps derived from the previous month's intergroup encounters, however this chapter focuses on behavioural responses in the aftermath of actual IGC. We used generalised linear mixed models to compare levels and patterns of self-directed, affiliative, and aggressive behaviour in the three hours after IGC to those at baseline, whilst controlling (where appropriate) for the effects of preferred resource availability, available social time, rank, and dyad sex, reproductive state, and social bond strength.

---

[3] Author contributions: JW, NK, and BM conceived the study. JW, NK, BM, and AE designed the study. JW and EA collected data. JW analysed data and wrote the manuscript. JW, NK, and BM revised manuscript drafts. MA and AE stewarded the field project of which this study was a part.

Contrary to all predictions we found that affiliative behaviour decreased in the immediate (one hour) aftermath of conflict. Self-scratching (a behavioural indicator of anxiety) increased in the hour following conflict; dyads in losing groups exchanged more affiliative behaviour than those in winning groups; individuals focused their post-conflict affiliative effort on their usual (strongly bonded) social partners; and conflict participation had no effect on the giving or receiving of affiliation or aggression. These results are consistent with studies of many other social species which suggest that IGC results in increased anxiety. However, we found no evidence that crested macaques use affiliative or aggressive behaviour to enhance group cohesion or to punish/reward group-mates following IGC. Rather, these findings indicate that in crested macaques the primary function of post-conflict social behaviour may be to relieve the associated physiological stress.

5.1 Introduction

Intergroup conflict (IGC) occurs in many social species and exerts a powerful selective force on intragroup social behaviour (Bowles, 2009; Hamilton, 1975; Majolo et al., 2016; Puurtinen & Mappes, 2009). In the long-term, theoretical models predict that intense conflict between groups favours the selection of behavioural traits within groups that amplify intergroup aggression and intragroup cooperation (Alexander & Borgia, 1978; Choi & Bowles, 2007). However, recent work on human and non-human animals indicates that IGC can also affect the immediate, short-term behaviour of individuals, even after the conflict has ended (Burton-Chellew et al., 2010; Mirville et al., 2020; Radford et al., 2016; Thompson et al., 2020). Much of this work has focussed on the influence of IGC on behaviours that promote cohesion and cooperation within groups (the ‘conflict-cohesion hypothesis’), both of which improve the odds of victory (Birch et al., 2019; Crofoot & Gilby, 2012; De Dreu et al., 2016; Nunn & Lewis, 2001). Indeed, several non-human animal studies have found evidence that exposure to, or conflict with rival groups increases social cohesion, as measured by affiliative behaviours such as allogrooming or body-contact (Radford et al., 2016). However, others report reduced affiliative behaviour, increased intragroup aggression, and/or no change at all (Radford et al., 2016). These mixed results suggest that the ‘conflict-cohesion hypothesis’ is not universally applicable, and that the function of post-IGC social behaviour differs by at least species, social system, and competitive regime.

Among these recent non-human animal studies, the strongest support for the 'conflict-cohesion hypothesis' comes from those that focus on post-IGC behaviour in cooperatively breeding species and eusocial insects, i.e. species with social systems characterised by extreme social tolerance and/or cooperation (Andersson, 1984; Kappeler & Silk, 2010). For example, social cohesion increased following IGC in green woodhoopoes (*Phoeniculus purpureus*) (Radford, 2008a, 2008b; Radford & Fawcett, 2014), cichlid fish (*Neolamprologus pulcher*) (Bruintjes et al., 2016), dampwood termites (*Zootermopsis angusticollis*) (Thompson et al., 2020), harvester ants (*Messor barbarous*) (Birch et al., 2019), and dwarf mongooses (*Helogale parvula*) (Morris-Drake et al., 2019). A similar study of banded mongooses (*Mungos mungo*) failed to find evidence of an increase in social cohesion, but did observe a decrease in male-female aggression following IGC (Preston et al., 2020). Finally, IGC also led to post-conflict increases in intragroup affiliation among Wied's black tufted-ear marmosets (*Callithrix kuhli*) (Schaffner & French, 1997), one of very few cooperatively breeding non-human primates (hereafter primates) (Burkart & van Schaik, 2010).

In contrast, among non-cooperatively breeding (and non-eusocial) species post-IGC behavioural responses are more varied and support for the 'conflict-cohesion hypothesis' is less compelling. Most of these studies focus on post-IGC affiliation and aggression in primate species, with mixed results. Several studies found that IGC had no significant effect on post-conflict affiliation or aggression at all (patas monkeys (*Erythrocebus patas*) (Chism & Rogers, 2004); ringtailed lemurs (*Lemur catta*) (Nunn & Deaner, 2004); and vervet monkeys (*Chlorocebus pygerythrus*) (Cheney, 1992)). A recent study of Javan gibbons (*Hylobates moloch*) even observed a decrease in pair-grooming following IGC (Yi et al., 2020). Furthermore, although numerous studies have reported significant changes in affiliative and aggressive intragroup behaviour following IGC, because no detailed data were available on partner choices and/or how these might relate to participation, it has not been possible to draw firm conclusions about the function of post-IGC behaviour from these studies. For example, allogrooming increased among blue monkeys (*Cercopithecus mitis*) (Cords, 2002), samango monkeys (*C. albogularis erythrarchus*) (Payne, Henzi, et al., 2003), and mountain gorillas (*Gorilla beringei beringei*) (Mirville et al., 2020) following IGC; but without partner choice information these increases only circumstantially support the 'conflict-cohesion hypothesis'. There are other potentially more parsimonious explanations. For example, IGC is known to cause substantial stress among primates. Chimpanzee (*Pan troglodytes*) IGC is associated with increased hypothalamic-pituitary-adrenal (HPA) axis activity (the physiological system most associated with stress (Novak et al., 2013)) (Samuni, Preis, et al., 2019; Wittig et al., 2016), Therefore, it is possible that, as with intragroup conflict, one potential function of post-IGC affiliation is to reduce anxiety and stress (which may manifest as increased intragroup aggression (e.g. Polizzi di Sorrentino, Schino, Massaro, et al., 2012)) (Kikusui et al., 2006; Radford et al., 2016): the 'tension-reduction hypothesis'.

Only a small number of studies have examined post-IGC social behaviour at a level of detail that allows firm conclusions to be drawn, and these indicate another possible function of post-IGC social behaviour: to incentivise the continued/future participation of group-mates (the 'social incentive hypothesis') (Arseneau-Robar et al., 2016; Cooper et al., 2004). For example, between episodes of intergroup aggression, female vervet monkeys (*Chlorocebus pygerythrus)* groomed males that had participated in the previous bout and aggressed those that had not (Arseneau-Robar et al., 2016). In subsequent aggressive bouts, these males participated at a level exceeding their personal baseline. Similarly, female bonnet macaques (*Macaca radiata*) groomed and mated more with participating than non-participating males, suggesting that they may have been rewarding IGC combatants (Cooper et al., 2004). However, no data were available on whether this influenced participation in subsequent IGC. Thus, there appear to be at least three plausible non-mutually exclusive hypotheses to explain the function of post-IGC social behaviour: 'conflict-cohesion', tension-reduction', and 'social incentive' (Radford et al., 2016).

Here, we investigate how IGC affects post-conflict intragroup behaviour in three groups of wild crested macaques (*Macaca nigra*) in Tangkoko Nature Reserve (TNR), Sulawesi, Indonesia. Crested macaques live in multi-male, multi-female (philopatric) groups of variable size. Although they are non-territorial they are a particularly suitable species in which to investigate the function of post-IGC social behaviour because (a) they have relatively stable, overlapping home ranges, (b) they have frequent intergroup encounters (IGEs) (Martínez-Iñigo, 2017), (c) both male and female macaques participate, and (d) female crested macaques have an unusually tolerant social style (Duboscq et al., 2013, 2017). This is important because the link between IGC and intragroup dynamics may be more pronounced and/or visible in species in which social interactions can occur between a broad range of individuals, largely unconstrained by rank or kinship.

In this study, we compare social and self-directed behaviour in the three hours following IGC to baseline levels and ask to what extent can any changes in occurrence and/or pattern be explained by the following three hypotheses: the 'conflict-cohesion' (H1), 'tension-reduction' (H2), and 'social incentive' (H3) hypotheses. These are not mutually exclusive, and we outline predictions for each (summarised in Table 5.1). When evaluating these predictions it is important to consider that individuals may have relatively inflexible time budgets and thus limited time each day for social activities (e.g. allogrooming; a key affiliative behaviour among primates) (Chism & Rogers, 2004). As such, it is useful to explore not only general increases/decreases in post-IGC social behaviour, but also/rather changes in how individuals allocate their social effort.

According to the 'conflict-cohesion' hypothesis (H1), the primary function of social behaviour following IGC is to increase group-wide social cohesion. Under this scenario, group-wide rates of affiliation should increase (Prediction 1.1) and members should affiliate with many individuals across the group (Prediction 1.2) rather than focusing on a few already well-bonded partners (Prediction 1.3), or on recent IGC combatants (Prediction 1.4) (Radford et al., 2016; Samuni, Mielke, et al., 2019). Furthermore, because intragroup aggression can have a destabilising effect on social cohesion (Flack et al., 2005; Wey & Blumstein, 2010), individuals may try to increase/maintain group cohesion by reducing intragroup aggression (Prediction 1.5).

According to the 'tension-reduction' hypothesis (H2), the primary function of social behaviour following IGC is to reduce stress and anxiety. Self-scratching is a well-established indicator of anxiety in primates (Maestripieri et al., 1992), including crested macaques (Neumann et al., 2013), and increases during ringtailed lemur territorial conflicts (Nunn & Deaner, 2004). If crested macaque encounters are similarly stressful, self-scratching should increase following IGC (Prediction 2.1), particularly in defeated groups (Prediction 2.2) given that losing is likely to be more stressful than winning (Radford, 2008b). In order to maximise the anxiolytic effects of social buffering (Kikusui et al., 2006) group-wide affiliation should increase (Prediction 2.3), particularly following lost conflicts (Prediction 2.4). Individuals should also affiliate with a select few partners (Prediction 2.5), those with whom they have the strongest social bonds (Prediction 2.6) (Young et al., 2014), rather than focusing on recent IGC combatants (Prediction 2.7). While the anxiety arising from IGC may result in post-conflict increases in intragroup aggression (Prediction 2.8) (Polizzi di Sorrentino, Schino, Massaro, et al., 2012), particularly among losing groups (Prediction 2.9) (Radford et al., 2016), the ‘tension-reduction’ hypothesis (H1) predicts that by buffering anxiety levels, increased post-IGC affiliative behaviour may inhibit this rise in aggression (Prediction 2.10).

Finally, according to the ‘social incentive’ hypothesis (H3) the primary function of social behaviour following IGC is to encourage future participation among group mates (Arseneau-Robar et al., 2016; Radford et al., 2016, p. 206). Under this scenario, post-IGC affiliative behaviour serves to reward combatants, and aggressive behaviour to punish non-combatants. As such, although no overall change in levels of affiliative (Prediction 3.1) and aggressive (Prediction 3.2) behaviour may occur, the affiliative behaviour that does occur should be preferentially focused on a small number of individual combatants (Predictions 3.3 and 3.4), and aggressive behaviour towards non-combatants (Prediction 3.5), regardless of existing social bond strength (Prediction 3.6).

Table 5.1 Hypotheses to test the function of post-IGC social interactions relative to baseline conditions.

Hypothesis	**Predictions**	**Rationale**
H1: Conflict-cohesion	1.1 Post-IGC affiliation rates are higher than baseline rates.	Affiliation reinforces social bonds between group-mates and increases social cohesion.
	1.2 Post-IGC, macaques affiliate with more partners than at baseline.	To promote group-wide social cohesion, individuals affiliate with many different partners, rather than focusing their social effort on a specific subset.
	1.3 Post-IGC affiliation rates are independent of social bond strength between individuals.	
	1.4 Post-IGC affiliation rates are independent of IGC participation.	
	1.5 Post-IGC aggression rates are lower than baseline rates.	Intragroup aggression disturbs in-group relationships and cohesion, potentially reducing the probability of cooperation and coalitionary support in future IGC.
H2: Tension-reduction	2.1 Post-IGC self-scratching rates are higher than baseline rates.	IGC is a stressful occurrence that induces anxiety and self-scratching is a reliable indicator of anxiety among macaques.
	2.2 Post-IGC self-scratching rates are higher among groups that lose than groups than win.	Losing an IGC causes more physiological stress than winning one.
	2.3 Post-IGC affiliation rates are higher than baseline rates.	Affiliative behaviour can buffer the effects of increased anxiety following stressful events.
	2.4 Post-IGC affiliation rates are higher among groups that lose than groups than win.	Losing an IGC causes more physiological stress than winning one.
	2.5 Post-IGC, macaques affiliate with fewer partners than at baseline.	Individuals focus their social effort on a small subset of group-mates (those with whom they have the strongest social bonds).
	2.6 Post-IGC affiliation rates are higher between group members with strong social bonds.	The anxiolytic effects of affiliation are maximised with strongly bonded social partners.
	2.7 Post-IGC affiliation rates are independent of IGC participation.	The receipt of post-IGC affiliation is linked primarily to the strength of pre-existing social bonds, not to IGC participation.
	2.8 Post-IGC aggression rates are higher than baseline rates.	Intragroup aggression may be a consequence of redirected aggression and/or increased stress/anxiety following IGC.
	2.9 Post-IGC aggression rates are higher among groups that lose than groups than win.	Losing an IGC causes more physiological stress than winning one.

Table 5.1 continued

Hypothesis	**Predictions**	**Rationale**
	2.10 Post-IGC aggression rates do not differ from baseline rates.	Post-IGC affiliation may inhibit a rise in aggression.
H3: Social incentive	3.1 Post-IGC affiliation rates do not differ from baseline rates.	Rather than engaging in more/less social behaviour, individuals focus their post-IGC social effort on a subset of group-mates.
	3.2 Post-IGC aggression rates do not differ from baseline rates.	
	3.3 Post-IGC, macaques affiliate with fewer partners than at baseline.	Individuals focus their social effort on a small subset of group-mates (combatants).
	3.4 IGC combatants receive more post-IGC affiliation than non-combatants.	Combatants are rewarded for their participation with social services (affiliation, grooming etc.).
	3.5 IGC non-combatants receive more post-IGC aggression than combatants.	Non-combatants are punished for their failure to participate.
	3.6 Post-IGC affiliation rates are independent of social bond strength between individuals.	The receipt of post-IGC affiliation is linked primarily to IGC participation, not to the strength of pre-existing social bonds.

5.2 Methods

We studied the behaviour and ranging patterns of crested macaques living in three neighbouring groups in the TNR, Sulawesi, Indonesia, from March 2018 through June 2019.

5.2.1 Ethical statement

See section 2.1.

5.2.2 Study site

See section 2.2.

5.2.3 Study subjects

See section 2.3.

5.2.4 Data collection

See section 2.4.

5.2.5 Behavioural sampling

See section 2.7.1.

5.2.6 Control variables

Because feeding competition can alter rates of affiliation, aggression, and reconciliation between primates (Janson & van Schaik, 1988; Koenig, 2002) we included a monthly measure of ripe fruit availability (the primary and preferred food item for crested macaques (O'Brien & Kinnaird, 1997; Ratna Sari, 2013) as a control variable in all social behaviour (affiliation and aggression) models. Dominance rank was included in all analyses to control for (a) the effect of rank on self-scratching in primates (Troisi & Schino, 1987; Whitehouse et al., 2017), and (b) the effect of rank on social attraction (Schino, 2001). Sex and female reproductive state can also influence crested macaque social behaviour; rates of social behaviour differ considerably between dyad sex combinations in crested macaques (Reed et al., 1997). For example, social interactions between adult males are rare, and maximally swollen females receive less social attention (including grooming) from other females, but are groomed more by males (Clark & Melfi, 2005). Swollen females are also more likely to be victims of aggressive sexual coercion (Martínez-Iñigo, 2017).

We accounted for this by including a composite control variable that specifies subject/dyad sex and subject/dyad reproductive status (S-RS) by combining the levels female (F0), female-maximally swollen (F1), and male (M). For example, a maximally swollen female subject is coded as 'F1' and a male-female (not maximally swollen) dyad is coded as 'M-F0' . Where appropriate we also included a measure of the social bond strength between partners as a control because strongly bonded dyads are more likely to associate with each other than weakly bonded dyads (Duboscq et al., 2013). Finally, we included in all models a control variable that quantified the proportion of each observation that was available for social interaction, i.e. the proportion of time not spent feeding or travelling.

5.2.7 Dyadic composite sociality index

We quantified the strength of the social bond between individuals using a dyadic composite sociality index (DCSI) (Sapolsky et al., 1997; Silk et al., 2013), calculated as described in section 2.10.7.

5.2.8 Dominance rank

We determined individual dominance ranks as described in section 2.10.6.

5.2.9 Ripe fruit availability

The availability of ripe fruit was estimated following the procedure described in section 2.10.4.

5.2.10 Female reproductive state

We specified the sexual swelling state of each adult female as described in section 2.10.5.

5.2.11 Intergroup encounters and outcome

Intergroup encounters were defined as described in sections 2.8.1 and 2.8.2. For these analyses, only encounters with a clear winner or loser were included in analyses (N = 231). We considered an encounter to have finished at the time of the last intergroup behavioural exchange and/or when the groups were out of sight of each other.

5.2.11.1 Intergroup encounter participation

Visibility permitting, we recorded the identity and behaviour of any participating individuals on an all-occurrence basis (see section 2.8.3). From a total of 183 recorded IGEs (see Appendix 3 for IGE summary data), full participation data were unavailable for 67 (36.6%) of these. The focal observations that followed these encounters were excluded from analyses that examined the effect of participation on post-IGE behaviour; they were retained for all other analyses.

5.2.12 Selection of focal observations for analysis

In order to test predictions about the function of post-IGC social behaviour it was crucial to establish a baseline condition against which to compare behaviour in the hours following IGC. Commonly, this would be the hour immediately before an IGC because it controls for several specific variables such as food abundance, terrain, and weather conditions, and because this is a regularly used baseline in other post-IGC behaviour studies: However, we previously demonstrated (Chapter 4) that crested macaques alter their behaviour prior to entering areas where IGEs are most likely to occur. One of the criteria for inclusion in the previous investigation was that the group experienced an IGE that day, at some time after the focal observation ended. In some cases, this occurred within an hour of the high-risk focal observation ending. As such, using the hour before an IGC as the baseline condition for the current analysis would unavoidably include “preparatory” high-risk focal observations that had already been found to be affected by impending IGE risk. We therefore decided to use the same baseline focal observations as the previous analysis (see section 4.2.13), which had already been shown to be a robust baseline sample of crested macaque behaviour in areas of little or no IGE risk.

Focal observations were assigned to the baseline risk condition only when the four criteria described in section 4.2.13 were met. Focal observations were assigned to the post-IGC condition only when the following two criteria were met: (1) the observation started within a three hour window following the end of an IGC, and (2) the group did not experience another IGC within that three hour window. Only focal follows in which the subject was in view for five minutes or more were included in analyses.

5.2.13 Data analysis

5.2.13.1 Self-scratching behaviour

To test whether macaques scratched more frequently in the three hours post-IGC than in the baseline condition (Prediction 2.1), we first ran a negative binomial generalised linear mixed model (GLMM) with a log link function and an offset for *observation duration* (M1). The log link function ensures positive fitted values, and the negative binomial distribution is appropriate for overdispersed count data (Zuur et al., 2009). We specified *self-scratching frequency* per individual as the dependent variable; *IGC condition* (factor with 4 levels: baseline vs. 1, 2, and 3 hours post-IGC) as the independent variable; and *daily subject rank* (continuous) as a control variable. To incorporate the dependency among observations of the same individuals within the same groups, we included random intercepts for *subject* nested in *group*. No random slopes were specified because their inclusion resulted in model convergence problems.

Second, to test whether IGC outcome affected post-conflict self-scratching frequency (Prediction 2.2), we used another negative binomial GLMM (M2), with a log link function and an offset for *observation duration*, to examine self-scratching in post-IGC hours only. A post-IGC model was needed because no outcome (the key variable of interest in Prediction 2.2) could be associated with the baseline condition. We specified *self-scratching frequency* per individual as the dependent variable; *IGC condition* (factor with 3 levels: 1, 2, and 3 hours post-IGC) and *outcome* (factor with 2 levels: lose vs. win) as independent variables; and *daily subject rank* (continuous) as a control variable. We included the two-way interaction *IGC condition x outcome*; and random intercepts for *subject* nested in *group*. No random slopes were specified because, as with the first self-scratching model, their inclusion resulted in model convergence problems.

5.2.13.2 Affiliative behaviour within dyads

To examine the effects of IGC on affiliative behaviour we created a dyadic matrix of all allogrooming, affiliation, and contact-sitting interactions between every paired combination of adult macaques. We then collapsed this into a single dyadic matrix indicating the presence or absence of any positive social behaviour (PSB) between these dyads. We used the *number of different PSB partners* an individual interacted with as the dependent variable in the PSB partner model (model M3), and the *presence/absence of PSB* (yes vs. no) as the dependent variable in both PSB rate models (M4 and M5). *Presence/absence of PSB* was chosen instead of rates or proportions of individual behaviours because the three separate dyadic matrices were too sparse to effectively compare specific affiliative behaviours.

First, to test whether macaques exchanged PSB with more or fewer partners following IGC (Predictions 1.2, 2.5, and 3.3) we fit a negative binomial GLMM with a log link function and an offset for *observation duration* (M3). We specified the *number of different PSB partners* as the dependent variable; *IGC condition* (factor with 4 levels: baseline vs. 1, 2, and 3 hours post-IGC) as the independent variable; *daily subject rank* (continuous), *daily subject S-RS* (factor with 3 levels: M, F0, F1), *monthly ripe fruit availability* (continuous), and *available social time per focal observation* (continuous) as control variables; and random intercepts for *subject* nested in *group*. No random slopes were specified because their inclusion resulted in model overfitting.

Second, to test whether the probability of dyads exchanging PSB changed following IGC (Predictions 1.1, 2.3, and 3.1) we fit a binomial GLMM with a logit link function and an offset for *observation duration* (M4). The logit link function ensures fitted values between 0 and 1, and the binomial distribution is typically used for 0/1 responses (Zuur et al., 2009). We specified the *occurrence of PSB* (yes vs. no) as the dependent variable; *IGC condition* (factor with 4 levels: baseline vs. 1, 2, and 3 hours post-IGC) as the independent variable; and *daily dyad S-RS* (factor with 7 levels: F0-F0, F0-F1, F0-M, F1-F0, F1-M, M-F0, M-F1 (M-M and F1-F1 combinations were dropped because very few were present in the data and their inclusion destabilised the model)), *DCSI* (continuous), *daily actor rank* (continuous), *daily receiver rank* (continuous), *monthly ripe fruit availability* (continuous), and *available social time per focal observation* (continuous) as control variables. To incorporate the dependency among observations of the same individuals within the same groups, we included *actor* nested in *group*, and *receiver* nested in *group* as crossed random intercepts. No random slopes were specified because their inclusion resulted in model convergence problems.

Third, we examined how IGC outcome (Prediction 2.4), social bond strength (Predictions 1.3, 2.5, 3.6), and participation in IGC (Predictions 1.4, 2.6, 3.4) affected the probability of dyads exchanging PSB in the two hours following IGC. The third hour post-IGC was excluded because there were no recorded instances of IGC participants giving or receiving PSB during this period. Using only post-IGC data with complete participant information, we fit a binomial GLMM with a logit link function and an offset for *observation duration* (M5). As with the previous PSB model, we used the *occurrence of PSB* (yes vs. no) as the dependent variable; *IGC condition* (factor with 2 levels: 1 and 2 hours post-IGC), *outcome* (factor with 2 levels), *DCSI* (continuous), *actor combatant* (factor with 2 levels; yes vs. no), and *receiver combatant* (factor with 2 levels; yes vs. no) as independent variables; and *daily dyad S-RS* (factor with 7 levels: F0-F0, F0-F1, F0-M, F1-F0, F1-M, M-F0, M-F1), *daily actor rank* (continuous), *daily receiver rank* (continuous), *monthly ripe fruit availability* (continuous), and *available social time per focal observation* (continuous) as control variables. The interaction terms *IGC condition x outcome*, *IGC condition x DCSI*, *IGC condition x actor combatant*, and *IGC condition x receiver combatant* were included. To incorporate the dependency among observations of the same individuals within the same groups, we included *actor* nested in *group*, and *receiver* nested in *group* as crossed random intercepts. No random slopes were specified because their inclusion resulted in model convergence problems.

5.2.13.3 Aggressive behaviour within dyads

To examine the effects of IGC on intragroup aggression, we created a dyadic matrix of aggressive behaviour between every paired combination of adult macaques. We used the *presence/absence of aggression* (yes vs. no) as the dependent variable instead of the frequency of aggressive behaviour because this rarely exceeded one per focal observation.

First, to test whether IGC affected the rate of post-conflict intragroup aggression (Predictions 1.5, 2.8, 2.10, and 3.2) we used a binomial GLMM with a logit link function and an offset for *observation duration* (M6). We specified the *occurrence of aggressive behaviour* (yes vs. no) as the dependent variable; *IGC condition* (factor with 4 levels: baseline vs. 1, 2, and 3 hours post-IGE) as the independent variable; and *daily dyad S-RS* (factor with 7 levels: F0-F0, F0-F1, F0-M, F1-F0, F1-M, M-F0, M-F1), *DCSI* (continuous), *daily actor rank* (continuous), *daily receiver rank* (continuous), *monthly ripe fruit availability* (continuous), and *available social time* *per focal observation* (continuous) as control variables. To incorporate the dependency among observations of the same individuals within the same groups, we included *actor* nested in *group*, and *receiver* nested in *group* as crossed random intercepts. Random slopes were omitted because their inclusion resulted in model convergence problems.

Finally, we examined how IGC outcome (Prediction 2.9), and participation in IGC (Predictions 3.4 and 3.6) affected the probability of post-conflict intragroup aggression between dyads. We used a binomial GLMM with a logit link function and an offset for *observation duration* (M7). We used the *occurrence of aggression* (yes vs. no) as the dependent variable; *outcome* (factor with 2 levels), *actor combatant* (factor with 2 levels; yes vs. no), and *receiver combatant* (factor with 2 levels; yes vs. no) as independent variables; and *DCSI* (continuous), *daily dyad S-RS* (factor with 8 levels: F0-F0, F0-F1, F0-M, F1-F0, F1-M, M-F0, M-F1, M-M), *daily actor rank* (continuous), *daily receiver rank* (continuous), *monthly ripe fruit availability* (continuous), and *available social time per focal observation* (continuous) as control variables. We also included the interaction term *IGC condition x outcome*. The interaction effects *IGC condition x actor combatant*, and *IGC condition x receiver combatant* were omitted because these data were sparse, and their inclusion led to model convergence failures. To incorporate the dependency among observations of the same individuals within the same groups, we included *actor* nested in *group*, and *receiver* nested in *group* as crossed random intercepts. As with all previous models, no random slopes were specified because their inclusion resulted in model convergence problems.

5.2.13.4 Hypothesis testing and model validation

We conducted all analyses in R version 3.6.1 (R Core Team, 2019) following the general procedure detailed in section 2.10.8. For these analyses we used the *Anova.glmmTMB* function from the 'glmmTMB' package (Brooks et al., 2017) to test the significance of the fixed effects, and the *confint* function to calculate profile likelihood confidence intervals around the fixed effect estimates (Bolker et al., 2009).

Binomial model estimates and confidence intervals were converted to odds ratios to aid in interpreting the values of the estimates, particularly for multi-level factors, and to show effect sizes (negative binomial model estimates and confidence intervals were converted to incident rate ratios) (see section 2.10.8). Where appropriate we present the results of interaction effects graphically, in addition to presenting tables of coefficients.

Model fit and assumptions were verified as described in section 2.10.8. We used the *collin.diag* function of the package 'misty' (Yanagida, 2020) to derive generalised variance inflation factors ($GVIF^{(1/(2 \times d.f.))}$) for each model, which did not reveal any collinearity problems (Zuur et al., 2009) (Table 5.2). Before fitting the models, we z-transformed all continuous variables using the *scale* function.

Table 5.2 Generalised variance inflation factors (GVIF) for models M1 - M7.

Model	**Model overview**	**Largest** $GVIF^{(1/(2 \times d.f.))}$
M1	Self-scratching (baseline vs. post-IGC)	1.00
M2	Self-scratching (IGC outcome)	1.61
M3	PSB partner number (baseline vs. post-IGC)	1.08
M4	PSB (baseline vs. post-IGC)	1.08
M5	PSB (IGC outcome, DCSI, and participation)	2.39
M6	Aggression (baseline vs. post-IGC)	1.13
M7	Aggression (IGC outcome and participation)	1.75

5.3 Results

Table 5.3 Summary of hypotheses, predictions, and support provided by this study.

Hypothesis	**Predictions**	**Supported?**
H1: Conflict-cohesion	1.1 Post-IGC affiliation rates are higher than baseline rates.	No
	1.2 Post-IGC, macaques affiliate with more partners than at baseline.	No
	1.3 Post-IGC affiliation rates are independent of social bond strength between individuals.	No
	1.4 Post-IGC affiliation rates are independent of IGC participation.	Yes
	1.5 Post-IGC aggression rates are lower than baseline rates.	No
H2: Tension-reduction	2.1 Post-IGC self-scratching rates are higher than baseline rates.	Yes
	2.2 Post-IGC self-scratching rates are higher among groups that lose than groups than win.	No
	2.3 Post-IGC affiliation rates are higher than baseline rates.	No
	2.4 Post-IGC affiliation rates are higher among groups that lose than groups than win.	Yes
	2.5 Post-IGC, macaques affiliate with fewer partners than at baseline.	No
	2.6 Post-IGC affiliation rates are higher between group members with strong social bonds.	Partially
	2.7 Post-IGC affiliation rates are independent of IGC participation.	Yes
	2.8 Post-IGC aggression rates are higher than baseline rates.	No
	2.9 Post-IGC aggression rates are higher among groups that lose than groups than win.	No
	2.10 Post-IGC aggression rates do not differ from baseline rates.	Yes
H3: Social incentive	3.1 Post-IGC affiliation rates do not differ from baseline rates.	No
	3.2 Post-IGC aggression rates do not differ from baseline rates.	Yes
	3.3 Post-IGC, macaques affiliate with fewer partners than at baseline.	No
	3.4 IGC combatants receive more post-IGC affiliation than non-combatants.	No
	3.5 IGC non-combatants receive more post-IGC aggression than combatants.	No
	3.6 Post-IGC affiliation rates are independent of social bond strength between individuals.	No

5.3.1 H1. Conflict-cohesion Hypothesis

Taken together, the results of models M1-M7 fail to support the conflict-cohesion hypothesis (H1) (Table 5.3). Contrary to Prediction 1.1, there was no post-IGC increase in intragroup affiliation. Rather, we found a significant decrease in affiliative behaviour between macaques in the first hour post-IGC (M4: Fig. 5.1 and Table 5.4), after which levels returned to baseline. Considering post-IGC patterns of affiliative behaviour; in the first hour post-IGC individuals preferentially exchanged affiliative behaviour with strongly bonded social partners (contrary to Prediction 1.3) (M5: Fig. 5.2 and Table 5.5), and as predicted this was unrelated to IGC participation (Prediction 1.4) (M5: Table 5.5). Finally, there was no increase in affiliative partner numbers following IGC (contrary to Prediction 1.2) (M3: Table 5.6).

5.3.2 H2. Tension-reduction Hypothesis

We found partial support for the tension-reduction hypothesis (H2) (Table 5.3). As predicted (Prediction 2.1), macaques scratched themselves more frequently in the hours following IGC than during the baseline condition. Self-scratching rate was higher in all three post-IGC hours, but only significantly higher than baseline during the first post-IGC hour (M1: Fig. 5.3 and Table 5.7), indicating that IGC is a short-term stressful event for crested macaques. However, contrary to Prediction 2.2, IGC outcome had no significant effect on self-scratching rate (M2: Table 5.8). We found no evidence of a group-wide increase in affiliation post-IGC (Prediction 2.3), but as predicted, post-IGC affiliation was more frequent among losing groups than winning groups (Prediction 2.4) (M5: Fig. 5.4 and Table 5.5). Furthermore, individuals directed their post-IGC social effort towards their usual social partners rather than towards IGC combatants (in support of Predictions 2.6 and 2.7), but only during the first post-IGC hour. Under these circumstances the tension-reduction hypothesis (H2) also predicts a reduction in the number of affiliative partners post-IGC (Prediction 2.5), as individuals focus on those with whom they have the strongest social bonds, but we found no evidence of this. Finally, contrary to Predictions 2.8 and 2.9, there was no significant increase in intragroup aggression following IGC (M6: Fig. 5.5 and Table 5.9), regardless of outcome (M7: Table 5.10), rather, aggression rates remained stable in the post-IGC hours (in support of Prediction 2.10).

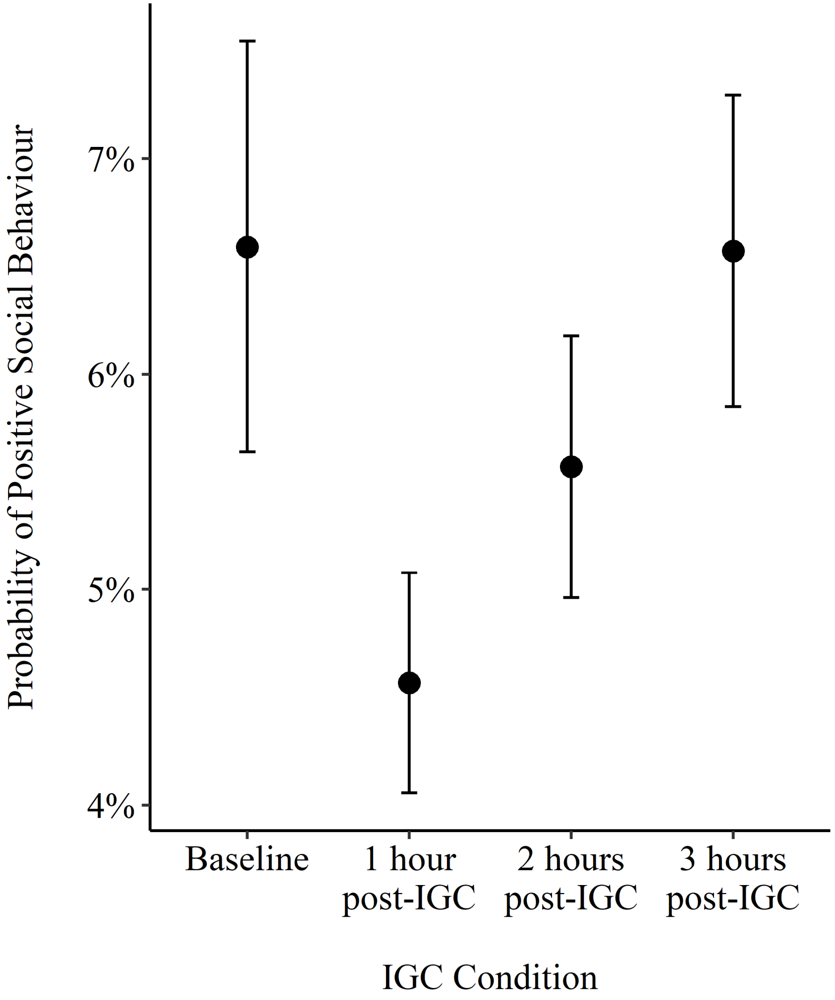

Figure 5.1 Predicted probability of PSB between crested macaques in the hours following IGC compared to baseline conditions (M4). Points and error bars represent estimated marginal means and their standard errors.

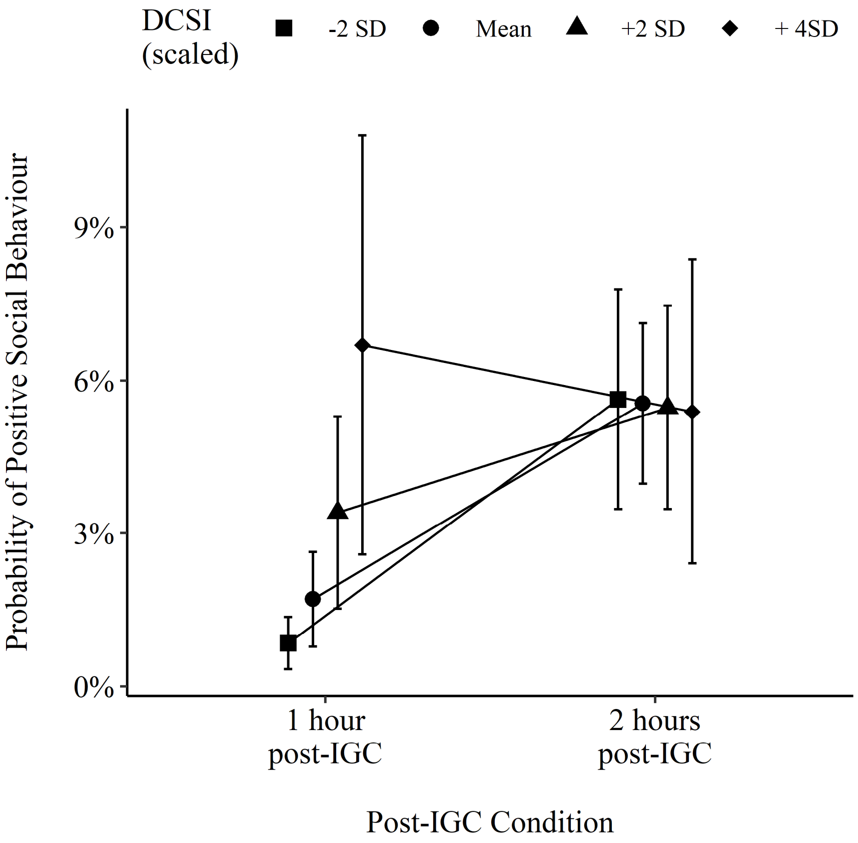

Figure 5.2 Predicted probability of PSB between crested macaques in the two hours following IGC as a function of social bond strength (DCSI) (M5). Shapes and error bars represent estimated marginal means and their standard errors.

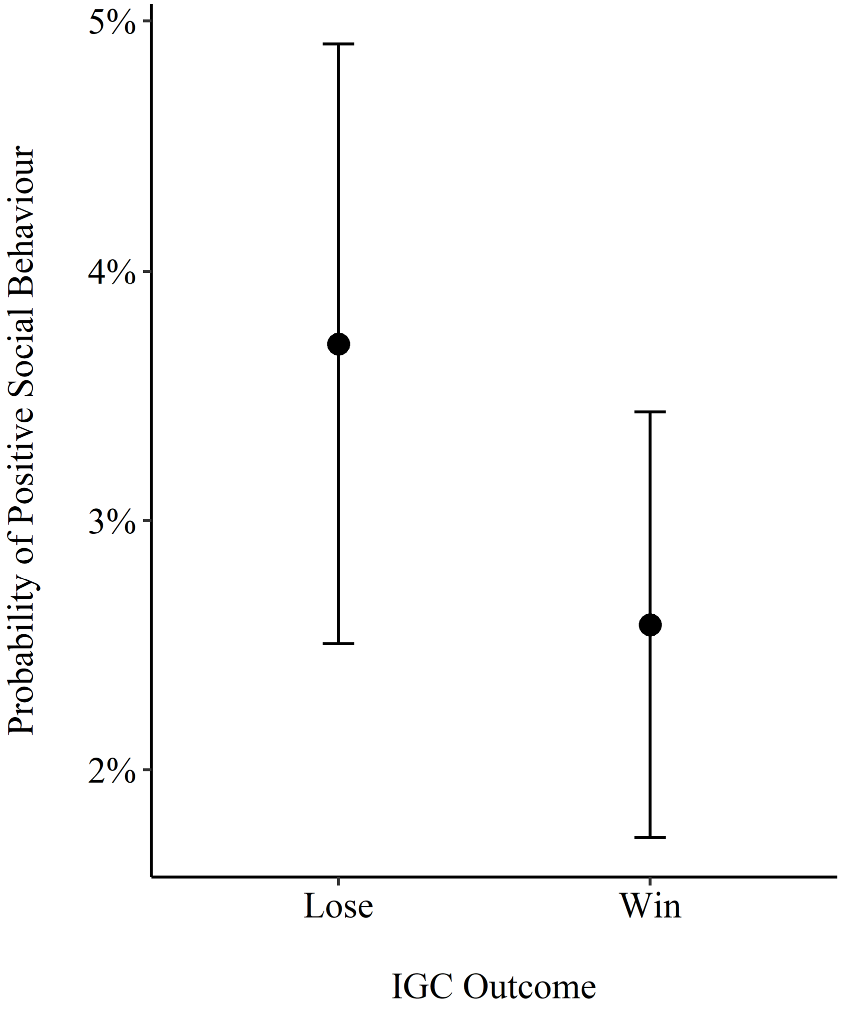

Figure 5.3 Crested macaque self-scratching frequency in the hours following IGC compared to baseline conditions (M1). Points and error bars represent estimated marginal means and their standard errors.

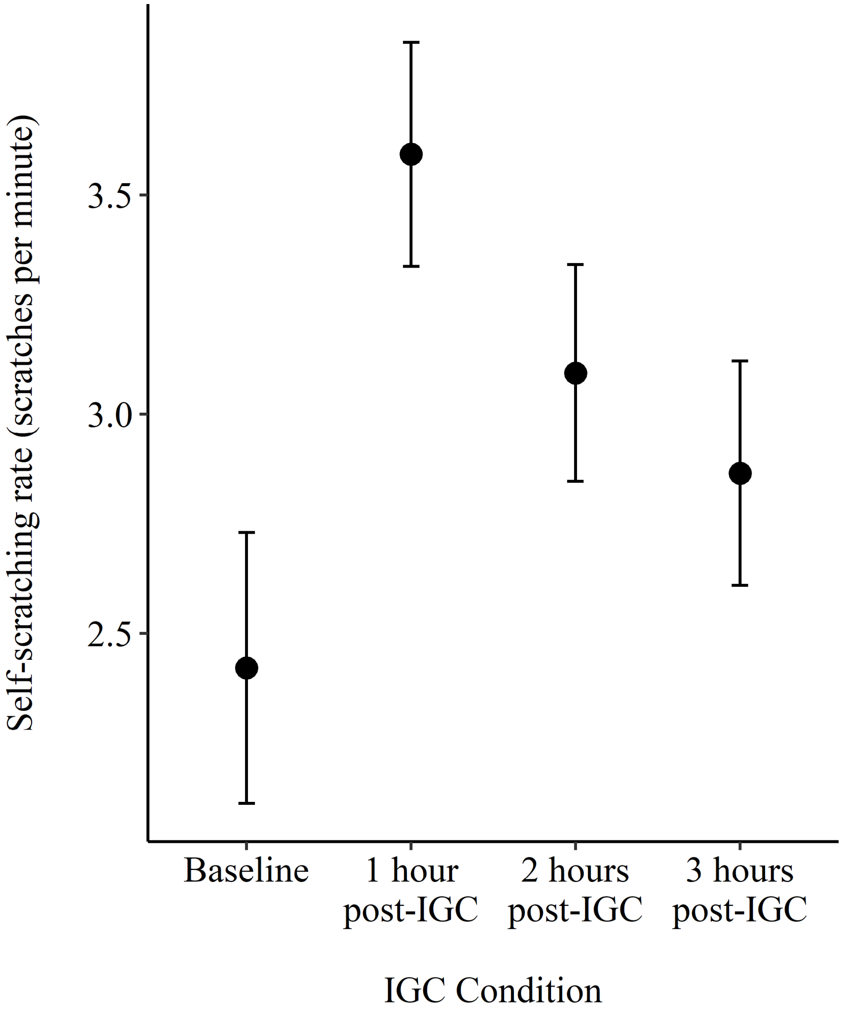

Figure 5.4 Predicted probability of PSB between crested macaques in the two hours following IGC as a function of IGC outcome (M5). Points and error bars represent estimated marginal means and their standard errors.

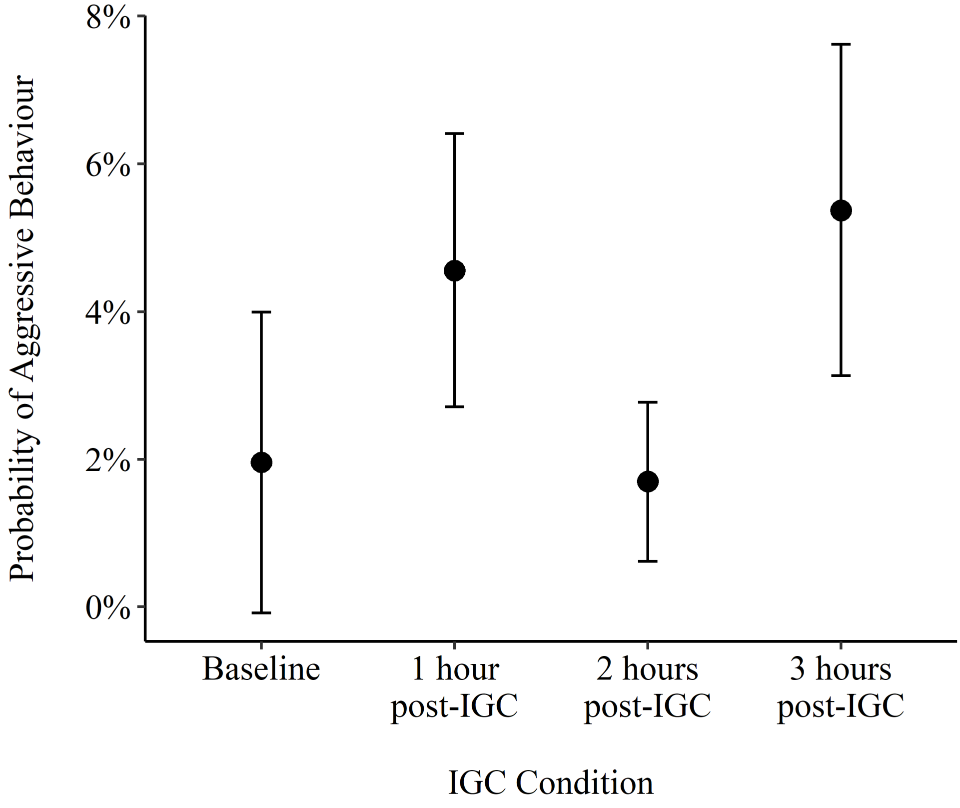

Figure 5.5 Predicted probability of aggressive behaviour between crested macaques in the hours following IGC compared to baseline conditions (M6). Points and error bars represent estimated marginal means and their standard errors.

5.3.3 Social Incentive Hypothesis

We found almost no evidence in support of the social incentive hypothesis (H3) (Table 5.3). This predicts that levels of affiliation and aggression will remain stable following IGC, but that post-IGC patterns of behaviour will change to reflect IGC participation. Intragroup aggression remained at baseline levels (in support of Prediction 3.2), but no other predictions were supported. Post-IGC affiliative behaviour declined (contrary to prediction 3.1), affiliative partner numbers remained the same (contrary to Prediction 3.3), and social effort was directed towards strongly bonded group-mates (contrary to Prediction 3.6) rather than IGC combatants (contrary to Prediction 3.4). Likewise, contrary to Prediction 3.5, non-combatants received no more aggression than combatants (M7: Table 5.10).

Table 5.4 GLMM (M4) investigating the influence of IGC on the probability of affiliation between crested macaque dyads.

Term	Levels	Est	SE	OR	OR 95% CI	LRT	df	*P* value
Test fixed effects								
Intercept		-4.89	0.14	[a]	[a]	[a]	[a]	[a]
IGC condition	1 hour post-IGC	-0.39	0.17	0.68	[0.49; 0.94]	**10.69**	**3**	**0.014**
	2 hours post-IGC	-0.18	0.17	0.84	[0.61; 1.17]			
	3 hours post-IGC	0	0.17	1	[0.72; 1.39]			
Control fixed effects								
DCSI[b]		**0.19**	**0.05**	**1.21**	**[1.11; 1.33]**	**17.34**	**1**	**<0.001**
Dyad Sex & Reproductive state	F0-F1	-0.27	0.18	0.76	[0.53; 1.07]	**31.54**	**6**	**<0.001**
	F0-M	-0.26	0.24	0.77	[0.47; 1.20]			
	F1-F0	-0.24	0.18	0.79	[0.54; 1.11]			
	F1-M	0.91	0.24	2.48	[1.52; 3.92]			
	M-F0	-0.94	0.31	0.39	[0.20; 0.69]			
	M-F1	0.34	0.28	1.4	[0.78; 2.35]			
Actor rank[b]		-0.04	0.05	0.96	[0.87; 1.07]	0.47	1	0.495
Receiver rank[b]		-0.04	0.06	0.96	[0.86; 1.07]	0.58	1	0.446
Ripe fruit availability[b]		-0.02	0.05	0.98	[0.89; 1.08]	0.22	1	0.641
Available social time[b]		**0.55**	**0.05**	**1.73**	**[1.57; 1.94]**	**105.00**	**1**	**<0.001**
Random effects	**Variance**		**SD**					
Actor within group	8.37 x 10-9		9.15 x 10-5					
Receiver within group	3.91 x 10-3		6.25 x 10-2					

The model was run with a binomial error structure and logit link function, controlling for repeated observations within actors nested in groups, and receivers in groups. The table shows fixed effects parameter estimates and standard errors (Est; SE); odds ratios and their 95% profile likelihood confidence intervals (OR; OR 95% CI); and LRT statistics, degrees of freedom, and p values (LRT; df; *P* value). Also shown are random effects variance and standard deviation (Variance; SD). [a] Not shown because of having no meaningful interpretation. [b] z-transformed; mean ± SD of the original value. Statistically significant (α = 0.05) P values are in bold. Dyad Sex & Reproductive state (F0=Female, F1=Female maximally swollen, M=Male).

Table 5.5 GLMM (M5) investigating the influence of IGC outcome, participation, and social bond strength on the probability of affiliation between crested macaque dyads.

Term	Levels	Est	SE	OR	OR 95% CI	LRT	df	*P* value
Test fixed effects								
Intercept		-5.03	0.19	[a]	[a]	[a]	[a]	[a]
IGC condition	2 hours post-IGC	[c]	[c]	[c]	[c]	[c]	[c]	[c]
DCSI[b]		[c]	[c]	[c]	[c]	[c]	[c]	[c]
IGC outcome	**Win**	**-0.38**	**0.23**	**0.68**	**[0.44; 1.07]**	**4.55**	**1**	**0.033**
Actor combatant		-1.85	1.04	0.16	[0.01; 0.78]	0.44	1	0.507
Receiver combatant		-0.35	0.56	0.7	[0.20; 1.91]	0.02	1	0.897
IGC condition x DCSI[b]		**-0.36**	**0.16**	**0.7**	**[0.50; 0.95]**	**5.09**	**1**	**0.024**
IGC condition x IGC outcome	2 hours post-IGC x Win	0.01	0.34	1.01	[0.52; 1.98]	0.002	1	0.969
IGC condition x Actor combatant		1.91	1.15	6.75	[0.95; 137.02]	2.76	1	0.097
IGC condition x Receiver combatant		0.65	0.71	1.92	[0.49; 8.33]	0.83	1	0.361
Control fixed effects								
Dyad Sex & Reproductive state	F0-F1	-0.45	0.31	0.64	[0.33; 1.13]	**26.81**	**7**	**<0.001**
	F0-M	-0.47	0.42	0.63	[0.25; 1.34]			
	F1-F0	-0.43	0.31	0.65	[0.34; 1.15]			
	F1-F1	0.42	0.49	1.52	[0.51; 3.66]			
	F1-M	1.28	0.37	3.6	[1.69; 7.34]			
	M-F0	-1.27	0.61	0.28	[0.07; 0.79]			
	M-F0	0.55	0.45	1.73	[0.66; 4.01]			
Actor rank[b]		-0.05	0.09	0.95	[0.79; 1.14]	0.33	1	0.565
Receiver rank[b]		-0.04	0.09	0.96	[0.80; 1.15]	0.20	1	0.651
Ripe fruit availability[b]		-0.07	0.09	0.93	[0.78; 1.10]	0.69	1	0.407
Available social time[b]		**0.56**	**0.09**	**1.75**	**[1.47; 2.11]**	**37.43**	**1**	**<0.001**

Table 5.5 continued

Random effects	**Variance**	**SD**
Actor within group	0.02	0.14
Receiver within group	0.02	0.13

The model was run with a binomial error structure and logit link function, controlling for repeated observations within actors nested in groups, and receivers in groups. The table shows fixed effects parameter estimates and standard errors (Est; SE); odds ratios and their 95% profile likelihood confidence intervals (OR; OR 95% CI); and LRT statistics, degrees of freedom, and p values (LRT; df; *P* value). Also shown are random effects variance and standard deviation (Variance; SD). [a] Not shown because of having no meaningful interpretation. [b] z-transformed; mean ± SD of the original value. [c] Not shown because of having no meaningful interpretation in the presence of a significant interaction. Statistically significant ($\alpha = 0.05$) P values are in bold. Dyad Sex & Reproductive state (F0=Female, F1=Female maximally swollen, M=Male).

Table 5.6 GLMM (M3) investigating the influence of IGC on affiliative partner numbers in crested macaques.

Term	**Levels**	**Est**	**SE**	**RR**	**RR 95% CI**	**LRT**	**df**	***P* value**
Test fixed effects								
Intercept		-2.48	0.19	[a]	[a]	[a]	[a]	[a]
IGC condition	1 hour post-IGC	-0.11	0.21	0.9	[0.59; 1.37]	2.92	3	0.405
	2 hours post-IGC	0.07	0.21	1.07	[0.71; 1.65]			
	3 hours post-IGC	0.15	0.22	1.16	[0.76; 1.79]			
Control fixed effects								
Subject rank[b]		-0.05	0.06	0.95	[0.85; 1.07]	0.57	1	0.45
Subject Sex & Reproductive status	F1	0.22	0.17	1.25	[0.88; 1.71]	**18.72**	**2**	**<0.001**
	M	-1.02	0.26	0.36	[0.21; 0.58]			
Ripe fruit availability[b]		-0.04	0.06	0.96	[0.85; 1.08]	0.43	1	0.514
Available social time[b]		**0.55**	**0.06**	**1.73**	**[1.53; 1.97]**	**73.07**	**1**	**<0.001**
Random effects	**Variance**		**SD**					
Subject within group	0.07		0.26					

The model was run with a negative binomial error structure and log link function, controlling for repeated observations within subjects nested in groups. The table shows fixed effects parameter estimates and standard errors (Est; SE); rate ratios and their 95% profile likelihood confidence intervals (RR; RR 95% CI); and LRT statistics, degrees of freedom, and p values (LRT; df; *P* value). Also shown are random effects variance and standard deviation (Variance; SD). [a] Not shown because of having no meaningful interpretation. [b] z-transformed; mean ± SD of the original value. Statistically significant (α = 0.05) P values are in bold. Subject Sex & Reproductive status (F1=Female max swollen, M=Male).

Table 5.7 GLMM (M1) investigating the influence of IGC on self-scratching rate in crested macaques.

Term	**Levels**	**Est**	**SE**	**RR**	**RR 95% CI**	**LRT**	**df**	***P* value**
Test fixed effects								
Intercept		-1.42	0.13	[a]	[a]	[a]	[a]	[a]
IGC condition	1 hour post-IGC	0.39	0.14	1.48	[1.13; 1.98]	**9.56**	**3**	**0.023**
	2 hours post-IGC	0.25	0.15	1.28	[0.97; 1.71]			
	3 hours post-IGC	0.17	0.15	1.19	[0.89; 1.60]			
Control fixed effects								
Subject rank[b]		0.04	0.04	1.04	[0.96; 1.12]	0.84	1	0.358
Random effects	**Variance**		**SD**					
Subject within group	0.03		0.17					

The model was run with a negative binomial error structure and log link function, controlling for repeated observations within subjects nested in groups. The table shows fixed effects parameter estimates and standard errors (Est; SE); rate ratios and their 95% profile likelihood confidence intervals (RR; RR 95% CI); and LRT statistics, degrees of freedom, and p values (LRT; df; *P* value). Also shown are random effects variance and standard deviation (Variance; SD). [a] Not shown because of having no meaningful interpretation. [b] z-transformed; mean ± SD of the original value. Statistically significant (α = 0.05) P values are in bold.

Table 5.8 GLMM (M2) investigating the influence of IGC outcome on self-scratching rate in crested macaques.

Term	Levels	Est	SE	RR	RR 95% CI	LRT	df	*P* value
Test fixed effects								
Intercept		-1.03	0.11	[a]	[a]	[a]	[a]	[a]
IGC condition	2 hours post-IGC	-0.27	0.17	0.76	[0.55; 1.06]	5.03	2	0.081
	3 hours post-IGC	-0.24	0.17	0.79	[0.56; 1.08]			
IGC outcome	Win	0.01	0.13	1.01	[0.78; 1.32]	0.66	1	0.416
IGC condition x IGC outcome	2 hours post-IGC x Win	0.18	0.21	1.2	[0.79; 1.80]	0.77	2	0.682
	3 hours post-IGC x Win	0.02	0.22	1.02	[0.67; 1.57]			
Control fixed effects								
Subject rank[b]		0.03	0.04	1.03	[0.94; 1.12]	0.34	1	0.561
Random effects	**Variance**	**SD**						
Subject within group	0.03	0.18						

The model was run with a negative binomial error structure and log link function, controlling for repeated observations within subjects nested in groups. The table shows fixed effects parameter estimates and standard errors (Est; SE); rate ratios and their 95% profile likelihood confidence intervals (RR; RR 95% CI); and LRT statistics, degrees of freedom, and p values (LRT; df; *P* value). Also shown are random effects variance and standard deviation (Variance; SD). [a] Not shown because of having no meaningful interpretation. [b] z-transformed; mean ± SD of the original value. Statistically significant (α = 0.05) P values are in bold.

Table 5.9 GLMM (M6) investigating the influence of IGC on aggression in crested macaques.

Term	**Levels**	**Est**	**SE**	**OR**	**OR 95% CI**	**LRT**	**df**	***P* value**
Test fixed effects								
Intercept		-6.42	1.11	[a]	[a]	[a]	[a]	[a]
IGC condition	1 hour post-IGC	0.87	1.11	2.39	[0.38; 46.67]	3.44	3	0.329
	2 hours post-IGC	-0.15	1.22	0.86	[0.09; 18.78]			
	3 hours post-IGC	1.05	1.12	2.86	[0.44; 56.35]			
Control fixed effects								
DCSI[b]		-0.4	0.26	0.67	[0.39; 1.09]	2.35	1	0.125
Dyad Sex & Reproductive state	F0-F1	-0.6	1.14	0.55	[0.03; 3.77]	7.69	8	0.465
	F0-M	-1.21	1.12	0.3	[0.02; 1.99]			
	F1-F0	0.32	1.15	1.38	[0.07; 10.07]			
	F1-F1	1.18	1.24	3.25	[0.15; 29.49]			
	F1-M	-0.02	1.14	0.98	[0.05; 6.85]			
	M-F0	0.65	0.71	1.92	[0.45; 7.80]			
	M-F0	1.52	0.81	4.57	[0.83; 22.00]			
	M-M	-0.02	0.89	0.98	[0.13; 5.03]			
Actor rank[b]		0.21	0.27	1.23	[0.73; 2.12]	0.62	1	0.430
Receiver rank[b]		-0.38	0.29	0.68	[0.39; 1.20]	1.73	1	0.189
Ripe fruit availability[b]		-0.03	0.27	0.97	[0.56; 1.60]	0.01	1	0.905
Available social time[b]		-0.13	0.26	0.88	[0.53; 1.47]	0.25	1	0.619
Random effects	**Variance**	**SD**						
Actor within group	1.22 x 10-9	3.49 x 10-5						
Receiver within group	1.94 x 10-10	1.39 x 10-5						

The model was run with a binomial error structure and logit link function, controlling for repeated observations within actors nested in groups, and receivers in groups. The table shows fixed effects parameter estimates and standard errors (Est; SE); odds ratios and their 95% profile likelihood confidence intervals (OR; OR 95% CI); and LRT statistics, degrees of freedom, and p values (LRT; df; *P* value). Also shown are random effects variance and standard deviation (Variance; SD). [a] Not shown because of having no meaningful interpretation. [b] z-transformed; mean ± SD of the original value. Statistically significant (α = 0.05) P values are in bold. Dyad Sex & Reproductive state (F0=Female, F1=Female maximally swollen, M=Male).

Table 5.10 GLMM (M7) investigating the influence of IGC outcome and participation on aggression in crested macaques.

Term	Levels	Estimate	SE	OR	OR 95% CI	LRT	df	*P* value
Test fixed effects								
Intercept		-6.47	1.06	[a]	[a]	[a]	[a]	[a]
IGC condition	2 hours post-IGC	1.26	1.2	3.53	[0.31; 43.27]	0.73	2	0.693
	3 hours post-IGC	0.57	1.16	1.77	[0.17; 19.94]			
IGC outcome	Win	0.18	1.05	1.2	[0.15; 11.54]	0.21	1	0.644
Actor combatant	Yes	0.05	0.94	1.05	[0.13; 5.84]	0.003	1	0.958
Receiver combatant	Yes	1.51	1.06	4.53	[0.47; 35.80]	2.04	1	0.153
IGC condition x IGC outcome	2 hours post-IGC x Win	-2.55	1.71	0.08	[0.00; 2.03]	2.72	2	0.257
	3 hours post-IGC x Win	0.12	1.46	1.13	[0.06; 21.33]			
Control fixed effects								
DCSI[b]		-0.2	0.36	0.82	[0.38; 1.64]	0.30	1	0.581
Dyad Sex & Reproductive state	F0-F1	-0.22	1.28	0.8	[0.03; 8.08]	5.87	8	0.662
	F0-M	-0.44	1.37	0.64	[0.02; 7.92]			
	F1-F0	0.95	1.34	2.59	[0.10; 31.67]			
	F1-F1	3.44	1.68	31.19	[0.84; 915.16]			
	F1-M	0.86	1.36	2.36	[0.09; 29.23]			
	M-F0	0.75	1.05	2.12	[0.23; 16.82]			
	M-F1	0.83	1.36	2.29	[0.09; 28.03]			
	M-M	0.89	1.12	2.44	[0.23; 21.97]			
Actor rank[b]		**0.86**	**0.42**	**2.36**	**[1.08; 5.75]**	**4.18**	**1**	**0.041**
Receiver rank[b]		-0.28	0.4	0.76	[0.34; 1.66]	0.49	1	0.485
Ripe fruit availability[b]		-0.09	0.36	0.91	[0.43; 1.80]	0.06	1	0.799
Available social time[b]		0.58	0.37	1.79	[0.89; 3.88]	2.52	1	0.113

Table 5.10 continued

Random effects	**Variance**	**SD**
Actor within group	9.88 x 10-10	3.14 x 10-5
Receiver within group	2.77 x 10-10	1.66 x 10-5

The model was run with a binomial error structure and logit link function, controlling for repeated observations within actors nested in groups, and receivers in groups. The table shows fixed effects parameter estimates and standard errors (Est; SE); odds ratios and their 95% profile likelihood confidence intervals (OR; OR 95% CI); and LRT statistics, degrees of freedom, and p values (LRT; df; *P* value). Also shown are random effects variance and standard deviation (Variance; SD). [a] Not shown because of having no meaningful interpretation. [b] z-transformed; mean ± SD of the original value. Statistically significant (α = 0.05) P values are in bold. Dyad Sex & Reproductive state (F0=Female, F1=Female maximally swollen, M=Male).

5.4 Discussion

The main findings of this study are that (1) affiliative behaviour between crested macaques decreased in the immediate aftermath (first hour) of IGC; (2) dyads in losing groups exchanged more affiliative behaviour than those in winning groups, (3) individuals focused their post-IGC affiliative behaviour on their strongly bonded social partners; and (4) IGC participation had no effect on the giving or receiving of post-conflict affiliative or aggressive behaviour.

As predicted by the tension-reduction hypothesis (H2: Table 5.1), individual macaques scratched themselves more following IGC (in the first hour) than they did in the baseline condition (Prediction 2.1), but no effect of IGC outcome was observed (contrary to Prediction 2.2). Contrary to all predictions (1.1, 2.3, and 3.1), dyads exchanged less affiliative behaviour in the hour post-IGC than at baseline, but both IGC outcome (Prediction 2.4) and social bond strength (Prediction 2.6) influenced patterns of affiliative behaviour in ways consistent with the tension-reduction hypothesis. As predicted by both the conflict-cohesion (H1) and tension-reduction hypotheses (H2), IGC participation had no significant effect on subsequent affiliative or aggressive behaviour (in support of Predictions 1.3 and 2.7 and contrary to Predictions 3.4 and 3.5). Furthermore, no change in aggressive behaviour was found in the post-IGC period compared to baseline (contrary to Predictions 1.5 and 2.8), even when IGC outcome was considered (Prediction 2.9). The social incentive hypothesis (H3) correctly predicted no change in levels of post-IGC aggression (Prediction 3.2), however no other social incentive predictions were supported. Likewise, only one prediction of the conflict-cohesion hypothesis (H1) was supported (Prediction 1.4). In sum, we found no evidence that crested macaques use grooming, affiliation, contact-sitting, and/or aggression to enhance in-group cohesion or to punish/reward group-mates in the aftermath of IGC. However, we did confirm several predictions of the tension-reduction hypothesis (H2), suggesting that in crested macaques the primary function of post-IGC social behaviour may be to relieve the physiological stress and anxiety associated with out-group conflict.

Intergroup conflict can be costly, and these results, showing that self-scratching increases in the hour post-IGC, indicate that crested macaques experience increased physiological stress in response to conflict with other groups. Many previous studies of primates (reviewed in Maestripieri et al., 1992), including other macaques, demonstrate that self-scratching is a reliable indicator of stress (Barbary macaques (*Macaca Sylvanus*): (Kaburu et al., 2012; Maréchal et al., 2011); Japanese macaques (*Macaca fuscata yakui*): (Majolo et al., 2009); and crested macaques (Aureli & Yates, 2010)), but it has rarely been used in the context of IGC. A study of semi-free-ranging ringtailed lemurs observed increased rates of self-directed behaviour, including self-scratching, during IGEs (Nunn & Deaner, 2004), but this study is one of the first to use this method to examine stress responses to IGC in wild primates. Long-term stress exposure can have negative effects on growth, reproduction, disease resistance, and longevity (Pride, 2005), but these can be reduced through positive social contact, particularly allogrooming (Terry, 1970). It is therefore surprising that our results show a significant decrease in PSB (affiliative gestures, touches, contact-sitting, and allogrooming) in the first hour following IGC, when we might expect to see an increase in response to elevated stress.

There are several possible explanations for the decrease in PSB following IGC, and for the apparent lack of effect of IGC participation. First, the familiarity of the study groups may affect intragroup behaviour following IGC. Encounters with unknown groups often elicit a more powerful response from territory-holders than those with more familiar neighbouring groups (see Christensen & Radford's (2018) review). Strangers could be more threatening for two main reasons: First, their appearance at territorial borders is less spatially and temporally predictable than that of neighbours (Jordan et al., 2007); and second, unfamiliar groups are more likely to usurp an entire territory than familiar neighbours. As such they represent a greater threat than neighbouring groups that are likely to return to their own territory following an incursion (Wilson, 1975): the "dear-enemy" effect (Fisher, 1954). In contrast, the "nasty-neighbour" effect proposes that familiar groups pose a greater threat if fluctuating resources levels in disputed territory encourage usurpation by neighbours (Temeles, 1990). The home ranges of the macaque groups at this study site overlapped considerably and the groups encountered one another frequently. In addition, food at this study site is abundant year-round (Kinnaird et al., 1999; O'Brien & Kinnaird, 1997; Ratna Sari, 2013), dispersing males often transfer in and out of the same groups throughout their lives (Marty, Hodges, Heistermann, et al., 2017), and two of our study groups (plus two other non-study groups) were closely related, having previously been part of the same group that fissioned several years before the study began. Therefore, it is probably safe to assume that groups were familiar with each other, which could explain why no increases in post-IGC affiliation or aggression were observed: Over and above the stress induced by any encounter with another group, perhaps encounters with familiar neighbours are not threatening enough to elicit an increase in affiliative or aggressive behaviour in this population.

However, if this were the case, we might expect PSB to remain unchanged after IGC, rather than to decrease. Individuals may forage more after IGEs to compensate for lost feeding time and increased energy expenditure. However, given that we controlled for available social time in all our analyses it seems unlikely that this is driving the decrease in post-IGC PSB among crested macaques. We might also expect to see an increase in intragroup aggression as individuals compete more fiercely for limited fall-back resources (in the case of losing groups). Very few studies report a decrease in social behaviour following IGEs, and our findings are in contrast with many of those for other species, where post-IGE PSB either increased (*Cercopithecus mitis*: (Cords, 2002); *Neolamprologus pulcher*: (Bruintjes et al., 2016); *Phoeniculus purpureus*: (Radford, 2008b); *Gorilla beringei beringei*: (Mirville et al., 2020); *Cercopithecus mitis erythrarchus*: (Payne, Henzi, et al., 2003); *Pan troglodytes verus*: (Samuni, Mielke, et al., 2019)), or did not change (*Erythrocebus patas*: (Chism & Rogers, 2004); *Lemur catta*: (Nunn & Deaner, 2004); *Cebus apella*: (Polizzi di Sorrentino, Schino, Massaro, et al., 2012); *Cercopithecus aethiops*: (Cheney, 1992)). Only Yi et al. (2020) found a post-IGC decrease in affiliative social behaviour, with a simultaneous increase in feeding behaviour, between pairs of Javan gibbons.

However, the species detailed above all have quite different social systems to each other, and to that of crested macaques. Furthermore, the nature of IGEs also differs considerably between these species. For example, affiliation between chimpanzees often increases pre- and post-IGC (Mitani et al., 2010; Samuni, Mielke, et al., 2019), with the likely function of increasing group cohesion and cooperation. Conflict between chimpanzee groups can be notoriously violent, if relatively infrequent, and can result in individual deaths and the usurpation of entire territories, which in turn has powerful fitness consequences for males and females (Langergraber et al., 2017; Mitani et al., 2010). Given that numerical superiority is one of the key determinants of IGC success in chimpanzees, affiliative behaviours that increase group cohesion may be highly adaptive. However, IGC among crested macaques at this study site is much more frequent, potentially injurious but rarely lethal (Martínez-Iñigo, 2017), and because food is abundant (O'Brien & Kinnaird, 1997; Ratna Sari, 2013) the costs of losing an encounter may be relatively low, compared to chimpanzees for example. Intragroup cohesion does not appear to be a key determinant of IGC success in crested macaques, with lethal coalitionary attacks being rare, and individuals of both sexes acting primarily to protect their own reproductive interests (this study; Martínez-Iñigo, 2017; Martínez-Iñigo et al., 2017). Although crested macaques are not cooperative breeders (for whom communal defence and collective action are crucial drivers of lifetime reproductive fitness (Bruintjes et al., 2016; Radford, 2008b), the high degree of social tolerance and relatedness between female group-mates (as the philopatric sex) may mean that most individuals are already prepared to support their close kin during IGC. As such, there may be little need of a social mechanism to increase group cohesion or incentivise participation in the context of IGC.

However, if there is little need for a cohesive behavioural mechanism in this situation, we might again anticipate no change in PSB post-IGC, rather than a decrease. Having taken into account dyad sex, female reproductive state, and the strength of social bonds, which are the primary determinants of PSB between crested macaques dyads under normal circumstances (this study; Clark & Melfi, 2005; Cowl et al., 2020; O'Brien & Kinnaird, 1997) the decrease in PSB was still evident. We therefore propose four non-mutually exclusive potential explanations for the observed decrease in PSB following IGC. First, that individuals increase vigilance at the expense of allogrooming in the aftermath of encounters. Because allogrooming (a key component of our PSB measure) can interfere with vigilance (Cords, 1995; Maestripieri, 1993; Mooring & Hart, 1995), it may be less common in the first hour post-IGC as individuals remain alert for the possible return of their rivals (both winners and losers). This could be investigated further by comparing time spent vigilant in the hours following IGC with baseline levels.

Second, there may be fewer opportunities (for losing groups) and less need (for winning groups) for intragroup affiliation following IGC. Losing groups generally move away from the IGC location and interindividual spacing tends to increase when travelling (*Papio* spp.; (Altmann & Altmann, 1973; Dunbar & Nathan, 1972);

Erythrocebus patas: (Hall, 1966); *Symphalangus syndactylus*: (Chivers, 1971); *Miopithecus talapoin*: (Gautier-Hion, 1970)). This reduces the likelihood of social exchange between individuals and could explain the decrease in PSB during the first post-IGC hour. Winning groups on the other hand may remain at the IGC location to feed on the contested resource, usually abundantly fruiting fig trees. Social behaviour may decrease in this case because although individuals may clump together to exploit the resource, they may be too busy feeding to engage in social behaviour. Indeed, this may partially explain our finding that although affiliative behaviour decreases in the first hour post-IGC for winning and losing groups, winning groups exchange even less affiliative behaviour than losing groups. Furthermore, the abundance of fruit may reduce intragroup (contest) feeding competition in both winning and losing groups to the extent that intragroup aggression also decreases/remains stable (Isbell, 1991).

Third, it may be that at times of increased anxiety (such as post-IGC) certain individuals avoid one another in anticipation of receiving aggression. There is limited evidence in the literature for an increase in intragroup aggression following IGC, and as with affiliative behaviour the results are inconsistent. In line with the results presented here, a study of ringtailed lemurs found no post-IGC increase in intragroup aggression (Nunn & Deaner, 2004), whilst agonistic interactions involving silverback male mountain gorillas decreased following long (vs. short) IGEs (Mirville et al., 2020), and post-IGC male-to-female aggression increased among bonnet macaques (Cooper et al., 2004). The latter study hypothesised that this aggression was the consequence of increased anxiety and/or functioned as herding behaviour. We have already demonstrated that anxiety increases post-IGC among crested macaques, and that females tend to avoid males pre-conflict; most likely to avoid aggressive sexual coercion/herding during between-group encounters (see Chapter 4). It follows that female macaques may also try to avoid males in the immediate aftermath of IGC when they may be the victims of further aggression: Possibly because males are in a general state of heightened anxiety and may redirect aggression received during IGC, and/or because males may try to punish/discourage female out-group copulations. Given that a great deal of the PSB between crested macaques takes the form of female-to-male grooming, and that the receipt of aggression is more likely upon approaching a potential aggressor (even to offer grooming), it is possible that PSB decreases post-IGC because females avoid males.

If this conflict-avoidance strategy works it would also be evidenced by an unchanged rate of intragroup aggression, which we see in these results.

Finally, affiliative behaviour may decrease following IGC simply because individuals have relatively inflexible time-budgets (Chism & Rogers, 2004). As such, “discretionary” activities, such as allogrooming, may be sacrificed in favour of maintenance activities like feeding. If time-budgets are limited in this way it follows that any remaining post-IGC social behaviour should serve an individual’s most immediate needs: which for crested macaques in this habitat may be tension-reduction (particularly for losing groups), rather than increasing group cohesion or socially incentivising future IGC participation. Our finding that individuals in losing groups still exchange more affiliative behaviour than those in winning groups supports this argument, as does our finding that individuals direct their time-limited social effort towards their most strongly bonded partners in the aftermath of conflict (which should maximise the effects of social buffering (Kikusui et al., 2006; Young et al., 2014)). Additionally, although we found almost no support for the conflict-cohesion hypothesis in this study, it is possible that by focussing their time-limited post-IGC social effort on strongly bonded social partners, crested macaques still manage to service their most important social relationships. In this respect, although post-IGC social behaviour may not actively increase social cohesion, it may function to maintain it, at least within specific social cliques

Considering our previous findings that female and male crested macaques appear to pursue their own reproductive interests in anticipation of potential IGC, rather than any collective goal, this time-limited tension-reduction scenario seems the most likely explanation of our results. In order to investigate this more thoroughly, future work should aim to quantify exactly how individuals participate, record in detail their behaviour during and immediately after IGC, and track participants over a considerably longer time-frame. This could be achieved with a larger team of individuals, spread around and throughout the competing groups, but this presents its own logistical and ethical problems as the number of observers increases. However, this would allow a more thorough understanding of whether the results presented here do in fact reflect a time-limited tension-reduction strategy, or whether some other form of social capital is exchanged in the aftermath of IGC, but perhaps in a different currency and/or at a later time.

The effect of IGC on intragroup social behaviour is still not well understood, and as the number of species examined increases it becomes clear that there is a great deal of variation in how species, groups, and individuals respond. These results begin to fill a gap in our understanding by providing the first information concerning the post-IGC responses of a Resident-Nepotistic-Tolerant (RNT) primate species (Sterck et al., 1997), and support the idea that a species' social system is a key factor in understanding the wide variation in responses. In common with Resident-Nepotistic (RN) species, RNT species experience high levels of intragroup contest competition, and we see the development of stable, linear, and nepotistic female hierarchies in both. However, unlike RN species, crested macaques also experience high intergroup contest competition, and this predicts the development of a more tolerant dominance regime (confirmed by Duboscq et al., 2013), in order to ensure the support of low-ranking individuals during IGC. This may explain the lack of evidence for the conflict-cohesion or social-incentive hypotheses in this study: if all individuals can benefit more or less equally from the spoils of IGC victory there may be little need for a behavioural mechanism that bolsters group cohesion and/or incentivises participation, particularly if time-budgets are limited by IGC. If this is the case it is more likely that as suggested here, individuals of RNT species will pursue behavioural strategies that most reliably maximise their own lifetime-reproductive fitness, such as buffering the deleterious effects of stress, rather than (or before) those that promote group-wide cohesion and collective action.

Chapter 6

General Discussion

6.1 Discussion

Intergroup competition is a pivotal factor in recent theoretical models of the evolution of social behaviour, particularly behaviour such as intragroup cooperation (Choi & Bowles, 2007; Puurtinen et al., 2015; Puurtinen & Mappes, 2009). Aggressive intergroup conflict (IGC) is one of the riskiest cooperative actions that an individual can undertake, and in many cases non-participants can receive the benefits of collective action (e.g. territory or resource defence) but incur none of the costs (Kitchen & Beehner, 2007; Nunn & Lewis, 2001). This renders the defence of commonly held resources vulnerable to a collective action problem (CAP) (Olson, 1965). If costly collective action produces a public good that cannot be monopolised by the individuals responsible for producing it, natural selection will favour free-riders over co-operators (Heinsohn & Packer, 1995), collective action will break down, and the public good will be lost to all (Rankin et al., 2007). Group-living animals in a diverse range of taxa rely on cooperative action in defence of resources against conspecifics (e.g. ants (*Formicidae* spp.) (Adams, 1990; Batchelor & Briffa, 2010; Birch et al., 2019; Hölldobler & Lumsden, 1980; Tanner, 2006), termites (Thompson et al., 2020), honeybees (*Apis mellifera*) (Rangel et al., 2010), birds (*Passeriformes* spp.) (Carlson, 1986; Langen & Vehrencamp, 1998; Strong et al., 2018; Woolfenden & Fitzpatrick, 1977), fish (Braga Goncalves & Radford, 2019; Bruintjes et al., 2016; Hellmann & Hamilton, 2019), and carnivores (*Carnivora* spp.) (Christensen et al., 2016; Dyble et al., 2019; Furrer et al., 2011; Morris-Drake et al., 2019; Mosser & Packer, 2009; Preston et al., 2020; Stewart et al., 2001). However, recent empirical work indicates that the CAP appears to be a particularly important selective pressure in the evolution of primate sociality and cooperation (Kitchen & Beehner, 2007; Nunn, 2000; Willems et al., 2013; Willems & van Schaik, 2015). Groups that win intergroup encounters (IGEs) tend to have greater access to fitness-enhancing resources (Mitani et al., 2010), and effective competition typically requires cooperation among individuals (De Dreu et al., 2016). Consequently, many researchers have hypothesised that intergroup hostility exerts a selective force on behaviours that promote intragroup cooperation, thereby overcoming the CAP (Alexander & Borgia, 1978; Bowles, 2009; Choi & Bowles, 2007). As such, many recent studies of interactions between groups of social animals have focused on the possible role of affiliative and aggressive behaviours in promoting intragroup cohesion and cooperation, but with conflicting results (e.g. Chism & Rogers, 2004; Mirville et al., 2020; Payne, Henzi, et al., 2003; Polizzi di Sorrentino, Schino, Massaro, et al., 2012; Preston et al., 2020; Samuni, Mielke, et al., 2019; Thompson et al., 2020; and Yi et al., 2020). While intergroup hostility and intragroup cooperation may be fundamentally linked in an evolutionary sense, the social and environmental conditions under which many group-living animals exist may elicit/demand different, or more varied responses. Despite a growing body of work, we still have an incomplete picture of this connection across different group living taxa. The goal of this thesis was to investigate how the threat and occurrence of IGC affects intragroup behaviour in wild crested macaques (*Macaca nigra*).

In Chapters 3 and 4, I first used the increase in a behavioural indicator of anxiety (self-scratching) to establish support for the view that crested macaques remember the location, timing, and outcome of recent IGEs, and that the prospect of encountering other groups can be stressful. Several studies show that non-human primates (hereafter primates) remember the locations of predator attacks and disturbance events, such as human persecution or large gatherings (Boinski et al., 2000; Fagan et al., 2013; Reisland & Lambert, 2016; Waterman et al., 2019), but very few have demonstrated the same with IGEs in the wild. I found that although both spacing and social behaviour changed in areas where IGEs were most likely to occur, there was little evidence that encounter risk prompted the expression of behaviours likely to facilitate future participation in IGEs. Rather, my findings suggest that when faced with the risk of intergroup hostility, individuals tend to behave in ways that maximise their own interests (physical safety and reproductive success) without the need for cooperative behaviour.

In Chapter 3, I found that groups altered their spacing and behavioural synchrony, but in different ways depending on their recent IGE win/loss record. Groups with the strongest records appear to spread out in high risk areas, a response most likely driven by low- and mid-ranking males prospecting for out-group mating/transfer opportunities. This would also explain the accompanying decrease in behavioural synchrony as different sex-age-rank classes pursue different agendas. I hypothesised that dominant groups might spread out to find, engage, and defeat rivals, reinforcing a profitable pattern of group dominance (Lemoine, Boesch, et al., 2020). However, if this were the case, we might expect to see an increase in active behavioural synchrony, which we do not here. In contrast, groups with the poorest win/loss records clump together and their behaviour becomes more synchronised. It is well established that small groups (that are likely to be subordinate) can overcome CAPs more easily than large groups (Olson, 1965), in which free-riding is often widespread and difficult to police. However, rather than functioning to promote effective collective action a more parsimonious explanation of the observed increase in spatial cohesion and behavioural synchrony among subordinate groups is that individuals try to take advantage of the dilution effect (Hamilton, 1971); crowding together in areas where the possibility of out-group attack is greatest.

Similarly, the patterns of social behaviour I observed in Chapter 4, as groups prepared to enter high encounter risk areas, are most likely explained by “selfish” motives. If coordinated collective action is important for IGC success in crested macaques we might expect to see an increase in behaviours that promote social cohesion and cooperation in advance of potential conflict. This should be particularly evident between adult males, the most frequent and aggressive participants. However, prior to entering high encounter risk areas I found that male-male social interactions ceased entirely. Male crested macaques exchange very little affiliative behaviour with one another at any time (Reed et al., 1997), but the total absence of interaction prior to entering high encounter risk areas suggests: (a) that the steep male dominance hierarchy (Marty, 2015) may inhibit affiliative social interaction at all times, regardless of IGE risk; and/or (b) that male crested macaques have no need of a behavioural mechanism to promote male collective action during IGC.

Because male reproductive fitness is primarily limited by access to sexually receptive females (Trivers, 1972) they may follow at least three IGE strategies, only the third of which (detailed below) would create any substantial selective pressure for cooperation in this species. First, they may directly defend their own reproductive interests by herding in-group females and aggressing out-group males (the mate-defence hypothesis: van Schaik et al., 1992; Wrangham, 1980). Second, they may use IGEs as opportunities to survey group transfer possibilities (Lazaro-Perea, 2001;

Majolo et al., 2005). Third, they may indirectly defend females (and increase female reproductive output (Williams et al., 2004)) by defending food resources (the hired-guns hypothesis: Fashing, 2001; Rubenstein, 1986). Overall, my findings provide strong support for the first of these possibilities, limited support for the second, and virtually none for the third.

First, in crested macaques dominant males can easily monopolise mating access (and crucially paternity) due to low female reproductive synchrony and clear, reliable signals of fertility (conspicuous sexual swellings) (Higham et al., 2012). This priority-of-access model (Altmann, 1962) is also evident in other primate species (Alberts et al., 2003; Altmann et al., 1996; Boesch et al., 2006; Setchell et al., 2005) and several studies have found that oestrus females, who could conceive offspring with out-group males, are more likely to be herded than those who are not (Byrne et al., 1987; Cheney & Seyfarth, 1977; Smuts & Smuts, 1993). Indeed, rather than, or in addition to attacking out-group rivals during IGEs, male crested macaques commonly herd swelling females one-on-one, and males of all rank display significantly more aggression towards swollen females than towards females in other reproductive states (Martínez-Iñigo, 2017; Reed et al., 1997). This appears to be an extremely effective strategy: Engelhardt et al. (2017) found no evidence of extragroup paternity or natal breeding in paternity tests of 63 infants from three groups of crested macaques (two of which I followed for this study) between 2006 and 2011. Furthermore, the mean proportion of alpha paternity was found to be 65% (Engelhardt et al., 2017). Under these conditions there may be very little incentive for male crested macaques to cooperate with each other in defence of mates: dominant males can protect their own reproductive interests without engaging in joint action, and non-dominant males have little chance of achieving mating success even if they do cooperate.

Second, intergroup transfer is a common and risky occurrence for male crested macaques (Marty, 2015). Intragroup competition over access to fertile females is high, male takeover attempts can be extremely violent, and alpha male tenures only last on average 12 months (Marty, Hodges, Agil, et al., 2017); one of the shortest tenures known for any primate species (average in multi-male multi-female groups is approximately 50 months (Lukas & Clutton-Brock, 2014)). Given the high potential for injury, and the extreme reproductive skew towards dominant males, immigration attempts that result in anything less than a successful takeover may be extremely costly in terms of lifetime reproductive fitness. As such, in common with chacma baboons (*Papio ursinus*) (Alberts & Altmann, 1995), males often wait until they have reached their physical peak before attempting to transfer into another group (Marty, Hodges, Agil, et al., 2017), rather than emigrating at or shortly after sexual maturity, as seen in most other primate species characterised by male natal dispersal (Pusey & Packer, 1986). In sum, the timing of male takeover attempts is of crucial importance in this species (Marty et al., 2016) and IGEs can be valuable opportunities to assess the relative strengths of out-group males. However, this strategy does not require cooperation between males either (even though low ranking males sometimes transfer together following a successful takeover by another more dominant individual (Marty et al., 2016)).

Finally, the males of several group-living primate species do cooperate to defend food resources for females during IGC, acting as 'hired-guns' (Scarry, 2013, 2017; Willems & van Schaik, 2015; Williams et al., 2004). However, there appear to be two main impediments to this in crested macaques: the antagonistic social relationships between males, and the abundance of food at this study site. Within social systems in which males are less closely related to each other than are resident females (like that of crested macaques), tolerance, friendship, and trust among resident males appears to play an important role in facilitating the emergence of collective action (Gilby & Wrangham, 2008). For unrelated males these qualities are likely achieved over time and through frequent, predictable social interactions (Kitchen, 2004). However, relations between male crested macaques are generally short-lived, infrequent, and antagonistic (Reed et al., 1997). In addition, the quick turnover and high reproductive skew associated with the alpha male position also means that relatedness among offspring (including males) is lower than it would be in species with longer alpha tenures. This likely hinders cooperation also (Widdig, 2013). As such, males may not associate with each other often enough, for long enough, or with enough tolerance to form the kind of bonds required to cooperatively defend food resources, for females or themselves.

Furthermore, the availability of food at this study site is extremely high, and very predictable year-round (Kinnaird et al., 1999; Kinnaird & O'Brien, 1995, 2005; O'Brien & Kinnaird, 1997; Ratna Sari, 2013), so much so that it may preclude the need for females to compete for it and thus for males to act as ‘hired-guns’ at all. Because female reproductive fitness is primarily restricted by access to the resources needed to raise offspring (Cheney & Seyfarth, 1987; Fashing, 2001; Trivers, 1972), females should experience a strong selective pressure to contest and win IGCs when these resources are at stake. However, the extraordinary density of fruiting trees in Tangkoko Nature Reserve (TNR) (Kinnaird et al., 1999; Kinnaird & O’Brien, 2005; Ratna Sari, 2013) may reduce the level of direct intergroup food competition to such an extent that the pressure for female crested macaques to compete and win is (at least partially) relieved.

In practice this may have given rise to a situation whereby groups that lose (or are denied) access to a contested food resource can simply travel to another nearby. While there are still costs associated with this (e.g. reduced opportunities for feeding and resting, and increased energy expenditure during travel), these are almost certainly outweighed by the potential costs of aggressive IGC (e.g. heightened anxiety, greatly increased energy expenditure for conflict participants, potential injury or death, and even the loss of offspring (Martínez-Iñigo, 2017; personal observation). In sum, it appears that an abundance of food at this study site may (a) release female crested macaques from the pressure to compete for resources with other groups, (b) release male crested macaques from the need to act as ‘hired-guns’, and as such, (c) remove any pressure for the evolution of female behaviours that promote collective action or incentivise future participation in IGC.

This idea is supported by the fact that I found no evidence of female attempts to incentivise male participation either before or after conflict. I investigated both possibilities and found evidence of neither (Chapters 4 and 5, respectively). Shortly before entering high encounter risk areas, social interactions between mixed-sex dyads decreased dramatically and the number of females from whom male macaques received affiliative behaviour decreased almost to zero. Neither did I observe any post-conflict punishment or reward associated with participation (via aggression or the giving/withholding of affiliative behaviour). These patterns strongly suggest the absence of any attempt by females to incentivise male or female participation, as has been observed in vervet monkeys (*Chlorocebus pygerythrus*) for example (Arseneau-Robar et al., 2016). Rather, the changes in social behaviour that I observed in the aftermath of IGC (Chapter 5) appear to function primarily to reduce stress and anxiety. Although the overall rate of affiliative behaviour decreased in the first hour following IGC, individuals in losing groups exchanged more affiliative behaviours than those in winning groups. Theory predicts that losing an encounter is more stressful than winning (Radford et al., 2016), however I found no evidence of this in my comparison of self-scratching rates between winning and losing groups. Individuals also focused their social effort on strongly bonded social partners, rather than on conflict participants. If post-conflict affiliation in crested macaques functions to increase group cohesion (in order to promote future collective action) we would expect to see an increase in the aftermath of conflict, and/or a change in patterns of social effort that reflect this, e.g. rapid affiliation with many different partners as described in blue monkeys (Cords, 2002), or a focus on conflict participants. I found evidence of neither.

6.2 Limitations and future directions

Throughout this study there are some limitations to consider. Among these was my inability to follow all three study groups every day. This makes it difficult to be certain about IGE rates and win/loss records. However, whenever possible my field assistant and I split up and followed two groups simultaneously. Also, I only collected data on three macaque groups. This allowed for large volumes of data to be collected on each group (essential for robust analyses of dyadic behavioural interactions), but at the cost of capturing a greater range of intergroup variation in response to conflict. However, I was able to sample three groups of considerably different size. This has the advantage of making my results more reliably applicable to other samples or populations of crested macaques than if I had studied groups of similar sizes.

Throughout the thesis my quantification of IGE risk relied on risk maps created from encounters that occurred in the preceding month. For example, for each group, focal observations that occurred in August 2018 were assigned risk values from the July 2018 risk map. This approach relies on the assumption that one month is a reasonable time window over which crested macaques remember previous encounters and that this alters their perception of encounter risk accordingly. In theory it may have been more parsimonious to construct weekly or even daily rolling risk maps. However, given the frequency with which each group was followed, one month was the smallest window in which enough data were collected to construct accurate risk maps.

Finally, my inability to include subadult individuals in observations and analyses may have biased some of my conclusions (Fedurek & Lehmann, 2017), particularly with respect to the effects of risk on group-wide spatial cohesion, and both risk and occurrence of conflict on dyadic social behaviour. The effect of excluding subadult females from the spatial cohesion analyses is unlikely to be too problematic because they tended to stay close to their older female relatives, particularly in the context of IGC. However, subadult males, particularly those approaching sexual maturity, are the class of individuals most likely to benefit from the information-gathering potential of IGEs (Marty, 2015; Marty et al., 2016). As such, these young males may be more motivated than the rest of their group to explore areas where the likelihood of IGE is high, and this may have skewed some of my group spread measurements. In terms of post-conflict social behaviour, the exclusion of young males is unlikely to be problematic because male macaques exchange so little social behaviour at any time (Reed et al., 1997; this study). Also, because they are highly unlikely to sire offspring in their own natal group (Engelhardt et al., 2017; Reed et al., 1997), sub-adult males have little incentive to defend mates or to act as hired-guns; either of which might garner social attention from group-mates. However, subadult females frequently exchange affiliative social behaviours with adult individuals, particularly older (presumably related) females. In order to investigate questions about partner choice throughout the thesis, both interaction partners had to be identified with certainty. This was not possible with all subadult individuals (including females). As a result, social interactions between adults and subadults were not included in analyses of affiliation rates. While this may have artificially deflated rates of intragroup affiliation, this effect is likely to be similar across groups. Furthermore, because subadult individuals rarely participate in IGC to the same extent as adults, interactions that involve them seem unlikely to serve the kind of strategic functions that I hypothesised throughout.

Moving forward, a more focused approach to phenological data collection might answer one of the most interesting questions raised by my study: are there any specific resources that reliably predict the escalation of intergroup aggression? If so, it would suggest that some resources are in fact limiting and that the pressure for collective action in crested macaques is not entirely absent. It may simply be that it does not occur frequently enough to exert a meaningful selection pressure on behaviours that would facilitate joint defence. For example, during the dry season reliable sources of fresh water are scarce. Groups often spent an unusually large proportion of the day at those locations, foraging less and resting/socialising nearby instead. The same was true of a few highly palatable, seasonally limited fruits such as mango (*Magnifera indica*). Anecdotally, the occurrence and frequency of IGEs increased considerably during the short mango fruiting window. Compared to *Ficus* spp. and *Dracontomelon dao* trees (the primary and preferred foods (Kinnaird & O'Brien, 1995, 2005; Lee, 1997; O'Brien & Kinnaird, 1997; Ratna Sari, 2013)), there were very few mango trees throughout the study area and the increase in intergroup hostility appeared to be centred around these locations. It is possible therefore, that in periods of scarcity male and female macaques may attempt to gain access to limited/highly palatable resources (Majolo et al., 2005), and that under these conditions we may see the emergence of (albeit temporary) behavioural mechanisms that facilitate intragroup cooperation and collective action. If this were the case it would suggest a more flexible, ecologically driven response to the need for collective action, which might go some way to explaining why intergroup coalitionary aggression does still occur (on rare occasions) in this population, despite the low level of resource competition.

Another way to approach this question might be to conduct a similar study with the large introduced population of crested macaques on the island of Bacan, in the North Mollucas, 300 km southeast of North Sulawesi. Little is known about this population by comparison, but population density is reportedly very high (Rosenbaum et al., 1998), which may mean that IGEs are frequent in this population also. However, like the study population, the Bacan population also enjoys an extremely high density of food resources (Rosenbaum et al., 1998). Although for comparative purposes it would be more instructive to study another population with less abundant resources it may still be illuminating to discover whether the patterns observed in this study are repeated elsewhere.

6.3 General conclusion

In this thesis I set out to investigate how the risk and occurrence of IGC influences intragroup social behaviour. What is most notable about my findings, especially when considered as a whole, is that I found no convincing evidence to indicate that IGC promotes cohesion and cooperation in crested macaques. Rather, I found that the particular ecological conditions under which this population exists (superabundant natural food resources), and the peculiarities of the male social system and reproductive strategy, seem to preclude the need for collective action in the context of IGC. In summary, I propose that this population of crested macaques have not experienced strong or sustained enough selective pressure to drive the evolution of behaviours that facilitate intragroup cohesion, cooperation, and collective action. These findings highlight the importance of examining a broad range of species and social systems when investigating the effect of intergroup competition on intragroup social evolution. In doing so I hope to have furthered our understanding of the factors that promote the evolution of cooperative behaviour in social primates by demonstrating a few limited effects of their absence.

Indeed, my findings suggest that not all groups that engage in IGC always have something worth fighting for, and that we need to find ways of incorporating this possibility into future models of intergroup hostility. A new meta-analysis of studies that link IGC with intragroup affiliation could focus on whether studies have considered, quantified, or controlled for the effect of territorial resource availability, both in space and time (i.e. considering seasonal supply and demand of specific limiting resources). The work involved in collecting data of this kind is considerable, but it may contribute to the emergence of a more thorough and coherent understanding of the factors that facilitate and impede collective action in group-living animals.

References

Abramson, I. S. (1982). On Bandwidth Variation in Kernel Estimates-A Square Root Law. *The Annals of Statistics*, *10*(4), 1217–1223. JSTOR.

Adams, E. S. (1990). Boundary disputes in the territorial ant Azteca trigona: effects of asymmetries in colony size. *Animal Behaviour*, *39*(2), 321–328. https://doi.org/10.1016/S0003-3472(05)80877-2

Agetsuma, N. (1995). Foraging Synchrony in a Group of Yakushima Macaques (Macaca fuscata yakui). *Folia Primatologica*, *64*(4), 167–179. https://doi.org/10.1159/000156850

Ai, C., & Norton, E. C. (2003). Interaction terms in logit and probit models. *Economics Letters*, *80*(1), 123–129. https://doi.org/10.1016/S0165-1765(03)00032-6

Albers, P. C. H., & de Vries, H. (2001). Elo-rating as a tool in the sequential estimation of dominance strengths. *Animal Behaviour*, *61*(2), 489–495. https://doi.org/10.1006/anbe.2000.1571

Alberts, S., & Altmann, J. (1995). Balancing Costs and Opportunities: Dispersal in Male Baboons. *American Naturalist*, *145*, 279–306. https://doi.org/10.1086/285740

Alberts, S. C., Watts, H. E., & Altmann, J. (2003). Queuing and queue-jumping: long-term patterns of reproductive skew in male savannah baboons, Papio cynocephalus. *Animal Behaviour*, *65*(4), 821–840. https://doi.org/10.1006/anbe.2003.2106

Alexander, R. D., & Borgia, G. (1978). Group Selection, Altruism, and the Levels of Organization of Life. *Annual Review of Ecology and Systematics*, *9*(1), 449–474. https://doi.org/10.1146/annurev.es.09.110178.002313

Allan, A. T. L., & Hill, R. A. (2018). What have we been looking at? A call for consistency in studies of primate vigilance. *American Journal of Physical Anthropology*, *165*(S65), 4–22. https://doi.org/10.1002/ajpa.23381

Altmann, J. (1974). Observational Study of Behavior: Sampling Methods. *Behaviour*, *49*(3/4), 227–267.

Altmann, J. (1980). Baboon mothers and infants Harvard University Press. *Cambridge, MA.[Google Scholar]*.

Altmann, J., Alberts, S. C., Haines, S. A., Dubach, J., Muruthi, P., Coote, T., Geffen, E., Cheesman, D. J., Mututua, R. S., Saiyalel, S. N., & others. (1996). Behavior predicts genes structure in a wild primate group. *Proceedings of the National Academy of Sciences*, *93*(12), 5797–5801.

Altmann, S. A. (1962). A field study of the sociology of rhesus monkeys, Macaca mulatta. *Annals of the New York Academy of Sciences*.

Altmann, S. A., & Altmann, J. (1973). *Baboon ecology*. University of Chicago Press.

Andersson, M. (1984). The Evolution of Eusociality. *Annual Review of Ecology and Systematics*, *15*, 165–189. https://doi.org/10.1146/annurev.ecolsys.15.1.165

Arseneau, T. J. M. (2010). *Causes and consequences of group dominance in social-territorial species: A study of eastern wolves(Canis lycaon) in Algonquin Provincial Park, Ontario, Canada* [MSc]. Trent University.

Arseneau-Robar, T. J. M., Müller, E., Taucher, A. L., van Schaik, C. P., Bshary, R., & Willems, E. P. (2018). Male monkeys use punishment and coercion to de-escalate costly intergroup fights. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1880), 20172323. https://doi.org/10.1098/rspb.2017.2323

Arseneau-Robar, T. J. M., Taucher, A. L., Schnider, A. B., van Schaik, C. P., & Willems, E. P. (2017). Intra- and interindividual differences in the costs and benefits of intergroup aggression in female vervet monkeys. *Animal Behaviour*, *123*, 129–137. https://doi.org/10.1016/j.anbehav.2016.10.034

Arseneau-Robar, T. Jean. M., Taucher, A. L., Müller, E., van Schaik, C. P., Bshary, R., & Willems, E. P. (2016). Female monkeys use both the carrot and the stick to promote male participation in intergroup fights. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1843), 20161817. https://doi.org/10.1098/rspb.2016.1817

Asher, L., & Collins, L. M. (2012). Assessing synchrony in groups: Are you measuring what you think you are measuring? *Applied Animal Behaviour Science*, *138*(3–4), 162–169. https://doi.org/10.1016/j.applanim.2012.02.004

Aureli, F., Schaffner, C. M., Verpooten, J., Slater, K., & Ramos-Fernandez, G. (2006). Raiding parties of male spider monkeys: Insights into human warfare? *American Journal of Physical Anthropology*, *131*(4), 486–497. https://doi.org/10.1002/ajpa.20451

Aureli, F., & Yates, K. (2010). Distress prevention by grooming others in crested black macaques. *Biology Letters*, *6*(1), 27–29. https://doi.org/10.1098/rsbl.2009.0513

Baniel, A., Cowlishaw, G., & Huchard, E. (2017). Male Violence and Sexual Intimidation in a Wild Primate Society. *Current Biology*, *27*(14), 2163-2168.e3. https://doi.org/10.1016/j.cub.2017.06.013

Banks, P. B. (2001). Predation-sensitive grouping and habitat use by eastern grey kangaroos: a field experiment. *Animal Behaviour*, *61*(5), 1013–1021. https://doi.org/10.1006/anbe.2001.1686

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, *68*(3), 255–278. https://doi.org/10.1016/j.jml.2012.11.001

Batchelor, T. P., & Briffa, M. (2010). Influences on resource-holding potential during dangerous group contests between wood ants. *Animal Behaviour*, *80*(3), 443–449. https://doi.org/10.1016/j.anbehav.2010.05.030

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Bejder, L., Samuels, A., Whitehead, H., Finn, H., & Allen, S. (2009). Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. *Marine Ecology Progress Series*, *395*, 177–185. https://doi.org/10.3354/meps07979

Benadi, G., Fichtel, C., & Kappeler, P. (2008). Intergroup relations and home range use in Verreaux's sifaka (*Propithecus verreauxi*). *American Journal of Primatology*, *70*(10), 956–965. https://doi.org/10.1002/ajp.20588

Beran, M. J., Pate, J. L., Washburn, D. A., & Rumbaugh, D. M. (2004). Sequential responding and planning in chimpanzees (Pan troglodytes) and rhesus macaques (Macaca mulatta). *Journal of Experimental Psychology: Animal Behavior Processes*, *30*(3), 203.

Birch, G., Cant, M. A., & Thompson, F. J. (2019). Behavioural response of workers to repeated intergroup encounters in the harvester ant Messor barbarus. *Insectes Sociaux*, *66*(3), 491–500. https://doi.org/10.1007/s00040-019-00710-2

Bleicher, S. S. (2017). The landscape of fear conceptual framework: definition and review of current applications and misuses. *PeerJ*, *5*, e3772. https://doi.org/10.7717/peerj.3772

Bode, N. W. F., Faria, J. J., Franks, D. W., Krause, J., & Wood, A. J. (2010). How perceived threat increases synchronization in collectively moving animal groups. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1697), 3065–3070. https://doi.org/10.1098/rspb.2010.0855

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï Forest: Behavioural ecology and evolution*. Oxford University Press, USA.

Boesch, C., Crockford, C., Herbinger, I., Wittig, R., Moebius, Y., & Normand, E. (2008). Intergroup conflicts among chimpanzees in Taï National Park: lethal violence and the female perspective. *American Journal of Primatology*, *70*(6), 519–532. https://doi.org/10.1002/ajp.20524

Boesch, C., Kohou, G., Néné, H., & Vigilant, L. (2006). Male competition and paternity in wild chimpanzees of the Taï forest. *American Journal of Physical Anthropology*, *130*(1), 103–115. https://doi.org/10.1002/ajpa.20341

Boinski, S., & Campbell, A. (1995). Use of Trill Vocalizations to Coordinate Troop Movement among White-Faced Capuchins: A Second Field Test. *Behaviour*, *132*(11/12), 875–901.

Boinski, S., & Garber, P. A. (2000). *On the move: how and why animals travel in groups*. University of Chicago Press.

Boinski, S., Treves, A., & Chapman, C. A. (2000). A critical evaluation of the influence of predators on primates: effects on group travel. *On the Move: How and Why Animals Travel in Groups. University of Chicago Press, Chicago*, 43–72.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*(3), 127–135. https://doi.org/10.1016/j.tree.2008.10.008

Bonanni, R., Valsecchi, P., & Natoli, E. (2010). Pattern of individual participation and cheating in conflicts between groups of free-ranging dogs. *Animal Behaviour*, *79*(4), 957–968.

Bourjade, M., Thierry, B., Call, J., & Dufour, V. (2012). Are monkeys able to plan for future exchange? *Animal Cognition*, *15*(5), 783–795. https://doi.org/10.1007/s10071-012-0502-1

Bowles, S. (2009). Did Warfare Among Ancestral Hunter-Gatherers Affect the Evolution of Human Social Behaviors? *Science*, *324*(5932), 1293–1298. https://doi.org/10.1126/science.1168112

Boydston, E. E., Morelli, T. L., & Holekamp, K. E. (2001). Sex differences in territorial behavior exhibited by the spotted hyena (Hyaenidae, Crocuta crocuta). *Ethology*, *107*(5), 369–385.

Braga Goncalves, I., & Radford, A. N. (2019). Experimental evidence that intruder and group member attributes affect outgroup defence and associated within-group interactions in a social fish. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1912), 20191261. https://doi.org/10.1098/rspb.2019.1261

Brambor, T., Clark, W. R., & Golder, M. (2006). Understanding Interaction Models: Improving Empirical Analyses. *Political Analysis*, *14*(1), 63–82. https://doi.org/10.1093/pan/mpi014

Braune, P., Schmidt, S., & Zimmermann, E. (2005). Spacing and group coordination in a nocturnal primate, the golden brown mouse lemur (Microcebus ravelobensis): the role of olfactory and acoustic signals. *Behavioral Ecology and Sociobiology*, *58*(6), 587–596. https://doi.org/10.1007/s00265-005-0944-4

Brockman, D. K. (1999). Reproductive behavior of female Propithecus verreauxi at Beza Mahafaly, Madagascar. *International Journal of Primatology*, *20*(3), 375–398.

Brooks, M., E., Kristensen, K., Benthem, K., J. ,van, Magnusson, A., Berg, C., W., Nielsen, A., Skaug, H., J., Mächler, M., & Bolker, B., M. (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal*, *9*(2), 378. https://doi.org/10.32614/RJ-2017-066

Brown, M. (2013). Food and range defence in group-living primates. *Animal Behaviour*, *85*(4), 807–816. https://doi.org/10.1016/j.anbehav.2013.01.027

Bruintjes, R., Lynton-Jenkins, J., Jones, J. W., & Radford, A. N. (2016). Out-Group Threat Promotes Within-Group Affiliation in a Cooperative Fish. *The American Naturalist*, *187*(2), 274–282. https://doi.org/10.1086/684411

Burkart, J. M., & van Schaik, C. P. (2010). Cognitive consequences of cooperative breeding in primates? *Animal Cognition*, *13*(1), 1–19. https://doi.org/10.1007/s10071-009-0263-7

Burton-Chellew, M. N., Ross-Gillespie, A., & West, S. A. (2010). Cooperation in humans: competition between groups and proximate emotions. *Evolution and Human Behavior*, *31*(2), 104–108. https://doi.org/10.1016/j.evolhumbehav.2009.07.005

Byrne, R., Whiten, A., & Henzi, S. (1987). One-male groups and intergroup interactions of mountain baboons. *International Journal of Primatology*, *8*(6), 615–633.

Calenge, C. (2011). Home range estimation in R: the adehabitatHR package. *Office National de La Classe et de La Faune Sauvage: Saint Benoist, Auffargis, France*.

Campbell, L. A. D., Tkaczynski, P. J., Lehmann, J., Mouna, M., & Majolo, B. (2018). Social thermoregulation as a potential mechanism linking sociality and fitness: Barbary macaques with more social partners form larger huddles. *Scientific Reports*, *8*(1), 6074.

Campos, F. A., & Fedigan, L. M. (2014). Spatial ecology of perceived predation risk and vigilance behavior in white-faced capuchins. *Behavioral Ecology*, *25*(3), 477–486. https://doi.org/10.1093/beheco/aru005

Carlson, A. (1986). Group Territoriality in the Rattling Cisticola, Cisticola chiniana. *Oikos*, *47*(2), 181–189. https://doi.org/10.2307/3566044

Caro, T., Roper, R., Young, M., & Dank, G. (1979). Inter-observer reliability. *Behaviour*, *69*(3–4), 303–315.

Carpenter, C. R. (1942). Sexual behavior of free ranging rhesus monkeys (Macaca mulatta). I. Specimens, procedures and behavioral characteristics of estrus. *Journal of Comparative Psychology*, *33*(1), 113.

Cassidy, K. A., Mech, L. D., MacNulty, D. R., Stahler, D. R., & Smith, D. W. (2017). Sexually dimorphic aggression indicates male gray wolves specialize in pack defense against conspecific groups. *Behavioural Processes*, *136*, 64–72. https://doi.org/10.1016/j.beproc.2017.01.011

Chapman, C. A. (1986). Boa constrictor Predation and Group Response in White-Faced Cebus Monkeys. *Biotropica*, *18*(2), 171. https://doi.org/10.2307/2388761

Cheney, D. L. (1987). Interactions and relationships between groups. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, T. Struhsaker, Thomas T., & R. W. Wrangham (Eds.), *Primate Societies* (pp. 267–281). iversity of Chicago Press.

Cheney, D. L. (1992). Intragroup cohesion and intergroup hostility: the relation between grooming distributions and intergroup competition among female primates. *Behavioral Ecology*, *3*(4), 334–345. https://doi.org/10.1093/beheco/3.4.334

Cheney, D. L., & Seyfarth, R. M. (1977). Behaviour of adult and immature male baboons during inter-group encounters. *Nature*, *269*(5627), 404–406. https://doi.org/10.1038/269404a0

Cheney, D. L., & Seyfarth, R. M. (1983). Nonrandom Dispersal in Free-Ranging Vervet Monkeys: Social and Genetic Consequences. *The American Naturalist*, *122*(3), 392–412. JSTOR.

Cheney, D. L., & Seyfarth, R. M. (1987). The Influence of Intergroup Competition on the Survival and Reproduction of Female Vervet Monkeys. *Behavioral Ecology and Sociobiology*, *21*(6), 375–386.

Cheney, D. L., & Seyfarth, R. M. (2009). Chapter 1 Stress and Coping Mechanisms in Female Primates. In *Advances in the Study of Behavior* (Vol. 39, pp. 1–44). Elsevier. https://doi.org/10.1016/S0065-3454(09)39001-4

Chism, J., & Rogers, W. (2004). Grooming and social cohesion in patas monkeys and other guenons. In M. E. Glenn & M. Cords (Eds.), *The guenons: Diversity and adaptation in African monkeys* (pp. 233–244). Springer.

Chivers, D. J. (1971). Spatial relations within the siamang group. *Proceedings of the 3rd International Congress of Primatology*, *3*, 14–21.

Choi, J.-K., & Bowles, S. (2007). The Coevolution of Parochial Altruism and War. *Science*, *318*(5850), 636–640. https://doi.org/10.1126/science.1144237

Christensen, C., Kern, J. M., Bennitt, E., & Radford, A. N. (2016). Rival group scent induces changes in dwarf mongoose immediate behavior and subsequent movement. *Behavioral Ecology*, *27*(6), 1627–1634. https://doi.org/10.1093/beheco/arw092

Christensen, C., & Radford, A. N. (2018). Dear enemies or nasty neighbors? Causes and consequences of variation in the responses of group-living species to territorial intrusions. *Behavioral Ecology*, *29*(5), 1004–1013. https://doi.org/10.1093/beheco/ary010

Ciuti, S., Northrup, J. M., Muhly, T. B., Simi, S., Musiani, M., Pitt, J. A., & Boyce, M. S. (2012). Effects of Humans on Behaviour of Wildlife Exceed Those of Natural Predators in a Landscape of Fear. *PLoS ONE*, *7*(11). https://doi.org/10.1371/journal.pone.0050611

Clark, F., & Melfi, V. (2005). Sexual swelling cycles in the Sulawesi crested black macaque (Macaca nigra). *Proceedings of the 7th Annual Symposium on Zoo Research, Twycross Zoo, Warwickshire, UK, 7-8th July 2005*, 102–112.

Clarke, M. F., da Silva, K. B., Lair, H., Pocklington, R., Kramer, D. L., McLaughlin, R. L., & Lair, H. (1993). Site Familiarity Affects Escape Behaviour of the Eastern Chipmunk, Tamias striatus. *Oikos*, *66*(3), 533. https://doi.org/10.2307/3544949

Clinchy, M., Zanette, L. Y., Roberts, D., Suraci, J. P., Buesching, C. D., Newman, C., & Macdonald, D. W. (2016). Fear of the human "super predator" far exceeds the fear of large carnivores in a model mesocarnivore. *Behavioral Ecology*, *27*(6), 1826–1832. https://doi.org/10.1093/beheco/arw117

Cohen, E. E. A., Ejsmond-Frey, R., Knight, N., & Dunbar, R. I. M. (2010). Rowers' high: behavioural synchrony is correlated with elevated pain thresholds. *Biology Letters*, *6*(1), 106–108. https://doi.org/10.1098/rsbl.2009.0670

Coleman, B. T., & Hill, R. A. (2014). Living in a landscape of fear: the impact of predation, resource availability and habitat structure on primate range use. *Animal Behaviour*, *88*, 165–173. https://doi.org/10.1016/j.anbehav.2013.11.027

Connor, R. C., Smolker, R. A., & Richards, A. F. (1992). Dolphin alliances and coalitions. *Coalitions and Alliances in Humans and Other Animals*, *414*, 443.

Connor, R. C., Smolker, R., & Bejder, L. (2006). Synchrony, social behaviour and alliance affiliation in Indian Ocean bottlenose dolphins, Tursiops aduncus. *Animal Behaviour*, *72*(6), 1371–1378. https://doi.org/10.1016/j.anbehav.2006.03.014

Conradt, L., & Roper, T. J. (2000). Activity synchrony and social cohesion: a fission-fusion model. *Proceedings of the Royal Society B: Biological Sciences*, *267*(1458), 2213–2218.

Conradt, L., & Roper, T. J. (2005). Consensus decision making in animals. *Trends in Ecology & Evolution*, *20*(8), 449–456. https://doi.org/10.1016/j.tree.2005.05.008

Cooksey, K., Sanz, C., Ebombi, T. F., Massamba, J. M., Teberd, P., Magema, E., Abea, G., Peralejo, J. S. O., Kienast, I., Stephens, C., & Morgan, D. (2020). Socioecological Factors Influencing Intergroup Encounters in Western Lowland Gorillas (Gorilla gorilla gorilla). *International Journal of Primatology*, *41*(2), 181–202. https://doi.org/10.1007/s10764-020-00147-6

Cooper, M. A., Aureli, F., & Singh, M. (2004). Between-Group Encounters among Bonnet Macaques (Macaca radiata). *Behavioral Ecology and Sociobiology*, *56*(3), 217–227.

Cords, M. (1995). Predator Vigilance Costs of Allogrooming in Wild Blue Monkeys. *Behaviour*, *132*(7/8), 559–569. JSTOR.

Cords, M. (2002). Friendship among adult female blue monkeys (Cercopithecus mitis). *Behaviour*, *139*(2), 291–314. https://doi.org/10.1163/156853902760102681

Cords, M., & Fuller, J. L. (2010). Infanticide in Cercopithecus mitis stuhlmanni in the Kakamega Forest, Kenya: Variation in the Occurrence of an Adaptive Behavior. *International Journal of Primatology*, *31*(3), 409–431. https://doi.org/10.1007/s10764-010-9400-z

Corti, P., & Shackleton, D. (2002). Relationship between predation-risk factors and sexual segregation in Dall's sheep (Ovis dalli dalli). *Canadian Journal of Zoology*, *80*, 2108–2117. https://doi.org/10.1139/Z02-207

Cowl, V. B., Jensen, K., Lea, J. M. D., Walker, S. L., & Shultz, S. (2020). Sulawesi Crested Macaque (Macaca nigra) Grooming Networks Are Robust to Perturbation While Individual Associations Are More Labile. *International Journal of Primatology*, *41*(1), 105–128. https://doi.org/10.1007/s10764-020-00139-6

Cowlishaw, G. (1994). Vulnerability To Predation in Baboon Populations. *Behaviour*, *131*(3–4), 293–304. https://doi.org/10.1163/156853994X00488

Cowlishaw, G. (1997). Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Animal Behaviour*, *53*(4), 667–686. https://doi.org/10.1006/anbe.1996.0298

Crofoot, M. C. (2012). Why Mob? Reassessing the Costs and Benefits of Primate Predator Harassment. *Folia Primatologica*, *83*(3–6), 252–273. https://doi.org/10.1159/000343072

Crofoot, M. C. (2013). The cost of defeat: Capuchin groups travel further, faster and later after losing conflicts with neighbors: Defeated Capuchin Groups Travel Further, Faster, Later. *American Journal of Physical Anthropology*, *152*(1), 79–85. https://doi.org/10.1002/ajpa.22330

Crofoot, M. C., & Gilby, I. C. (2012). Cheating monkeys undermine group strength in enemy territory. *Proceedings of the National Academy of Sciences*, *109*(2), 501–505. https://doi.org/10.1073/pnas.1115937109

Crofoot, M. C., Gilby, I. C., Wikelski, M. C., & Kays, R. W. (2008). Interaction location outweighs the competitive advantage of numerical superiority in Cebus capucinus intergroup contests. *Proceedings of the National Academy of Sciences*, *105*(2), 577–581. https://doi.org/10.1073/pnas.0707749105

Crofoot, M. C., & Wrangham, R. W. (2010). Intergroup aggression in primates and humans: the case for a unified theory. In *Mind the gap* (pp. 171–195). Springer.

Dannock, R. J., Pays, O., Renaud, P.-C., Maron, M., & Goldizen, A. W. (2019). Assessing blue wildebeests' vigilance, grouping and foraging responses to perceived predation risk using playback experiments. *Behavioural Processes*, *164*, 252–259. https://doi.org/10.1016/j.beproc.2019.05.021

Davies, T. M., Marshall, J. C., & Hazelton, M. L. (2018). Tutorial on kernel estimation of continuous spatial and spatiotemporal relative risk. *Statistics in Medicine*, *37*(7), 1191–1221.

De Dreu, C. K. W., Gross, J., Méder, Z., Giffin, M., Prochazkova, E., Krikeb, J., & Columbus, S. (2016). In-group defense, out-group aggression, and coordination failures in intergroup conflict. *Proceedings of the National Academy of Sciences*, *113*(38), 10524–10529. https://doi.org/10.1073/pnas.1605115113

Dekleva, M., van den Berg, L., Spruijt, B. M., & Sterck, E. H. M. (2012). Take it or leave it: Transport of tools for future use by long-tailed macaques (Macaca fascicularis). *Behavioural Processes*, *90*(3), 392–401. https://doi.org/10.1016/j.beproc.2012.04.003

Dixson, A. (2002). Sexual selection by cryptic female choice and the evolution of primate sexuality. *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews*, *11*(S1), 195–199.

Duboscq, J., Micheletta, J., Agil, M., Hodges, K., Thierry, B., & Engelhardt, A. (2013). Social Tolerance in Wild Female Crested Macaques (*Macaca nigra)* in Tangkoko-Batuangus Nature Reserve, Sulawesi, Indonesia: Social Tolerance in *M. nigra* Females. *American Journal of Primatology*, *75*(4), 361–375. https://doi.org/10.1002/ajp.22114

Duboscq, J., Neumann, C., Agil, M., Perwitasari-Farajallah, D., Thierry, B., & Engelhardt, A. (2017). Degrees of freedom in social bonds of crested macaque females. *Animal Behaviour*, *123*, 411–426. https://doi.org/10.1016/j.anbehav.2016.11.010

Dugatkin, L. A. (1997). Winner and loser effects and the structure of dominance hierarchies. *Behavioral Ecology*, *8*(6), 583–587. https://doi.org/10.1093/beheco/8.6.583

Dunbar, R. I. M. (1991). Functional Significance of Social Grooming in Primates. *Folia Primatologica*, *57*, 121–131. https://doi.org/10.1159/000156574

Dunbar, R. I. M., Baron, R., Frangou, A., Pearce, E., van Leeuwen, E. J. C., Stow, J., Partridge, G., MacDonald, I., Barra, V., & van Vugt, M. (2012). Social laughter is correlated with an elevated pain threshold. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1731), 1161–1167. https://doi.org/10.1098/rspb.2011.1373

Dunbar, R. I. M., & Dunbar, P. (1988). Maternal time budgets of gelada baboons. *Animal Behaviour*, *36*(4), 970–980.

Dunbar, R. I. M., & Nathan, M. F. (1972). Social Organization of the Guinea Baboon, *Papio papio*. *Folia Primatologica*, *17*(5–6), 321–334. https://doi.org/10.1159/000155453

Duranton, C., & Gaunet, F. (2016). Behavioural synchronization from an ethological perspective: Overview of its adaptive value. *Adaptive Behavior*, *24*(3), 181–191. https://doi.org/10.1177/1059712316644966

Dyble, M., Houslay, T. M., Manser, M. B., & Clutton-Brock, T. (2019). Intergroup aggression in meerkats. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1917), 20191993. https://doi.org/10.1098/rspb.2019.1993

Eckardt, W., Stoinski, T. S., Rosenbaum, S., Umuhoza, M. R., & Santymire, R. (2016). Validating faecal glucocorticoid metabolite analysis in the Virunga mountain gorilla using a natural biological stressor. *Conservation Physiology*, *4*(1), cow029. https://doi.org/10.1093/conphys/cow029

Emlen, S. T., & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science*, *197*(4300), 215–223.

Engel, J., & Lamprecht, J. (1997). Doing What Everybody Does? A Procedure for Investigating Behavioural Synchronization. *Journal of Theoretical Biology*, *185*(2), 255–262. https://doi.org/10.1006/jtbi.1996.0359

Engelhardt, A., & Farajallah, D. P. (2008). Reproductive biology of Sulawesi crested black macaques (Macaca nigra). *Folia Primatologica*, *79*(5), 326–326.

Engelhardt, A., Heistermann, M., Hodges, K., Nürnberg, P., & Niemitz, C. (2006). Determinants of male reproductive success in wild long-tailed macaques (Macaca fascicularis)—male monopolisation, female mate choice or post-copulatory mechanisms? *Behavioral Ecology and Sociobiology*, *59*(6), 740–752. https://doi.org/10.1007/s00265-005-0104-x

Engelhardt, A., Muniz, L., Perwitasari-Farajallah, D., & Widdig, A. (2017). Highly Polymorphic Microsatellite Markers for the Assessment of Male Reproductive Skew and Genetic Variation in Critically Endangered Crested Macaques (Macaca nigra). *International Journal of Primatology*, *38*(4), 672–691. https://doi.org/10.1007/s10764-017-9973-x

Enomoto, T. (1981). Male aggression and the sexual behavior of Japanese monkeys. *Primates*, *22*(1), 15–23.

Fagan, W. F., Lewis, M. A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G., LaDage, L., Schlägel, U. E., Tang, W., Papastamatiou, Y. P., Forester, J., & Mueller, T. (2013). Spatial memory and animal movement. *Ecology Letters*, *16*(10), 1316–1329. https://doi.org/10.1111/ele.12165

Fashing, P. (2001). Male and female strategies during intergroup encounters in guerezas (Colobus guereza): evidence for resource defense mediated through males and a comparison with other primates. *Behavioral Ecology and Sociobiology*, *50*(3), 219–230. https://doi.org/10.1007/s002650100358

Fedurek, P., & Lehmann, J. (2017). The effect of excluding juveniles on apparent adult olive baboons (Papio anubis) social networks. *PLOS ONE*, *12*(3), e0173146. https://doi.org/10.1371/journal.pone.0173146

Fieberg, J., & Kochanny, C. O. (2005). Quantifying home-range overlap: the importance of the utilization distribution. *The Journal of Wildlife Management*, *69*(4), 1346–1359.

Fischer, J. W., Walter, W. D., & Avery, M. L. (2013). Brownian Bridge Movement Models to Characterize Birds' Home Ranges. *The Condor*, *115*(2), 298–305. https://doi.org/10.1525/cond.2013.110168

Fisher, J. (1954). Evolution and bird sociality. *Evolution as a Process*, 71–83.

Flack, J. C., Krakauer, D. C., & de Waal, F. B. M. (2005). Robustness mechanisms in primate societies: a perturbation study. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1568), 1091–1099. https://doi.org/10.1098/rspb.2004.3019

Fooden, J. (1980). Classification and distribution of living macaques (Macaca lecépède, 1799). *The Macaques: Studies in Ecology, Behaviour and Evolution*.

Fragaszy, D. M., Boinski, S., & Whipple, J. (1992). Behavioral sampling in the field: Comparison of individual and group sampling methods. *American Journal of Primatology*, *26*(4), 259–275. https://doi.org/10.1002/ajp.1350260404

Franz, M., McLean, E., Tung, J., Altmann, J., & Alberts, S. C. (2015). Self-organizing dominance hierarchies in a wild primate population. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1814), 20151512. https://doi.org/10.1098/rspb.2015.1512

Furrer, R. D., Kyabulima, S., Willems, E. P., Cant, M. A., & Manser, M. B. (2011). Location and group size influence decisions in simulated intergroup encounters in banded mongooses. *Behavioral Ecology*, *22*(3), 493–500.

Garber, P. A., & Kowalewski, M. K. (2011). Collective Action and Male Affiliation in Howler Monkeys (Alouatta caraya). In R. W. Sussman & C. R. Cloninger (Eds.), *Origins of Altruism and Cooperation* (pp. 145–165). Springer New York. https://doi.org/10.1007/978-1-4419-9520-9_8

Gautier-Hion, A. (1970). The social organization of a band of talapoins (Miopithecus talapoin) in the northeast of Gabon. *Folia Primatologica*, *12*(2), 116–141.

Gautrais, J., Michelena, P., Sibbald, A., Bon, R., & Deneubourg, J.-L. (2007). Allelomimetic synchronization in Merino sheep. *Animal Behaviour*, *74*(5), 1443–1454. https://doi.org/10.1016/j.anbehav.2007.02.020

Gavrilets, S. (2015). Collective action problem in heterogeneous groups. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1683), 20150016. https://doi.org/10.1098/rstb.2015.0016

Gavrilets, S., & Fortunato, L. (2014). A solution to the collective action problem in between-group conflict with within-group inequality. *Nature Communications*, *5*(1). https://doi.org/10.1038/ncomms4526

Gebo, D., Chapman, C., Chapman, L., & Lambert, J. (1994). Locomotory response to predator threat in red colobus. *Primates*, *35*, 219–223. https://doi.org/10.1007/BF02382057

Gibson, K. N., Vick, L. G., Palma, A. C., Carrasco, F. M., Taub, D., & Ramos-Fernández, G. (2008). Intra-community infanticide and forced copulation in spider monkeys: a multi-site comparison between Cocha Cashu, Peru and Punta Laguna, Mexico. *American Journal of Primatology*, *70*(5), 485–489. https://doi.org/10.1002/ajp.20511

Gibson, L., & Koenig, A. (2012). Neighboring groups and habitat edges modulate range use in Phayre's leaf monkeys (Trachypithecus phayrei crepusculus). *Behavioral Ecology and Sociobiology*, *66*(4), 633–643. https://doi.org/10.1007/s00265-011-1311-2

Gilby, I., & Wrangham, R. (2008). Association Patterns Among Wild Chimpanzees (Pan Troglodytes Schweinfurthii) Reflect Sex Differences in Cooperation. *Behavioral Ecology and Sociobiology*, *62*. https://doi.org/10.1007/s00265-008-0612-6

Gittleman, J. L., & Thompson, S. D. (1988). Energy Allocation in Mammalian Reproduction. *American Zoologist*, *28*(3), 863–875. https://doi.org/10.1093/icb/28.3.863

Goodall, J. (1986). The chimpanzees of Gombe: Patterns of behavior. *Cambridge Mass*.

Grinnell, J. (2002). Modes of cooperation during territorial defense by African lions. *Human Nature*, *13*(1), 85–104. https://doi.org/10.1007/s12110-002-1015-4

Gros-Louis, J., Perry, S., & Manson, J. H. (2003). Violent coalitionary attacks and intraspecific killing in wild white-faced capuchin monkeys (Cebus capucinus). *Primates*, *44*(4), 341–346.

Grueter, C. C. (2013). No effect of inter-group conflict on within-group harmony in non-human primates. *Communicative & Integrative Biology*, *6*(6), e26801. https://doi.org/10.4161/cib.26801

Gumert, M. D. (2007). Payment for sex in a macaque mating market. *Animal Behaviour*, *74*(6), 1655–1667. https://doi.org/10.1016/j.anbehav.2007.03.009

Hale, A. M., Williams, D. A., & Rabenold, K. N. (2003). Territoriality and neighbor assessment in brown jays (Cyanocorax morio) in Costa Rica. *The Auk*, *120*(2), 446–456.

Hall, K. R. (1966). Behaviour and ecology of the wild patas monkey, Erythrocebus patas, in Uganda. *Journal of Zoology*, *148*(1), 15–87.

Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology*, *31*(2), 295–311. https://doi.org/10.1016/0022-5193(71)90189-5

Hamilton, W. D. (1975). Innate social aptitudes of man: an approach from evolutionary genetics. *Biosocial Anthropology*, *53*, 133–155.

Hankerson, S. J., & Caine, N. G. (2004). Pre-retirement predator encounters alter the morning behavior of captive marmosets (Callithrix geoffroyi). *American Journal of Primatology*, *63*(2), 75–85. https://doi.org/10.1002/ajp.20040

Harrington, F. H., & Mech, L. D. (1979). Wolf Howling and Its Role in Territory Maintenance. *Behaviour*, *68*(3/4), 207–249.

Harris, T. R. (2006). Between-Group Contest Competition for Food in a Highly Folivorous Population of Black and White Colobus Monkeys (Colobus guereza). *Behavioral Ecology and Sociobiology*, *61*(2), 317–329.

Hartig, F. (2019). *DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models*. https://CRAN.R-project.org/package=DHARMa

Heinsohn, R., & Packer, C. (1995). Complex cooperative strategies in group-territorial African lions. *Science*, *269*(5228), 1260–1262.

Heithaus, M. R., & Dill, L. M. (2002). *Food availability and tiger shark predation risk influence bottlenose dolphin habitat use*. *83*(2), 12.

Hellmann, J. K., & Hamilton, I. M. (2019). Intragroup social dynamics vary with the presence of neighbors in a cooperatively breeding fish. *Current Zoology*, *65*(1), 21–31. https://doi.org/10.1093/cz/zoy025

Herbert-Read, J. E., Buhl, J., Hu, F., Ward, A. J. W., & Sumpter, D. J. T. (2015). Initiation and spread of escape waves within animal groups. *Royal Society Open Science*, *2*(4), 140355. https://doi.org/10.1098/rsos.140355

Higham, J. P., Heistermann, M., Saggau, C., Agil, M., Perwitasari-Farajallah, D., & Engelhardt, A. (2012). Sexual signalling in female crested macaques and the evolution of primate fertility signals. *BMC Evolutionary Biology*, *12*, 89. https://doi.org/10.1186/1471-2148-12-89

Hijmans, R. J. (2020). *raster: Geographic Data Analysis and Modeling*. https://CRAN.R-project.org/package=raster

Hill, D. (1994). Affiliative Behaviour Between Adult Males of the Genus Macaca. *Behaviour*, *130*, 293–308. https://doi.org/10.1163/156853994X00578

Hilser, H., Sampson, H., Melfi, V., & Tasirin, J. S. (2013). Sulawesi crested black macaque Macaca nigra Species Action Plan: Draft 1. *Selamatkan Yaki–Pacific Institute, Manado, Indonesia*.

Hölldobler, B., & Lumsden, C. J. (1980). Territorial strategies in ants. *Science*, *210*(4471), 732–739.

Horne, J. S., Garton, E. O., Krone, S. M., & Lewis, J. S. (2007). Analyzing Animal Movements Using Brownian Bridges. *Ecology*, *88*(9), 2354–2363. https://doi.org/10.1890/06-0957.1

Huchard, E., Canale, C. I., Le Gros, C., Perret, M., Henry, P.-Y., & Kappeler, P. M. (2012). Convenience polyandry or convenience polygyny? Costly sex under female control in a promiscuous primate. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1732), 1371–1379. https://doi.org/10.1098/rspb.2011.1326

Isbell, L. A. (1990). Sudden short-term increase in mortality of vervet monkeys (Cercopithecus aethiops) due to leopard predation in Amboseli National Park, Kenya. *American Journal of Primatology*, *21*(1), 41–52. https://doi.org/10.1002/ajp.1350210105

Isbell, L. A. (1991). Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behavioral Ecology*, *2*(2), 143–155. https://doi.org/10.1093/beheco/2.2.143

Jack, K. M., Brown, M. R., Buehler, M. S., Cheves Hernadez, S., Ferrero Marín, N., Kulick, N. K., & Lieber, S. E. (2020). Cooperative rescue of a juvenile capuchin (Cebus imitator) from a Boa constrictor. *Scientific Reports*, *10*(1). https://doi.org/10.1038/s41598-020-73476-4

Janson, C. H. (1988). Intra-specific food competition and primate social structure: a synthesis. *Behaviour*, *105*(1–2), 1–17.

Janson, C. H., & van Schaik, C. P. (1988). Recognizing the many faces of primate food competition: methods. *Behaviour*, *105*(1/2), 165–186.

Johnson, C. L., Hilser, H., Linkie, M., Rahasia, R., Rovero, F., Pusparini, W., Hunowu, I., Patandung, A., Andayani, N., Tasirin, J., Nistyantara, L. A., & Bowkett, A. E. (2020). Using occupancy-based camera-trap surveys to assess the Critically Endangered primate Macaca nigra across its range in North Sulawesi, Indonesia. *Oryx*, *54*(6), 784–793. https://doi.org/10.1017/S0030605319000851

Johnstone, R. A., Cant, M. A., Cram, D., & Thompson, F. J. (2020). Exploitative leaders incite intergroup warfare in a social mammal. *Proceedings of the National Academy of Sciences*, *117*(47), 29759–29766. https://doi.org/10.1073/pnas.2003745117

Jordan, N. R., Cherry, M. I., & Manser, M. B. (2007). Latrine distribution and patterns of use by wild meerkats: implications for territory and mate defence. *Animal Behaviour*, *73*(4), 613–622. https://doi.org/10.1016/j.anbehav.2006.06.010

Kaburu, S. S. K., MacLarnon, A., Majolo, B., Qarro, M., & Semple, S. (2012). *Dominance rank and self-scratching among wild female Barbary macaques (Macaca sylvanus)*. *47*(1), 6.

Kappeler, P. M., & Silk, J. (Eds.). (2010). *Mind the gap: tracing the origins of human universals*. Springer.

Kelsall, J. E., & Diggle, P. J. (1995). Kernel estimation of relative risk. *Bernoulli*, *1*(1–2), 3–16.

Kerhoas, D., Perwitasari-Farajallah, D., Agil, M., Widdig, A., & Engelhardt, A. (2014). Social and ecological factors influencing offspring survival in wild macaques. *Behavioral Ecology*, *25*(5), 1164–1172. https://doi.org/10.1093/beheco/aru099

Kernohan, B. J., Gitzen, R. A., & Millspaugh, J. J. (2001). Analysis of animal space use and movements. In *Radio tracking and animal populations* (pp. 125–166). Elsevier.

Kikusui, T., Winslow, J. T., & Mori, Y. (2006). Social buffering: relief from stress and anxiety. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *361*(1476), 2215–2228. https://doi.org/10.1098/rstb.2006.1941

King, A. J., & Cowlishaw, G. (2009). All together now: behavioural synchrony in baboons. *Animal Behaviour*, *78*(6), 1381–1387. https://doi.org/10.1016/j.anbehav.2009.09.009

Kinnaird, M. F., & O'Brien, T. (2000). The Tana River Crested mangabey and the sulawesi crested black macaque. Comparative movement patterns of two semi terrestrial cercopithecine primates. *On the Move. How and Why Animals Travel in Groups*, 327–350.

Kinnaird, M. F., & O'Brien, T. G. (1995). *Variation in Fruit Resources and the Effects on Vertebrate Frugivores: The Role of Disturbance Regimes in Sulawesi*. Wildlife Conservation Society.

Kinnaird, M. F., & O'Brien, T. G. (2005). Fast Foods of the Forest: The Influence of Figs on Primates and Hornbills Across Wallace's Line. In J. L. Dew & J. P. Boubli (Eds.), *Tropical Fruits and Frugivores* (pp. 155–184). Springer-Verlag. https://doi.org/10.1007/1-4020-3833-X_9

Kinnaird, M. F., O'Brien, T. G., & Suryadi, S. (1999). The importance of figs to Sulawesi's imperiled wildlife. *Tropical Biodiversity*, *6*(1 & 2), 5–18.

Kitchen, D. M. (2004). Alpha male black howler monkey responses to loud calls: effect of numeric odds, male companion behaviour and reproductive investment. *Animal Behaviour*, *67*(1), 125–139. https://doi.org/10.1016/j.anbehav.2003.03.007

Kitchen, D. M., & Beehner, J. (2007). Factors affecting individual participation in group-level aggression among non-human primates. *Behaviour*, *144*(12), 1551–1581. https://doi.org/10.1163/156853907782512074

Kitchen, D. M., Cheney, D. L., & Seyfarth, R. M. (2004). Factors Mediating Inter-Group Encounters in Savannah Baboons (Papio cynocephalus ursinus). *Behaviour*, *141*(2), 197–218. JSTOR.

Koch, F., Signer, J., Kappeler, P. M., & Fichtel, C. (2016). Intergroup encounters in Verreaux's sifakas (Propithecus verreauxi): who fights and why? *Behavioral Ecology and Sociobiology*, *70*(5), 797–808. https://doi.org/10.1007/s00265-016-2105-3

Koda, H., Shimooka, Y., & Sugiura, H. (2008). Effects of caller activity and habitat visibility on contact call rate of wild Japanese macaques (*Macaca fuscata*). *American Journal of Primatology*, *70*(11), 1055–1063. https://doi.org/10.1002/ajp.20597

Koenig, A. (2002). Competition for Resources and Its Behavioral Consequences Among Female Primates. *International Journal of Primatology*, *23*(4), 759–783. https://doi.org/10.1023/A:1015524931226

Kotler, B. P., Brown, J. S., Bleicher, S. S., & Embar, K. (2016). Intercontinental-wide consequences of compromise-breaking adaptations: the case of desert rodents. *Israel Journal of Ecology & Evolution*, *62*(3–4), 186–195. https://doi.org/10.1080/15659801.2015.1125832

Koyama, N. F., Caws, C., & Aureli, F. (2006). Interchange of Grooming and Agonistic Support in Chimpanzees. *International Journal of Primatology*, *27*(5), 1293–1309. https://doi.org/10.1007/s10764-006-9074-8

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

Krebs, C. J. (1989). *Ecological Methodology* (2nd.). Harper & Row.

Kurihara, Y., & Hanya, G. (2018). Within-Population Variations in Home Range Use and Food Patch Use of Japanese Macaques: A Perspective of Intergroup Hostility. *Folia Primatologica*, *89*(6), 397–414. https://doi.org/10.1159/000493574

LaBarge, L. R., Allan, A. T. L., Berman, C. M., Margulis, S. W., & Hill, R. A. (2020). Reactive and pre-emptive spatial cohesion in a social primate. *Animal Behaviour*, *163*, 115–126. https://doi.org/10.1016/j.anbehav.2020.03.005

Langen, T. A., & Vehrencamp, S. L. (1998). Ecological Factors Affecting Group and Territory Size in White-Throated Magpie-Jays. *The Auk*, *115*(2), 327–339. https://doi.org/10.2307/4089191

Langergraber, K. E., Watts, D. P., Vigilant, L., & Mitani, J. C. (2017). Group augmentation, collective action, and territorial boundary patrols by male chimpanzees. *Proceedings of the National Academy of Sciences*, *114*(28), 7337–7342. https://doi.org/10.1073/pnas.1701582114

Laundré, J. W., Hernández, L., & Altendorf, K. B. (2001). Wolves, elk, and bison: reestablishing the 'landscape of fear' in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology*, *79*(8), 1401–1409. https://doi.org/10.1139/cjz-79-8-1401

Laundré, J. W., Hernández, L., & Ripple, W. J. (2010). The landscape of fear: ecological implications of being afraid. *Open Ecology Journal*, *3*, 1–7.

Lawson, A. B., & Williams, F. L. R. (1993). Applications of extraction mapping in environmental epidemiology. *Statistics in Medicine*, *12*(13), 1249–1258. https://doi.org/10.1002/sim.4780121306

Lazaro-Perea, C. (2001). Intergroup interactions in wild common marmosets, Callithrix jacchus: territorial defence and assessment of neighbours. *Animal Behaviour*, *62*(1), 11–21. https://doi.org/10.1006/anbe.2000.1726

Lee, R. J. (1997). *The impact of hunting and habitat disturbance on the population dynamics and behavioral ecology of the crested black macaque (Macaca nigra)* [PhD Thesis].

Lehmann, L., & Feldman, M. W. (2008). War and the evolution of belligerence and bravery. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1653), 2877–2885. https://doi.org/10.1098/rspb.2008.0842

Lemoine, S., Boesch, C., Preis, A., Samuni, L., Crockford, C., & Wittig, R. M. (2020). Group dominance increases territory size and reduces neighbour pressure in wild chimpanzees. *Royal Society Open Science*, *7*(5), 200577. https://doi.org/10.1098/rsos.200577

Lemoine, S., Preis, A., Samuni, L., Boesch, C., Crockford, C., & Wittig, R. M. (2020). Between-Group Competition Impacts Reproductive Success in Wild Chimpanzees. *Current Biology*, *30*(2), 312-318.e3. https://doi.org/10.1016/j.cub.2019.11.039

Lenth, R., Singmann, H., Love, J., Buerkner, P., & Herve, M. (2019). *R Package emmeans*. CRAN.

Lewis, R. J. (2006). Scent marking in sifaka: no one function explains it all. *American Journal of Primatology*, *68*(6), 622–636. https://doi.org/10.1002/ajp.20256

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, *68*(4), 619–640.

Lindburg, D. G. (1971). The rhesus monkey in North India: an ecological and behavioral study. *Primate Behavior: Developments in Field and Laboratory Research*, *2*, 1–106.

Lukas, D., & Clutton-Brock, T. (2014). Costs of mating competition limit male lifetime breeding success in polygynous mammals. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1786), 20140418. https://doi.org/10.1098/rspb.2014.0418

Mackinnon, J. (1974). The behaviour and ecology of wild orang-utans (Pongo pygmaeus). *Animal Behaviour*, *22*(1), 3–74. https://doi.org/10.1016/S0003-3472(74)80054-0

Maestripieri, D. (1993). Vigilance Costs of Allogrooming in Macaque Mothers. *The American Naturalist*, *141*(5), 744–753. https://doi.org/10.1086/285503

Maestripieri, D., Schino, G., Aureli, F., & Troisi, A. (1992). A modest proposal: displacement activities as an indicator of emotions in primates. *Animal Behaviour*, *44*(5), 967–979. https://doi.org/10.1016/S0003-3472(05)80592-5

Majolo, B., de Bortoli Vizioli, A., & Lehmann, J. (2016). The effect of intergroup competition on intragroup affiliation in primates. *Animal Behaviour*, *114*, 13–19. https://doi.org/10.1016/j.anbehav.2016.01.009

Majolo, B., deBortoli Vizioli, A., Martínez-Íñigo, L., & Lehmann, J. (2020). Effect of Group Size and Individual Characteristics on Intergroup Encounters in Primates. *International Journal of Primatology*. https://doi.org/10.1007/s10764-019-00119-5

Majolo, B., Ventura, R., & Koyama, N. F. (2005). Sex, rank and age differences in the Japanese macaque (Macaca fuscata yakui) participation in inter-group encounters. *Ethology*, *111*(5), 455–468.

Majolo, B., Ventura, R., & Koyama, N. F. (2009). Anxiety level predicts post-conflict behaviour in wild Japanese macaques (Macaca fuscata yakui). *Ethology*, *115*(10), 986–995.

Makin, D. F., Payne, H. F. P., Kerley, G. I. H., & Shrader, A. M. (2012). Foraging in a 3-D world: how does predation risk affect space use of vervet monkeys? *Journal of Mammalogy*, *93*(2), 422–428. https://doi.org/10.1644/11-MAMM-A-115.1

Maréchal, L., Semple, S., Majolo, B., Qarro, M., Heistermann, M., & MacLarnon, A. (2011). Impacts of tourism on anxiety and physiological stress levels in wild male Barbary macaques. *Biological Conservation*, *144*(9), 2188–2193. https://doi.org/10.1016/j.biocon.2011.05.010

Mares, R., Young, A. J., & Clutton-Brock, T. H. (2012). Individual contributions to territory defence in a cooperative breeder: weighing up the benefits and costs. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1744), 3989–3995. https://doi.org/10.1098/rspb.2012.1071

Markham, A. C., Guttal, V., Alberts, S. C., & Altmann, J. (2013). When good neighbors don't need fences: temporal landscape partitioning among baboon social groups. *Behavioral Ecology and Sociobiology*, *67*(6), 875–884. https://doi.org/10.1007/s00265-013-1510-0

Martínez-Iñigo, L. (2017). *Intergroup encounters in crested macaques (Macaca nigra)* [PhD Thesis]. University of Lincoln.

Martínez-Iñigo, L., Agil, M., Engelhardt, A., Malgorzata Pilot, & Majolo, B. (2017). *Resource and mate defence influence the outcome of intergroup encounters in wild crested macaques (Macaca nigra)* [Poster]. Unpublished. http://rgdoi.net/10.13140/RG.2.2.18384.05124

Marty, P. R. (2015). *Male migration and alpha male takeovers in crested macaques, Macaca nigra* [PhD Thesis]. Niedersächsische Staats-und Universitätsbibliothek Göttingen.

Marty, P. R., Hodges, K., Agil, M., & Engelhardt, A. (2016). Determinants of immigration strategies in male crested macaques (Macaca nigra). *Scientific Reports*, *6*(1). https://doi.org/10.1038/srep32028

Marty, P. R., Hodges, K., Agil, M., & Engelhardt, A. (2017). Alpha male replacements and delayed dispersal in crested macaques (*Macaca nigra*): Alpha Male Replacements in Crested Macaques. *American Journal of Primatology*, *79*(7), e22448. https://doi.org/10.1002/ajp.22448

Marty, P. R., Hodges, K., Heistermann, M., Agil, M., & Engelhardt, A. (2017). *Is social dispersal stressful? A study in male crested macaques (Macaca nigra) | Elsevier Enhanced Reader*. https://doi.org/10.1016/j.yhbeh.2016.10.018

May, R., van Dijk, J., Forland, J. M., Andersen, R., & Landa, A. (2008). Behavioural patterns in ewe–lamb pairs and vulnerability to predation by wolverines. *Applied Animal Behaviour Science*, *112*(1), 58–67. https://doi.org/10.1016/j.applanim.2007.07.009

Maynard Smith, J. (1982). *Evolution and the theory of games*. Cambridge university press Cambridge.

McGraw, W. S., Plavcan, J. M., & Adachi-Kanazawa, K. (2002). Adult female Cercopithecus diana employ canine teeth to kill another adult female C. diana. *International Journal of Primatology*, *23*(6), 1301–1308.

Mech, L. D. (1977). Productivity, mortality, and population trends of wolves in northeastern Minnesota. *Journal of Mammalogy*, *58*(4), 559–574.

Mech, L. D. (1994). Buffer Zones of Territories of Gray Wolves as Regions of Intraspecific Strife. *Journal of Mammalogy*, *75*(1), 199–202. https://doi.org/10.2307/1382251

Micheletta, J., Engelhardt, A., Matthews, L., Agil, M., & Waller, B. M. (2013). Multicomponent and Multimodal Lipsmacking in Crested Macaques (*Macaca nigra*): Lipsmacking Behavior in Crested Macaques. *American Journal of Primatology*, *75*(7), 763–773. https://doi.org/10.1002/ajp.22105

Mills, M. G. L. (1983). Behavioural mechanisms in territory and group maintenance of the brown hyaena, Hyaena brunnea, in the southern Kalahari. *Animal Behaviour*, *31*(2), 503–510. https://doi.org/10.1016/S0003-3472(83)80072-4

Millspaugh, J. J., Nielson, R. M., McDONALD, L., Marzluff, J. M., Gitzen, R. A., Rittenhouse, C. D., Hubbard, M. W., & Sheriff, S. L. (2006). Analysis of Resource Selection Using Utilization Distributions. *Journal of Wildlife Management*, *70*(2), 384–395. https://doi.org/10.2193/0022-541X(2006)70[384:AORSUU]2.0.CO;2

Mirville, M. O., Ridley, A. R., Samedi, J. P. M., Vecellio, V., Ndagijimana, F., Stoinski, T. S., & Grueter, C. C. (2020). Intragroup Behavioral Changes Following Intergroup Conflict in Mountain Gorillas (Gorilla beringei beringei). *International Journal of Primatology*, *41*(2), 382–400. https://doi.org/10.1007/s10764-020-00130-1

Mitani, J. C., Watts, D. P., & Amsler, S. J. (2010). Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. *Current Biology*, *20*(12), R507–R508. https://doi.org/10.1016/j.cub.2010.04.021

Mooring, M. S., & Hart, B. L. (1995). Costs of allogrooming in impala: distraction from vigilance. *Animal Behaviour*, *49*(5), 1414–1416.

Morris-Drake, A., Christensen, C., Kern, J. M., & Radford, A. N. (2019). Experimental field evidence that out-group threats influence within-group behavior. *Behavioral Ecology*. https://doi.org/10.1093/beheco/arz095

Mosser, A., & Packer, C. (2009). Group territoriality and the benefits of sociality in the African lion, Panthera leo. *Animal Behaviour*, *78*(2), 359–370. https://doi.org/10.1016/j.anbehav.2009.04.024

Muller, M. N., Kahlenberg, S. M., & Wrangham, R. W. (2009). Male aggression against females and sexual coercion in chimpanzees. *Sexual Coercion in Primates and Humans: An Evolutionary Perspective on Male Aggression against Females. Harvard University Press, Cambridge*, 184–217.

Neumann, C., Agil, M., Widdig, A., & Engelhardt, A. (2013). Personality of Wild Male Crested Macaques (Macaca nigra). *PLoS ONE*, *8*(8), e69383. https://doi.org/10.1371/journal.pone.0069383

Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., Widdig, A., & Engelhardt, A. (2011). Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. *Animal Behaviour*, *82*(4), 911–921. https://doi.org/10.1016/j.anbehav.2011.07.016

Neumann, C., & Kulik, L. (2014). *EloRating: Animal Dominance Hierarchies by Elo-Rating. R Package, Version 0.43*.

Nielson, R. M. H., Sawyer, H., & McDonald, T. L. (2013). *BBMM: Brownian bridge movement model* (R package version 3.0) [Computer software]. https://CRAN.R-project.org/package=BBMM

Nilsen, E. B., Linnell, J. D. C., & Andersen, R. (2004). Individual Access to Preferred Habitat Affects Fitness Components in Female Roe Deer Capreolus capreolus. *Journal of Animal Ecology*, *73*(1), 44–50. JSTOR.

Novak, M. A., Hamel, A. F., Kelly, B. J., Dettmer, A. M., & Meyer, J. S. (2013). Stress, the HPA axis, and nonhuman primate well-being: A review. *Applied Animal Behaviour Science*, *143*(2–4), 135–149. https://doi.org/10.1016/j.applanim.2012.10.012

Nowak, K., le Roux, A., Richards, S. A., Scheijen, C. P. J., & Hill, R. A. (2014). Human observers impact habituated samango monkeys' perceived landscape of fear. *Behavioral Ecology*, *25*(5), 1199–1204. https://doi.org/10.1093/beheco/aru110

Nowak, K., Wimberger, K., Richards, S. A., Hill, R. A., & le Roux, A. (2017). Samango Monkeys (Cercopithecus albogularis labiatus) Manage Risk in a Highly Seasonal, Human-Modified Landscape in Amathole Mountains, South Africa. *International Journal of Primatology*, *38*(2), 194–206. https://doi.org/10.1007/s10764-016-9913-1

Nunn, C. L. (2000). Collective benefits, free-riders, and male extra-group conflict. *Primate Males*, 192–204.

Nunn, C. L., & Deaner, R. O. (2004). Patterns of participation and free riding in territorial conflicts among ringtailed lemurs (Lemur catta). *Behavioral Ecology and Sociobiology*, *57*(1), 50–61. https://doi.org/10.1007/s00265-004-0830-5

Nunn, C. L., & Lewis, R. J. (2001). Cooperation and collective action in animal behaviour. In R. Noë, J. A. R. A. M. van Hooff, & P. Hammerstein (Eds.), *Economics in nature: Social dilemmas, mate choice and biological markets* (pp. 42–66). Cambridge University Press.

O'Brien, T. G., & Kinnaird, M. F. (1996). Changing populations of birds and mammals in North Sulawesi. *Oryx*, *30*(2), 150–156. https://doi.org/10.1017/S0030605300021530

O'Brien, T. G., & Kinnaird, M. F. (1997). Behavior, Diet, and Movements of the Sulawesi Crested Black Macaque (Macaca nigra). *International Journal of Primatology*, *18*(3), 31.

O'Brien, T., & Kinnaird, M. F. (2000). Differential vulnerability of large birds and mammals to hunting in North Sulawesi, Indonesia, and the outlook for the future. *Hunting for Sustainability in Tropical Forests*, 199–213.

Olson, M. (1965). *The Logic of Collective Action: Public Goods and the Theory of Groups* (21. printing, Vol. 24). Harvard Univ. Press.

Palagi, E., & Norscia, I. (2011). Scratching around stress: Hierarchy and reconciliation make the difference in wild brown lemurs (*Eulemur fulvus*). *Stress*, *14*(1), 93–97. https://doi.org/10.3109/10253890.2010.505272

Palombit, R. A. (2014). Sexual conflict in nonhuman primates. In *Advances in the Study of Behavior* (Vol. 46, pp. 191–280). Elsevier.

Parsons, M. H., & Blumstein, D. T. (2010). Familiarity Breeds Contempt: Kangaroos Persistently Avoid Areas with Experimentally Deployed Dingo Scents. *PLOS ONE*, *5*(5), e10403. https://doi.org/10.1371/journal.pone.0010403

Paulus, A. (2009). Impacts of ecotourism on the behaviour of Sulawesi Crested Black Macaques (Macaca nigra) and Spectral Tarsiers (Tarsius specrum) in the Tangkoko-Bantuangus nature reserve, North Sulawesi, Indonesia. *Plymouth: The University of Plymouth*.

Payne, H. F. P., Henzi, S. P., & Lawes, M. (2003). Competition and the Exchange of Grooming Among Female Samango Monkeys (Cercopithecus Mitis Erythrarchus). *Behaviour*, *140*(4), 453–471. https://doi.org/10.1163/156853903322127931

Payne, H. F. P., Lawes, M. J., & Henzi, S. P. (2003). Fatal Attack on an Adult Female Cercopithecus mitis erythrarchus: Implications for Female Dispersal in Female-Bonded Societies. *International Journal of Primatology*, *24*(6), 1245–1250. https://doi.org/10.1023/B:IJOP.0000005990.39403.96

Peet, R. K. (1974). The Measurement of Species Diversity. *Annual Review of Ecology and Systematics*, *5*(1), 285–307. https://doi.org/10.1146/annurev.es.05.110174.001441

Petit, O., & Thierry, B. (1994). Reconciliation in a group of black macaques Macaca nigra. *Dodo: Journal of the Wildlife Preservation Trusts*.

Pisor, A. C., & Surbeck, M. (2019). The evolution of intergroup tolerance in nonhuman primates and humans. *Evolutionary Anthropology: Issues, News, and Reviews*, *28*(4), 210–223. https://doi.org/10.1002/evan.21793

Polizzi di Sorrentino, E., Schino, G., Massaro, L., Visalberghi, E., & Aureli, F. (2012). Between-group hostility affects within-group interactions in tufted capuchin monkeys. *Animal Behaviour*, *83*(2), 445–451. https://doi.org/10.1016/j.anbehav.2011.11.016

Polizzi di Sorrentino, E., Schino, G., Tiddi, B., & Aureli, F. (2012). Scratching as a Window into the Emotional Responses of Wild Tufted Capuchin Monkeys. *Ethology*, *118*(11), 1072–1084. https://doi.org/10.1111/eth.12008

Preston, E. F. R., Thompson, F. J., Ellis, S., Kyambulima, S., Croft, D. P., & Cant, M. A. (2020). Network-level consequences of outgroup threats in banded mongooses: Grooming and aggression between the sexes. *Journal of Animal Ecology*, *n/a*(n/a). https://doi.org/10.1111/1365-2656.13323

Pride, R. E. (2005). High faecal glucocorticoid levels predict mortality in ring-tailed lemurs (Lemur catta). *Biology Letters*. https://doi.org/10.1098/rsbl.2004.0245

Pusey, A., & Packer, C. (1986). Dispersal and philopatry. Primate societies. *Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW & Struhsaker TT*, 150–166.

Puurtinen, M., Heap, S., & Mappes, T. (2015). The joint emergence of group competition and within-group cooperation. *Evolution and Human Behavior*, *36*(3), 211–217. https://doi.org/10.1016/j.evolhumbehav.2014.11.005

Puurtinen, M., & Mappes, T. (2009). Between-group competition and human cooperation. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1655), 355–360. https://doi.org/10.1098/rspb.2008.1060

R Core Team. (2019). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Radford, A. N. (2003). Territorial vocal rallying in the green woodhoopoe: influence of rival group size and composition. *Animal Behaviour*, *66*(6), 1035–1044. https://doi.org/10.1006/anbe.2003.2292

Radford, A. N. (2008a). Type of threat influences postconflict allopreening in a social bird. *Current Biology*, *18*(3), R114–R115. https://doi.org/10.1016/j.cub.2007.12.025

Radford, A. N. (2008b). Duration and outcome of intergroup conflict influences intragroup affiliative behaviour. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1653), 2787–2791. https://doi.org/10.1098/rspb.2008.0787

Radford, A. N. (2011). Preparing for battle? Potential intergroup conflict promotes current intragroup affiliation. *Biology Letters*, *7*(1), 26–29. https://doi.org/10.1098/rsbl.2010.0507

Radford, A. N., & Fawcett, T. (2014). Conflict between Groups Promotes Later Defense of a Critical Resource in a Cooperatively Breeding Bird. *Current Biology*, *24*(24), 2935–2939. https://doi.org/10.1016/j.cub.2014.10.036

Radford, A. N., Majolo, B., & Aureli, F. (2016). Within-group behavioural consequences of between-group conflict: a prospective review. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1843), 20161567. https://doi.org/10.1098/rspb.2016.1567

Rampim, L. E., Sartorello, L. R., Fragoso, C. E., Haberfeld, M., & Devlin, A. L. (2020). Antagonistic interactions between predator and prey: mobbing of jaguars (Panthera onca) by white-lipped peccaries (Tayassu pecari). *Acta Ethologica*, *23*(1), 45–48. https://doi.org/10.1007/s10211-020-00335-w

Rangel, J., Griffin, S., & Seeley, T. (2010). *Nest-site defense by competing honey bee (Apis mellifera) swarms during house-hunting*.

Rankin, D. J., Bargum, K., & Kokko, H. (2007). The tragedy of the commons in evolutionary biology. *Trends in Ecology & Evolution*, *22*(12), 643–651. https://doi.org/10.1016/j.tree.2007.07.009

Ratna Sari, I. (2013). *Anthropogenic effects on habitat use, activity budget, and energy balance in <i>Macaca nigra<i> at Tangkoko Nature Reserve, North Sulawesi, Indonesia*. Georg-August University.

Reed, C., O'Brien, T. G., & Kinnaird, M. F. (1997). *Male Social Behavior and Dominance Hierarchy in the Sulawesi Crested Black Macaque (Macaca nigra)*. 15.

Reeve, H. K., & Holldobler, B. (2007). The emergence of a superorganism through intergroup competition. *Proceedings of the National Academy of Sciences*, *104*(23), 9736–9740. https://doi.org/10.1073/pnas.0703466104

Reisland, M. A., & Lambert, J. E. (2016). Sympatric Apes in Sacred Forests: Shared Space and Habitat Use by Humans and Endangered Javan Gibbons (Hylobates moloch). *PLOS ONE*, *11*(1), e0146891. https://doi.org/10.1371/journal.pone.0146891

Riley, E. P. (2010). The endemic seven: Four decades of research on the Sulawesi macaques. *Evolutionary Anthropology: Issues, News, and Reviews*, *19*(1), 22–36. https://doi.org/10.1002/evan.20246

Riley, E. P., MacKinnon, K. C., Garber, P. A., Setchell, J. M., & Fernandez-Duque, E. (2014). *Code of Best Practices for Field Primatology* [International Primatological Society and American Society of Primatologists Steering Committee]. International Primatological Society and American Society of Primatologists Steering Committee. https://www.researchgate.net/publication/268515707_Code_of_Best_Practices_for_Field_Primatology

Rincon, A. V., Deschner, T., Schülke, O., & Ostner, J. (2019). *Oxytocin increases after affiliative interactions in male Barbary macaques* [Preprint]. Animal Behavior and Cognition. https://doi.org/10.1101/695064

Robinson, E. J. H., & Barker, J. L. (2017). Inter-group cooperation in humans and other animals. *Biology Letters*, *13*(3), 20160793. https://doi.org/10.1098/rsbl.2016.0793

Rogers, A. C., Langmore, N. E., & Mulder, R. A. (2007). Function of pair duets in the eastern whipbird: cooperative defense or sexual conflict? *Behavioral Ecology*, *18*(1), 182–188. https://doi.org/10.1093/beheco/arl070

Rogers, A. C., & Mulder, R. A. (2004). Breeding ecology and social behaviour of an antiphonal duetter, the eastern whipbird (Psophodes olivaceus). *Australian Journal of Zoology*, *52*(4), 417–435.

Rook, A. J., & Penning, P. D. (1991). Synchronisation of eating, ruminating and idling activity by grazing sheep. *Applied Animal Behaviour Science*, *32*(2–3), 157–166. https://doi.org/10.1016/S0168-1591(05)80039-5

Rosenbaum, B., O'Brien, T. G., Kinnaird, M. F., & Supriatna, J. (1998). Population densities of Sulawesi crested black macaques (Macaca nigra) on Bacan and Sulawesi, Indonesia: Effects of habitat disturbance and hunting. *American Journal of Primatology*, *44*(2), 89–106. https://doi.org/10.1002/(SICI)1098-2345(1998)44:2<89::AID-AJP1>3.0.CO;2-S

Rosenbaum, S., Vecellio, V., & Stoinski, T. (2016). Observations of severe and lethal coalitionary attacks in wild mountain gorillas. *Scientific Reports*, *6*(1). https://doi.org/10.1038/srep37018

Rubenstein, D. I. (1986). Ecology and sociality in horses and zebras. In D. I. Rubenstein & R. W. Wrangham (Eds.), *Ecological Aspects of Social Evolution.* (pp. 282–302). Princeton University Press.

Saito, C., Sato, S., Suzuki, S., Sugiura, H., Agetsuma, N., Takahata, Y., Sasaki, C., Takahashi, H., Tanaka, T., & Yamagiwa, J. (1998). Aggressive intergroup encounters in two populations of Japanese macaques (Macaca fuscata). *Primates*, *39*(3), 303–312. https://doi.org/10.1007/BF02573079

Samuni, L., Mielke, A., Preis, A., Crockford, C., & Wittig, R. M. (2019). Intergroup Competition Enhances Chimpanzee (Pan troglodytes verus) In-group Cohesion. *International Journal of Primatology*, *41*(2), 342–362. https://doi.org/10.1007/s10764-019-00112-y

Samuni, L., Preis, A., Deschner, T., Wittig, R. M., & Crockford, C. (2019). Cortisol and oxytocin show independent activity during chimpanzee intergroup conflict. *Psychoneuroendocrinology*, *104*, 165–173.

Sanchez, M. M., McCormack, K. M., & Howell, B. R. (2015). Social buffering of stress responses in nonhuman primates: Maternal regulation of the development of emotional regulatory brain circuits. *Social Neuroscience*, *10*(5), 512–526. https://doi.org/10.1080/17470919.2015.1087426

Sapolsky, R. M., Alberts, S. C., & Altmann, J. (1997). *Hypercortisolism associated with social subordinance or social isolation amon...* 7.

Scarf, D., Danly, E., Morgan, G., Colombo, M., & Terrace, H. S. (2011). Sequential planning in rhesus monkeys (Macaca mulatta). *Animal Cognition*, *14*(3), 317–324. https://doi.org/10.1007/s10071-010-0365-2

Scarry, C. J. (2013). Between-group contest competition among tufted capuchin monkeys, Sapajus nigritus, and the role of male resource defence. *Animal Behaviour*, *85*(5), 931–939. https://doi.org/10.1016/j.anbehav.2013.02.013

Scarry, C. J. (2017). Male resource defence during intergroup aggression among tufted capuchin monkeys. *Animal Behaviour*, *123*, 169–178. https://doi.org/10.1016/j.anbehav.2016.10.015

Scarry, C. J., & Tujague, M. P. (2012). Consequences of Lethal Intragroup Aggression and Alpha Male Replacement on Intergroup Relations and Home Range Use in Tufted Capuchin Monkeys (Cebus apella nigritus). *American Journal of Primatology*, *74*(9), 804–810. https://doi.org/10.1002/ajp.22030

Schaffner, C. M., & French, J. A. (1997). Group size and aggression: ‘recruitment incentives’ in a cooperatively breeding primate. *Animal Behaviour*, *54*(1), 171–180. https://doi.org/10.1006/anbe.1996.0413

Schino, G. (2001). Grooming, competition and social rank among female primates: a meta-analysis. *Animal Behaviour*, *62*(2), 265–271. https://doi.org/10.1006/anbe.2001.1750

Schino, G. (2007). Grooming and agonistic support: a meta-analysis of primate reciprocal altruism. *Behavioral Ecology*, *18*(1), 115–120. https://doi.org/10.1093/beheco/arl045

Schino, G., Troisi, A., Perretta, G., & Monaco, V. (1991). Measuring anxiety in nonhuman primates: Effect of lorazepam on macaque scratching. *Pharmacology Biochemistry and Behavior*, *38*(4), 889–891. https://doi.org/10.1016/0091-3057(91)90258-4

Schoof, V. A., & Jack, K. M. (2013). The association of intergroup encounters, dominance status, and fecal androgen and glucocorticoid profiles in wild male white-faced capuchins (Cebus capucinus). *American Journal of Primatology*, *75*(2), 107–115.

Schreier, A. L., & Swedell, L. (2012). Ecology and sociality in a multilevel society: Ecological determinants of spatial cohesion in hamadryas baboons. *American Journal of Physical Anthropology*, *148*(4), 580–588. https://doi.org/10.1002/ajpa.22076

Setchell, J. M., Charpentier, M., & Wickings, E. J. (2005). Mate guarding and paternity in mandrills: factors influencing alpha male monopoly. *Animal Behaviour*, *70*(5), 1105–1120. https://doi.org/10.1016/j.anbehav.2005.02.021

Seyfarth, R. M. (1978). Social Relationships Among Adult Male and Female Baboons. Ii. Behaviour Throughout the Female Reproductive Cycle. *Behaviour*, *64*(3–4), 227–247. https://doi.org/10.1163/156853978X00044

Shaffer, C. A. (2013). Activity Patterns, Intergroup Encounters, and Male Affiliation in Free-Ranging Bearded Sakis (Chiropotes sagulatus). *International Journal of Primatology*, *34*(6), 1190–1208. https://doi.org/10.1007/s10764-013-9727-3

Sherman, P. T. (2003). Intergroup Infanticide in Cooperatively Polyandrous White-winged Trumpeters (Psophia leucoptera). *The Wilson Journal of Ornithology*, *115*(3), 339–342. https://doi.org/10.1676/02-125

Shimada, M., Uno, T., Nakagawa, N., Fujita, S., & Izawa, K. (2009). Case Study of a One-Sided Attack by Multiple Troop Members on a Nontroop Adolescent Male and the Death of Japanese Macaques (Macaca fuscata). *Aggressive Behavior*, *35*, 334–341. https://doi.org/10.1002/ab.20308

Sicotte, P. (1993). Inter-group encounters and female transfer in mountain gorillas: Influence of group composition on male behavior. *American Journal of Primatology*, *30*(1), 21–36. https://doi.org/10.1002/ajp.1350300103

Sicotte, P., Teichroeb, J. A., & Saj, T. L. (2007). Aspects of Male Competition in Colobus vellerosus: Preliminary Data on Male and Female Loud Calling, and Infant Deaths After a Takeover. *International Journal of Primatology*, *28*(3), 627–636. https://doi.org/10.1007/s10764-007-9141-9

Silk, J., Cheney, D. L., & Seyfarth, R. M. (2013). A practical guide to the study of social relationships: A Practical Guide to the Study of Social Relationships. *Evolutionary Anthropology: Issues, News, and Reviews*, *22*(5), 213–225. https://doi.org/10.1002/evan.21367

Silverman, B. W. (1986). *Density Estimation for Statistics and Data Analysis*. Chapman & Hall.

Singmann, H., Bolker, B., Westfall, J., & Aust, F. (2017). *afex: Analysis of Factorial Experiments.*

Smith, A. C., Buchanan-Smith, H. M., Surridge, A. K., & Mundy, N. I. (2005). Factors Affecting Group Spread within Wild Mixed-Species Troops of Saddleback and Mustached Tamarins. *International Journal of Primatology*, *26*(2), 337–355. https://doi.org/10.1007/s10764-005-2928-7

Smuts, B. B. (1985). *Sex and friendship in baboons*. Transaction Publishers.

Smuts, B. B., Cheney, D. L., Seyfarth, R. M., & Wrangham, R. W. (2008). *Primate societies*. University of Chicago Press.

Smuts, B. B., & Smuts, R. W. (1993). Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Advances in the Study of Behavior*, *22*(22), 1–63.

Sommer, V., & Reichard, U. (1997). Group encounters in wild gibbons (Hylobates lar): agonism, affiliation, and the concept of infanticide. *Behaviour*, *134*(15–16), 1135–1174.

Stanford, C. B. (1995). The influence of chimpanzee predation on group size and anti-predator behaviour in red colobus monkeys. *Animal Behaviour*, *49*(3), 577–587. https://doi.org/10.1016/0003-3472(95)80191-X

Sterck, E. H. M., Watts, D. P., & van Schaik, C. P. (1997). The Evolution of Female Social Relationships in Nonhuman Primates. *Behavioral Ecology and Sociobiology*, *41*(5), 291–309. JSTOR.

Steventon, J., Liebenberg, L., Derbecker, M., Bapat, V., & Miles, D. (2011). CyberTracker. *Retrieved 23rd August*.

Stewart, P. D., Macdonald, D. W., Newman, C., & Cheeseman, C. L. (2001). Boundary faeces and matched advertisement in the European badger (Meles meles): a potential role in range exclusion. *Journal of Zoology*, *255*(2), 191–198. https://doi.org/10.1017/S0952836901001261

Stillfried, M., Gras, P., Börner, K., Göritz, F., Painer, J., Röllig, K., Wenzler, M., Hofer, H., Ortmann, S., & Kramer-Schadt, S. (2017). Secrets of Success in a Landscape of Fear: Urban Wild Boar Adjust Risk Perception and Tolerate Disturbance. *Frontiers in Ecology and Evolution*, *5*. https://doi.org/10.3389/fevo.2017.00157

Strong, M. J., Sherman, B. L., & Riehl, C. (2018). Home field advantage, not group size, predicts outcomes of intergroup conflicts in a social bird. *Animal Behaviour*, *143*, 205–213. https://doi.org/10.1016/j.anbehav.2017.07.006

Sugiura, H., Saito, C., Sato, S., Agetsuma, N., Takahashi, H., Tanaka, T., Furuichi, T., & Takahata, Y. (2000). Variation in intergroup encounters in two populations of Japanese macaques. *International Journal of Primatology*, *21*(3), 519–535.

Supriatna, J., & Andayani, N. (2008). Macaca nigra. *IUCN Red List of Threatened Species*.

Suzuki, S., Hill, D. A., & Sprague, D. S. (1998). Intertroop Transfer and Dominance Rank Structure of Nonnatal Male Japanese Macaques in Yakushima, Japan. *International Journal of Primatology*, *19*(4), 703–722. https://doi.org/10.1023/A:1020329010009

Tanner, C. J. (2006). Numerical assessment affects aggression and competitive ability: a team-fighting strategy for the ant Formica xerophila. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1602), 2737–2742. https://doi.org/10.1098/rspb.2006.3626

Tarr, B., Launay, J., Cohen, E., & Dunbar, R. I. M. (2015). Synchrony and exertion during dance independently raise pain threshold and encourage social bonding. *Biology Letters*, *11*(10), 20150767. https://doi.org/10.1098/rsbl.2015.0767

Teas, J. (1984). Rhesus monkey aggression and grooming social dynamics. *Female Primates: Studies by Women Primatologists. New York: Alan R. Liss. p*, 237–247.

Tello, N. S., Huck, M., & Heymann, E. W. (2002). Boa constrictor attack and successful group defence in moustached tamarins, Saguinus mystax. *Folia Primatologica*, *73*(2/3), 146.

Temeles, E. J. (1990). Northern Harriers on Feeding Territories Respond More Aggressively to Neighbors than to Floaters. *Behavioral Ecology and Sociobiology*, *26*(1), 57–63. JSTOR.

Terry, R. L. (1970). Primate grooming as a tension reduction mechanism. *The Journal of Psychology*, *76*(1), 129–136.

Thierry, B., Bynum, E. L., Baker, S., Kinnaird, M. F., Matsumura, S., Muroyama, Y., O'Brien, T. G., Petit, O., & Watanabe, K. (2000). The Social Repertoire of Sulawesi Macaques. *Primate Research*, *16*(3), 203–226. https://doi.org/10.2354/psj.16.203

Thierry, B., Iwaniuk, A. N., & Pellis, S. M. (2000). The influence of phylogeny on the social behaviour of macaques (Primates: Cercopithecidae, genus Macaca). *Ethology*, *106*(8), 713–728.

Thompson, F. J., Hunt, K. L., Wright, K., Rosengaus, R. B., Cole, E. L., Birch, G., Maune, A. L., & Cant, M. A. (2020). Who goes there? Social surveillance as a response to intergroup conflict in a primitive termite. *Biology Letters*, *16*(7), 20200131. https://doi.org/10.1098/rsbl.2020.0131

Thompson, F. J., Marshall, H. H., Vitikainen, E. I. K., & Cant, M. A. (2017). Causes and consequences of intergroup conflict in cooperative banded mongooses. *Animal Behaviour*, *126*, 31–40. https://doi.org/10.1016/j.anbehav.2017.01.017

Thomson, J. A., Hess, D. L., Dahl, K. D., Iliff-Sizemore, S. A., Stouffer, R. L., & Wolf, D. P. (1992). The Sulawesi crested black macaque (Macaca nigra) menstrual cycle: changes in perineal tumescence and serum estradiol, progesterone, follicle-stimulating hormone, and luteinizing hormone levels. *Biology of Reproduction*, *46*(5), 879–884.

Tórrez-Herrera, L. L., Davis, G. H., & Crofoot, M. C. (2020). Do Monkeys Avoid Areas of Home Range Overlap Because They Are Dangerous? A Test of the Risk Hypothesis in White-Faced Capuchin Monkeys (Cebus capucinus). *International Journal of Primatology*. https://doi.org/10.1007/s10764-019-00110-0

Trivers, R. L. (1972). Parental investment and sexual selection. *Sexual Selection & the Descent of Man, Aldine de Gruyter, New York*, 136–179.

Troisi, A., & Schino, G. (1987). Environmental and social influences on autogrooming behaviour in a captive group of Java monkeys. *Behaviour*, *100*(1–4), 292–302.

Turchin, P. (2018). *Historical dynamics: Why states rise and fall* (Vol. 26). Princeton University Press.

van Noordwijk, M. A., & van Schaik, C. P. (1985). Male migration and rank acquisition in wild long-tailed macaques (Macaca fascicularis). *Animal Behaviour*, *33*(3), 849–861. https://doi.org/10.1016/S0003-3472(85)80019-1

van Schaik, C. P. (1983). Why Are Diurnal Primates Living in Groups? *Behaviour*, *87*(1/2), 120–144.

van Schaik, C. P. (1996). Social evolution in primates: the role of ecological factors and male behaviour. *Proceedings-British Academy*, *88*, 9–32.

van Schaik, C. P., Assink, P. R., & Salafsky, N. (1992). Territorial behavior in Southeast Asian langurs: resource defense or mate defense? *American Journal of Primatology*, *26*(4), 233–242.

van Schaik, C. P., & Mitrasetia, T. (1990). Changes in the behaviour of wild long-tailed macaques (Macaca fascicularis) after encounters with a model python. *Folia Primatologica*, *55*(2), 104–108.

van Vugt, M. (2009). Sex Differences in Intergroup Competition, Aggression, and Warfare. *Annals of the New York Academy of Sciences*, *1167*(1), 124–134. https://doi.org/10.1111/j.1749-6632.2009.04539.x

Ventura, R., Majolo, B., Koyama, N. F., Hardie, S., & Schino, G. (2006). Reciprocation and interchange in wild Japanese macaques: grooming, cofeeding, and agonistic support.

American Journal of Primatology, *68*(12), 1138–1149. https://doi.org/10.1002/ajp.20314

Waterman, J. O., Campbell, L. A. D., Maréchal, L., Pilot, M., & Majolo, B. (2019). Effect of human activity on habitat selection in the endangered Barbary macaque. *Animal Conservation*. https://doi.org/10.1111/acv.12543

Watts, D. P., Muller, M., Amsler, S. J., Mbabazi, G., & Mitani, J. C. (2006). Lethal intergroup aggression by chimpanzees in Kibale National Park, Uganda. *American Journal of Primatology*, *68*(2), 161–180. https://doi.org/10.1002/ajp.20214

Wey, T. W., & Blumstein, D. T. (2010). Social cohesion in yellow-bellied marmots is established through age and kin structuring. *Animal Behaviour*, *79*(6), 1343–1352. https://doi.org/10.1016/j.anbehav.2010.03.008

Whitehouse, J., Micheletta, J., & Waller, B. M. (2017). Stress behaviours buffer macaques from aggression. *Scientific Reports*, *7*(1), 11083. https://doi.org/10.1038/s41598-017-10754-8

Widdig, A. (2013). The Impact of male reproductive skew on kin structure and sociality in multi-male groups. *Evolutionary Anthropology: Issues, News, and Reviews*, *22*(5), 239–250. https://doi.org/10.1002/evan.21366

Willems, E. P., Arseneau, T. Jean. M., Schleuning, X., & van Schaik, C. P. (2015). Communal range defence in primates as a public goods dilemma. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1683), 20150003. https://doi.org/10.1098/rstb.2015.0003

Willems, E. P., Hellriegel, B., & van Schaik, C. P. (2013). The collective action problem in primate territory economics. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1759), 20130081. https://doi.org/10.1098/rspb.2013.0081

Willems, E. P., & Hill, R. A. (2009). Predator-Specific Landscapes of Fear and Resource Distribution: Effects on Spatial Range Use. *Ecology*, *90*(2), 546–555.

Willems, E. P., & van Schaik, C. P. (2015). Collective action and the intensity of between-group competition in nonhuman primates. *Behavioral Ecology*, *26*(2), 625–631. https://doi.org/10.1093/beheco/arv001

Williams, J. M., Oehlert, G. W., Carlis, J. V., & Pusey, A. E. (2004). Why do male chimpanzees defend a group range? *Animal Behaviour*, *68*(3), 523–532. https://doi.org/10.1016/j.anbehav.2003.09.015

Wilson, E. (1975). Sociobiology: The New Synthesis.-Belknap Press of Harvard University Press. *Cambridge, MA*.

Wilson, M. L., & Wrangham, R. W. (2003). Intergroup Relations in Chimpanzees. *Annual Review of Anthropology*, *32*(1), 363–392. https://doi.org/10.1146/annurev.anthro.32.061002.120046

Wiltermuth, S. S., & Heath, C. (2009). Synchrony and cooperation. *Psychological Science*, 1–5.

Wittig, R. M., Crockford, C., Lehmann, J., Whitten, P. L., Seyfarth, R. M., & Cheney, D. L. (2008). Focused grooming networks and stress alleviation in wild female baboons. *Hormones and Behavior*, *54*(1), 170–177. https://doi.org/10.1016/j.yhbeh.2008.02.009

Wittig, R. M., Crockford, C., Weltring, A., Langergraber, K. E., Deschner, T., & Zuberbühler, K. (2016). Social support reduces stress hormone levels in wild chimpanzees across stressful events and everyday affiliations. *Nature Communications*, *7*(1), 13361. https://doi.org/10.1038/ncomms13361

Woolfenden, G. E., & Fitzpatrick, J. W. (1977). Dominance in the Florida Scrub Jay. *The Condor*, *79*(1), 1–12. https://doi.org/10.2307/1367524

Worton, B. J. (1989). Kernel Methods for Estimating the Utilization Distribution in Home-Range Studies. *Ecology*, *70*(1), 164–168. https://doi.org/10.2307/1938423

Wrangham, R. W. (1980). An Ecological Model of Female-Bonded Primate Groups. *Behaviour*, *75*(3/4), 262–300.

Wrangham, R. W. (1999). Evolution of coalitionary killing. *American Journal of Physical Anthropology*, *110*(S29), 1–30.

Wrangham, R. W., Crofoot, M. C., Lundy, R., & Gilby, I. (2007). Use of Overlap Zones among Group-Living Primates: A Test of the Risk Hypothesis. *Behaviour*, *144*(12,), 1599–1619.

Wrangham, R. W., Wilson, M. L., & Muller, M. N. (2006). Comparative rates of violence in chimpanzees and humans. *Primates*, *47*(1), 14–26. https://doi.org/10.1007/s10329-005-0140-1

Yanagida, T. (2020). *misty: Miscellaneous Functions 'T. Yanagida'*. https://CRAN.R-project.org/package=misty

Yi, Y., Fichtel, C., Kim, E., & Choe, J. C. (2020). Impacts of Intergroup Interactions on Intragroup Behavioral Changes in Javan Gibbons (Hylobates moloch). *International Journal of Primatology*, *41*(2), 363–381. https://doi.org/10.1007/s10764-019-00116-8

Young, C., Majolo, B., Heistermann, M., Schülke, O., & Ostner, J. (2014). Responses to social and environmental stress are attenuated by strong male bonds in wild macaques. *Proceedings of the National Academy of Sciences*, *111*(51), 18195–18200. https://doi.org/10.1073/pnas.1411450111

Zhang, H., Gross, J., De Dreu, C., & Ma, Y. (2019). Oxytocin promotes coordinated out-group attack during intergroup conflict in humans. *ELife*, *8*. https://doi.org/10.7554/eLife.40698

Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer New York. https://doi.org/10.1007/978-0-387-87458-6

Appendices

Appendix 1: Predator encounters

During the study, across all groups, we observed 41 predators in 35 separate encounters over 226 observation days, with a mean rate of 0.18 ± 0.46 (mean ± SD) predator encounters per day (range: 0 – 3), and no fatal or injurious attacks.

Appendix 2: Tourist encounters

During the study, across all groups, we observed 978 tourists in 177 separate encounters over 226 observation days, with a mean rate of 4.33 ± 9.53 (mean ± SD) tourists per day and a mean encounter rate of 0.78 ± 1.60 (mean ± SD) tourist encounters per day. Two of the study groups, PB1B and R1 were regularly visited by tourists. The third group, R3 were not (Table A.1). Fig. A.1 shows the locations of all observed tourist-macaque encounters in Tangkoko Nature Reserve (TNR) from March 2018 through June 2019.

Table A.1 Tourist-macaque encounters in TNR from March 2018 through June 2019.

Group	**Total number of tourists**	**Total number of tourist-macaque encounters**	**Number of tourists per day (mean ± SD), range (min – max)**	**Tourist encounters per day (mean ± SD), range (min – max)**
PB1B	440	81	3.60 ± 8.14 (0 – 57)	0.69 ± 1.52 (0 - 12)
R1	436	75	4.33 ± 8.50 (0 – 47)	0.74 ± 1.25 (0 – 6)
R3	71	18	1.28 ± 4.02 (0 – 20)	0.25 ± 0.82 (0 – 5)

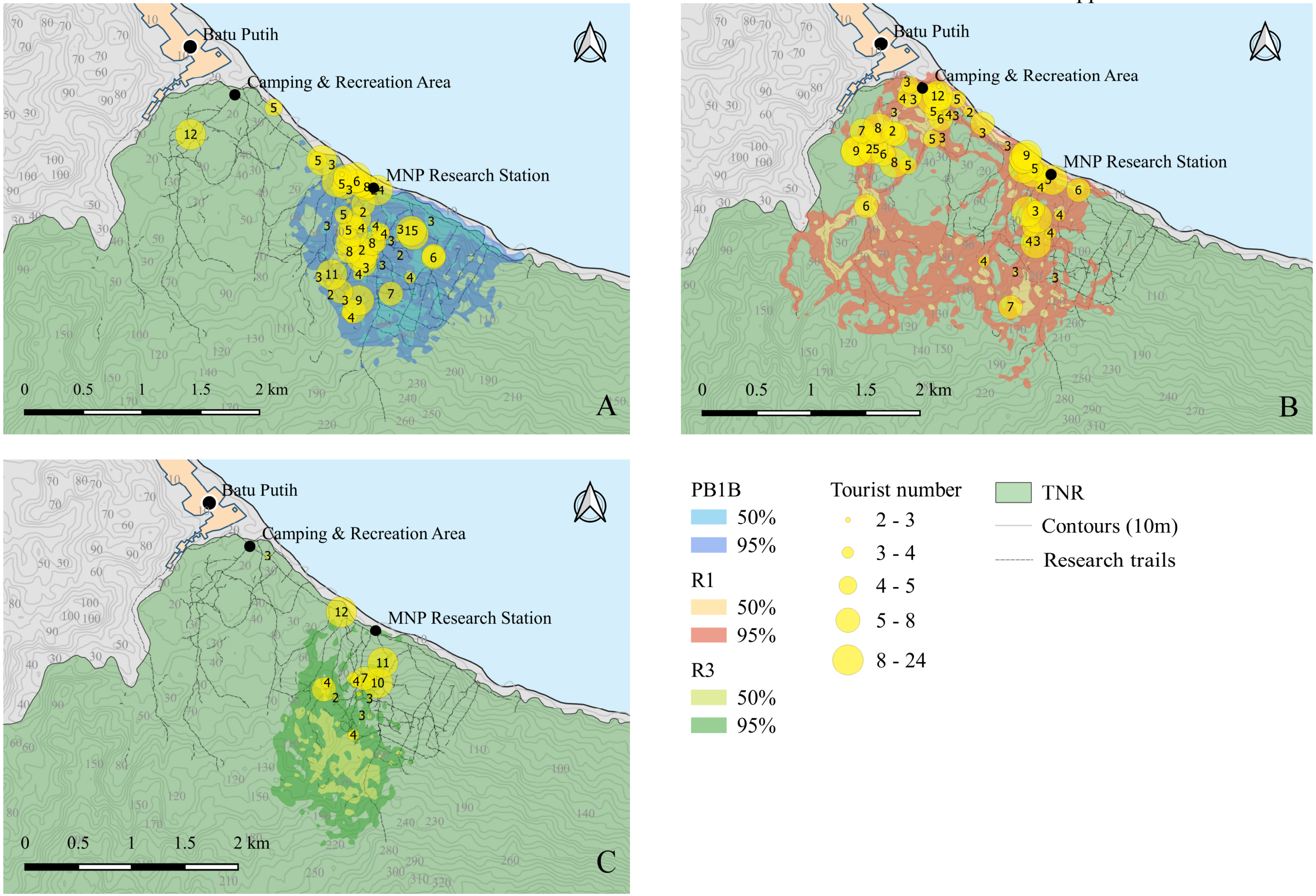

Figure A.1 Tourist-macaque encounters in TNR from March 2018 through June 2019 for groups PB1B (panel A), R1 (panel B), and R3 (panel C).

Appendix 3: IGEs

During the study, across all groups, we observed 183 intergroup encounters (IGEs) over 226 observation days, with a mean rate of 0.74 ± 0.66 (mean ± SD) IGEs per day (range: 0 – 3) (Table A.2 and Fig. A.2).

Table A.2 Summary of IGEs between wild crested macaque groups in TNR from March 2018 through June 2019. The total number of IGEs by group do not sum to 183, the total number recorded across the study, because (depending on the identity of both groups) a single encounter may be counted twice in the by-group tally, whilst it is only ever counted once in the across-group tally.

Group	Total number of recorded IGEs	Number of IGEs per day (mean ± SD), range (min – max)
PB1B	91	0.63 ± 0.64 (0 – 2)
R1	114	0.77 ± 0.55 (0 – 3)
R3	57	0.46 ± 0.55 (0 – 2)

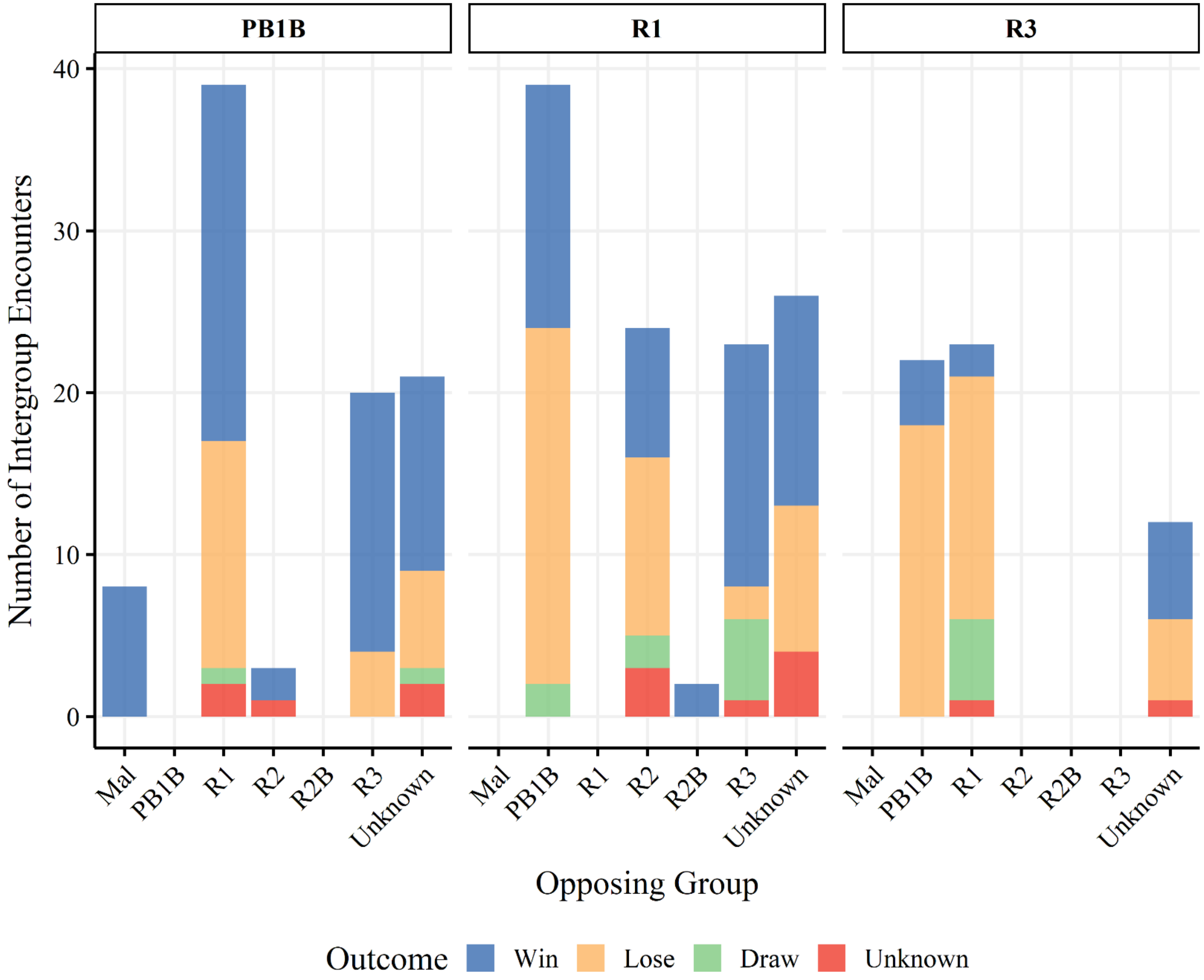

Figure A.2 Summary of crested macaque IGEs in TNR from March 2018 through June 2019.

Appendix 4: Home range & overlap

Table A.3 Utilisation Distribution Overlap Index (UDOI) values for crested macaque groups in TNR from March 2018 through June 2019.

Group pair	**UDOI**
PB1B – R1	0.23
PB1B – R3	0.02
R1 -R3	0.16

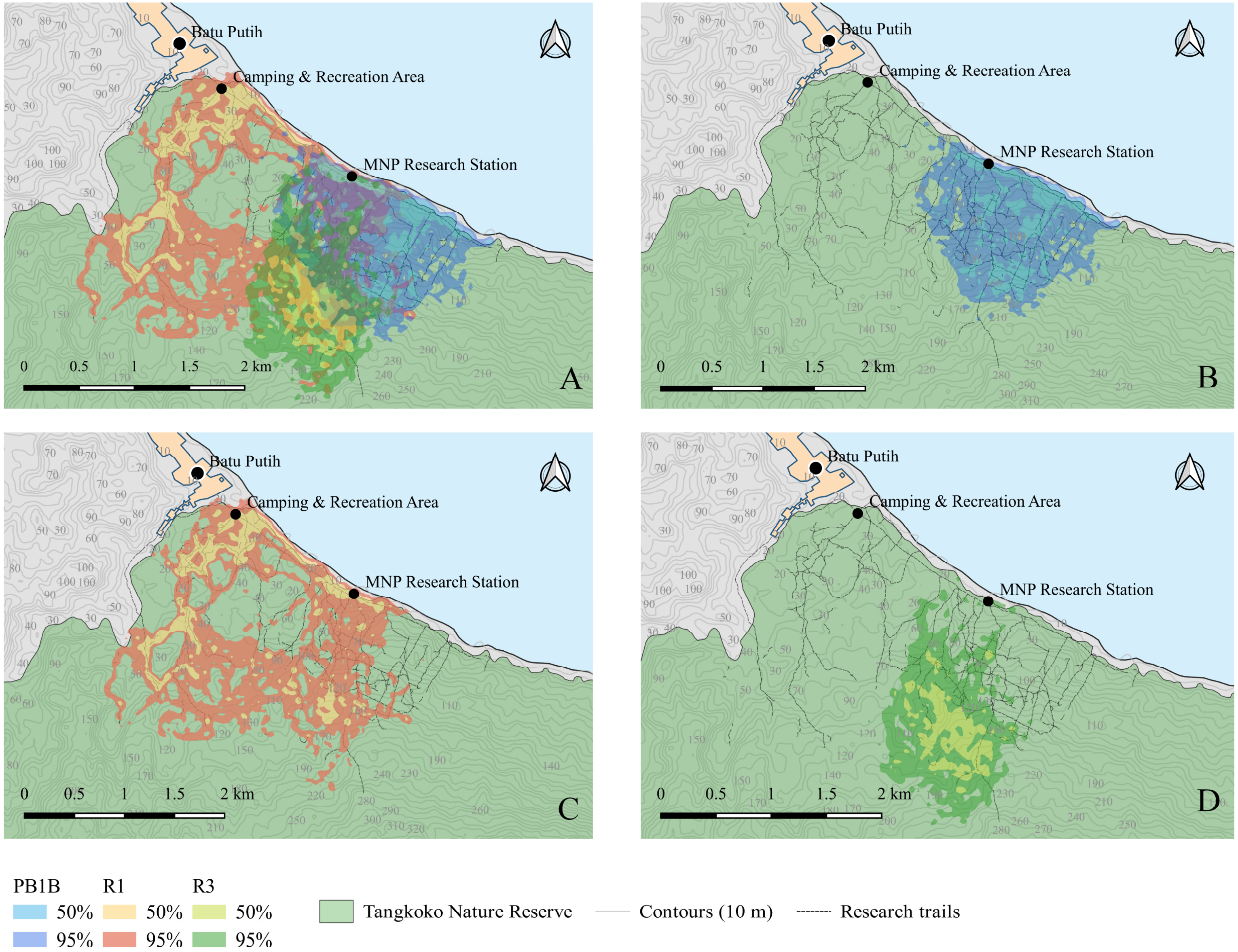

Figure A.3 Crested macaque home range estimates (and overlaps) in TNR from March 2018 through June 2019 for all 3 study groups (panel A), PB1B (panel B), R1 (panel C), and R3 (panel D).

Appendix 5: Relative IGE risk

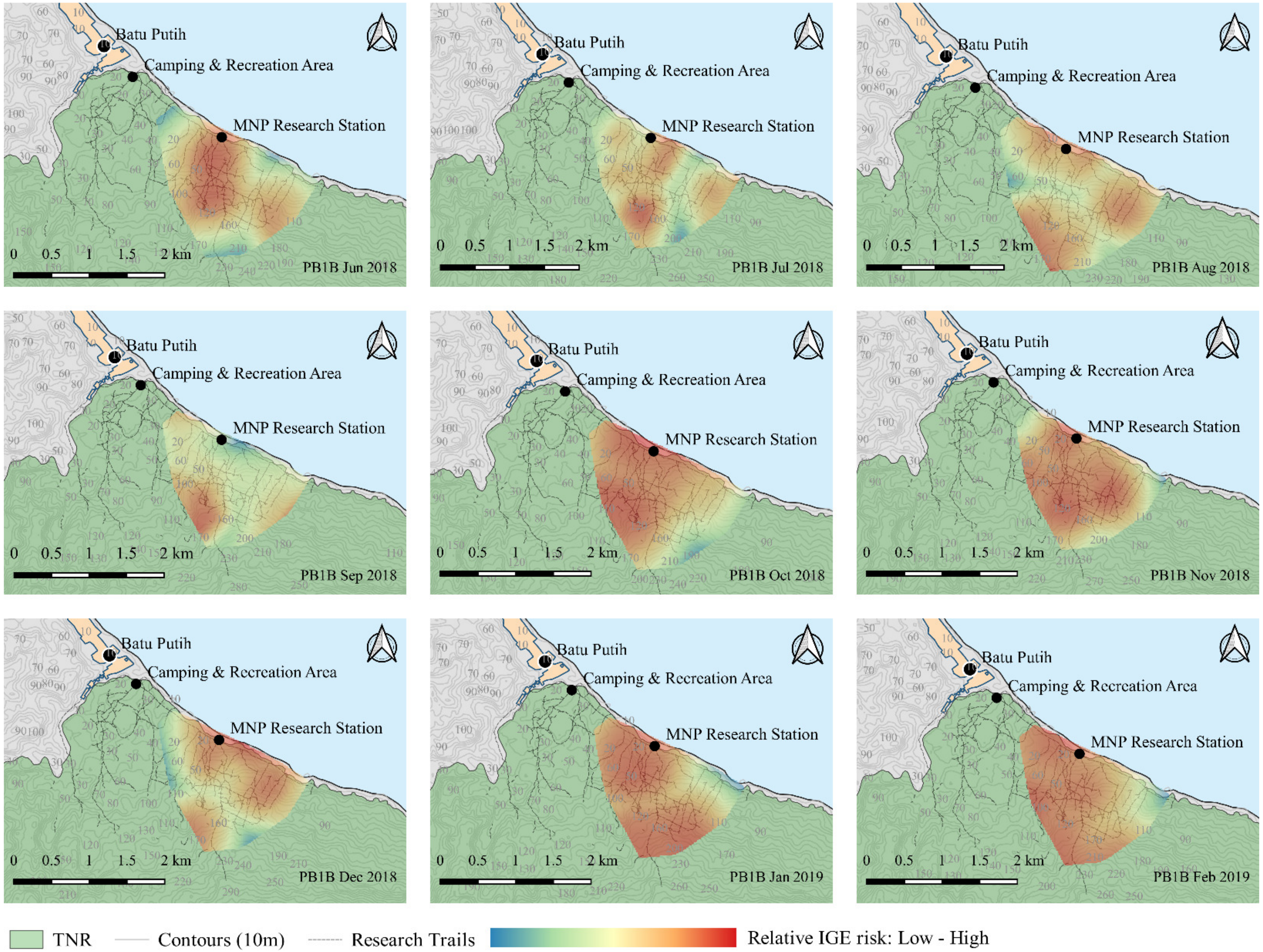

Figure A.4 Crested macaque monthly IGE relative risk maps in TNR (PB1B Jun 2018-Feb 2019).

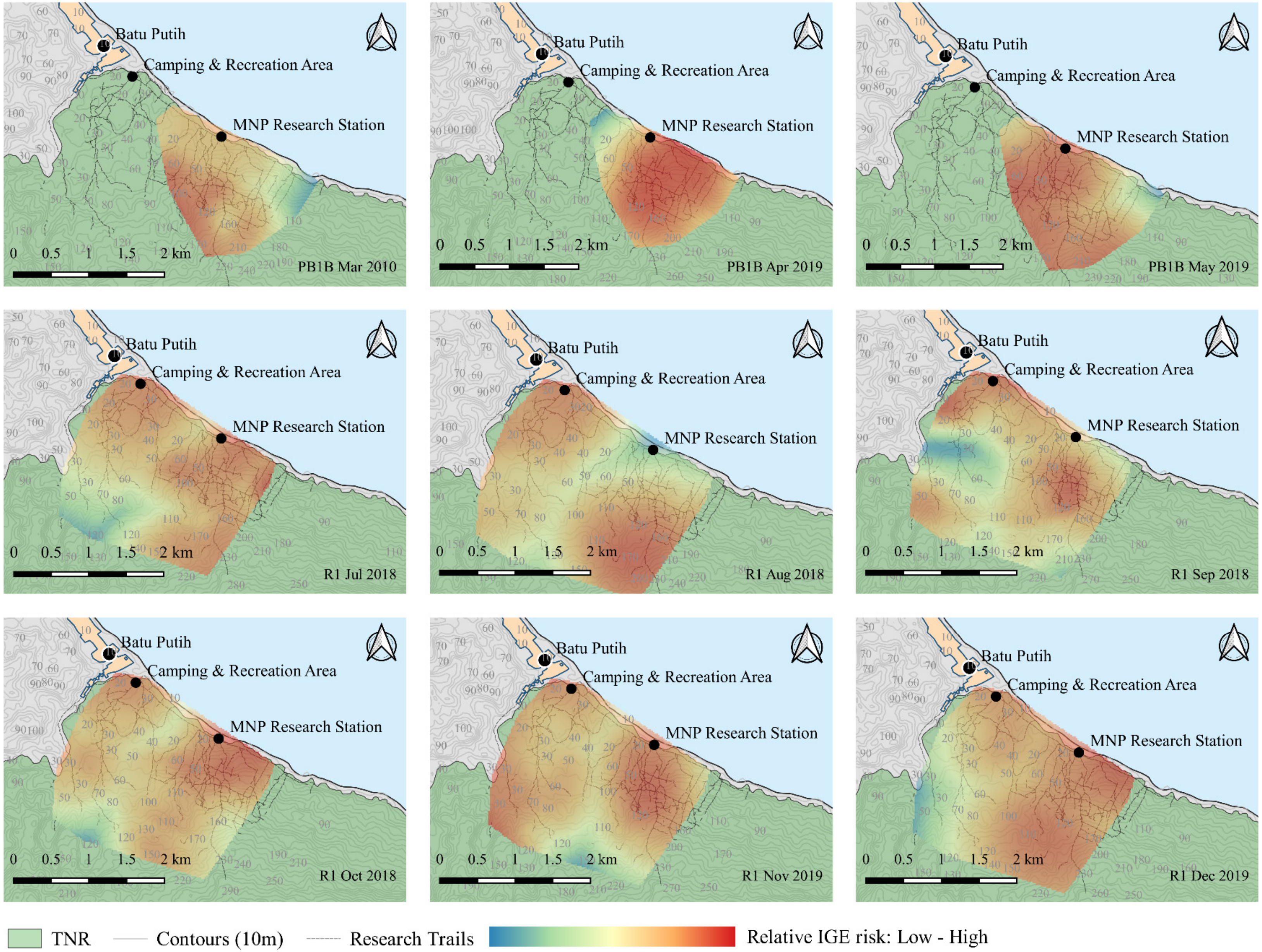

Figure A.5 Crested macaque monthly IGE relative risk maps in TNR (PB1B Mar 2019-May 2019; R1 Jul 2018-Dec 2018).

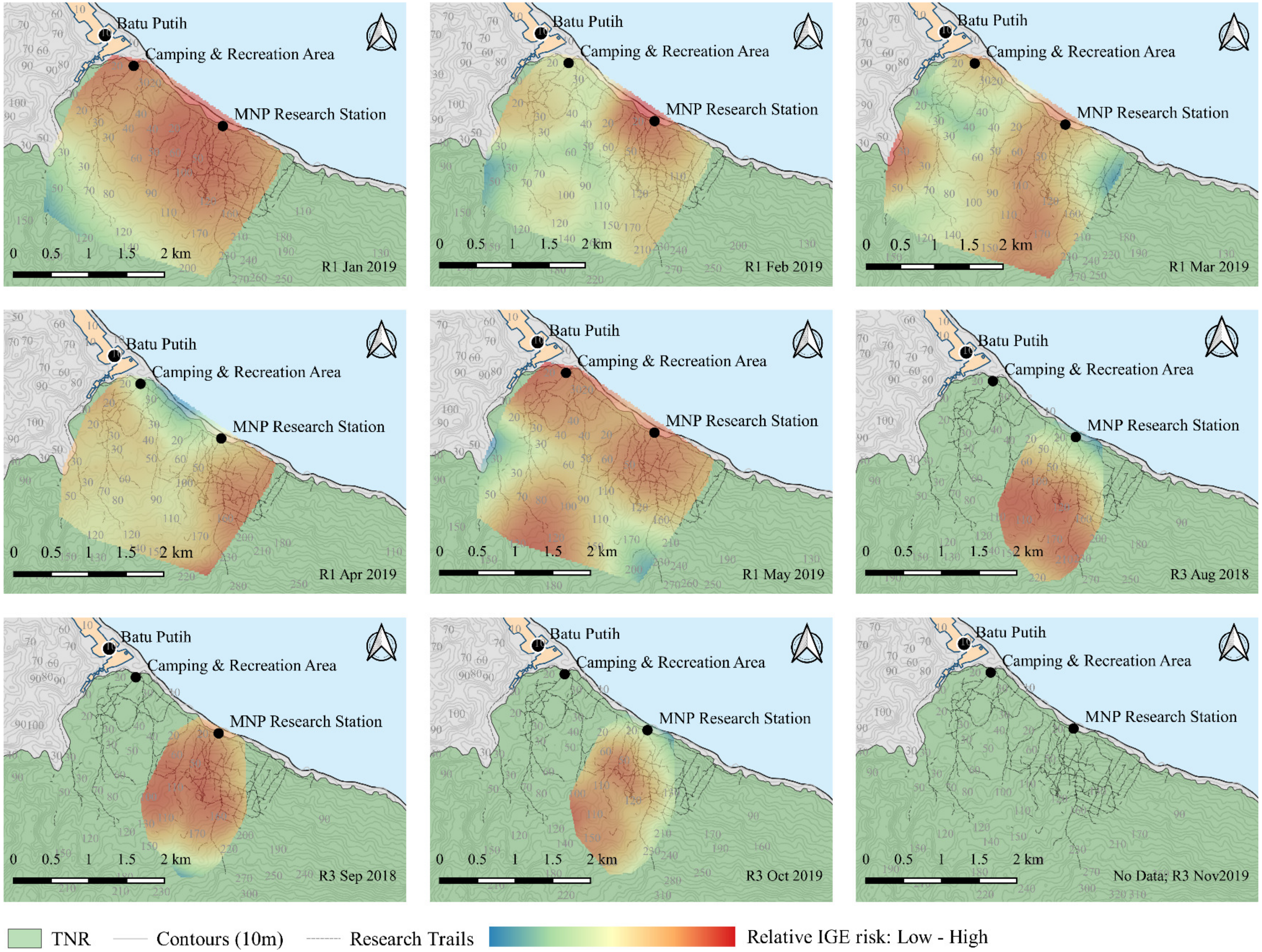

Figure A.6 Crested macaque monthly IGE relative risk maps in TNR (R1 Jan2019-May 2019; R3 Aug 2018-Nov 2018).

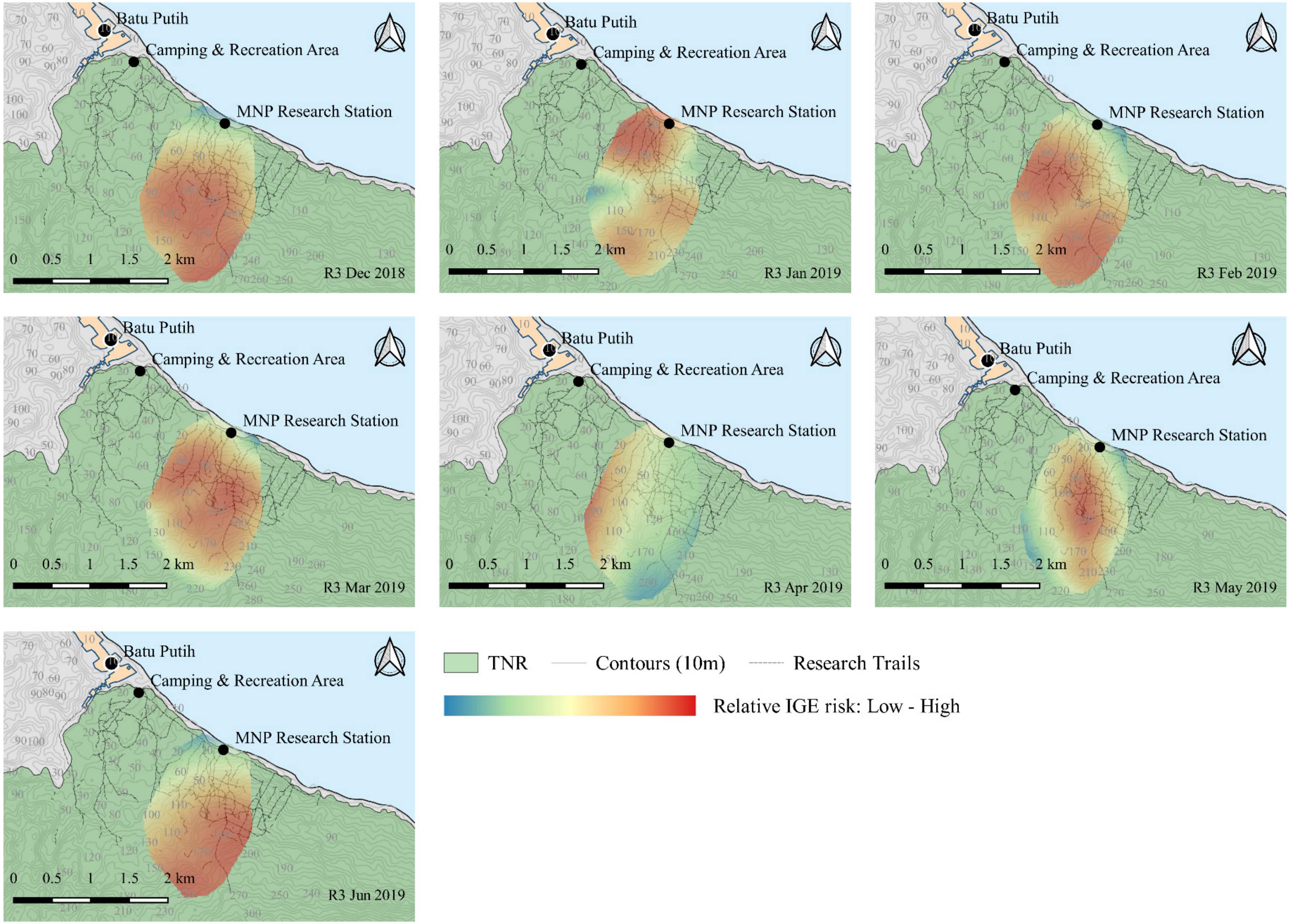

Figure A.7 Crested macaque monthly IGE relative risk maps in TNR (R3 Dec2018-Jun 2019).