The Functions and Consequences of Intergroup Aggression among Argentine Tufted Capuchin Monkeys (*Cebus apella* [*Sapajus*] *nigritus*)

A Dissertation Presented

by

Clara JoAnn Scarry

to

The Graduate School

in Partial Fulfillment of the

Requirements

for the Degree of

Doctor of Philosophy

in

Anthropology

(Physical Anthropology)

Stony Brook University

August 2012

Stony Brook University
The Graduate School

Clara JoAnn Scarry

We, the dissertation committee for the above candidate for the
Doctor of Philosophy degree, hereby recommend
acceptance of this dissertation.

Charles H. Janson, Ph.D. – Dissertation Advisor
Professor & Associate Dean, Biological Sciences Division,
University of Montana

Andreas Koenig, Ph.D. – Dissertation Advisor
Professor, Department of Anthropology

Diane M. Doran-Sheehy, Ph.D. – Chairperson of Defense
Professor & Chair, Department of Anthropology

David P. Watts, Ph.D. – External Member
Professor, Department of Anthropology, Yale University

This dissertation is accepted by the Graduate School

Charles Taber
Interim Dean of the Graduate School

Abstract of the Dissertation

The Functions and Consequences of Intergroup Aggression among Argentine Tufted Capuchin Monkeys (*Cebus apella* [*Sapajus*] *nigritus*)

by

Clara JoAnn Scarry

Doctor of Philosophy

in

Anthropology

(Physical Anthropology)

Stony Brook University

2012

Intergroup encounters provide dramatic examples of cooperative behavior, in which unrelated individuals may coordinate aggression when mutualistic benefits arise from defending access to resources. While between-group competition over mates and resources are pivotal factors in theoretical models of the evolution of primate behavior, systematic study of these interactions has been limited due to the relative rarity of intergroup encounters and the logistical difficulties of studying multiple social groups simultaneously. Here I examine the nature and consequences of between-group competition in tufted capuchin monkeys (*Cebus apella* [*Sapajus*] *nigritus*) in Iguazú National Park, Argentina. I followed four neighboring groups, collecting explicit measures of the foraging and social contexts and consequences of intergroup aggression – through both naturalistic observations and field experiments. Within this population, males and females demonstrate concordant strategies during intergroup encounters, responding aggressively only in the presence of a high-quality food resource. Overall, males respond more strongly to the presence of neighboring groups, demonstrating no differences between dominant and subordinate males in either willingness to participate in or lead intergroup aggression. Females also participate, but they are less likely to lead aggressive encounters, allowing larger-bodied males to incur higher energetic costs and risk of potential injury. Collective defense by resident males allows groups to predictably win encounters against groups with fewer males, overcoming the potential benefits of a home-field advantage. Individuals appear able to assess the potential for winning an encounter and are more likely to participate during encounters against competitively weaker groups. When facing a competitively stronger group, most individuals flee, although females bearing the additional energetic burden of caring for a young infant appear more willing to attempt to maintain access to the resource, leading intergroup aggression despite a numerical disadvantage. Because dominant groups – those with more adult males – are better able to defend their core area, they share fewer of the resources within these areas, and individuals in dominant groups have higher *per capita* access to food, which may offset the costs of large group size. These results suggest the need to expand existing models of the evolution of intragroup social relationships to incorporate the potential for ecological variation and between-group contest competition over food resources to affect male-female relationships.

For my parents,
John and Margaret Scarry,
who never gave voice to doubt

Table of Contents

List of Figures

List of Tables

Acknowledgements

As with any dissertation – or any other goal that requires eight years to complete – I could not have undertaken this project without the support of many, many people. First and foremost, I have to thank my committee: my co-advisors, Charlie Janson and Andreas Koenig, Diane Doran-Sheehy, and David Watts.

Charlie Janson took a huge chance by bringing to Iguazú a first-year graduate student with virtually no field experience, zero command of the Spanish language, and two sprained ankles. What was supposed to be a single field season somehow turned into a dissertation, for which I am deeply grateful because – in spite of this seemingly foolhardy choice – Charlie is one of the smartest people I have ever met. Because he has the added distinction of being one of the clearest spoken, I walk away from conversations with Charlie understanding concepts I'm convinced should have remained beyond my ken. Although it has been said before, I'll repeat it here: Stony Brook suffered an enormous loss when Charlie left for Big Sky Country, and I am lucky to have had the chance to continue working with and learning from him over the last seven years.

When I came back from the field, Andreas Koenig rescued me from exile, generously opening his lab and his advisorial door to me. If Charlie taught me the theory, then Andreas has taught me the practice and to be practical, and any failure in my application of those lessons is due to my own disorganized nature and not my teacher. But for Andreas, I would still be drafting endless outlines of chapters, instead of writing acknowledgements. Yet Andreas has pushed me not only to develop my chapters, but also to develop myself. He has created opportunities for me to teach, given me free reign to learn statistical techniques because they seemed fun, and generally taught me how to be an advisor and a scientist.

Although she is not officially an "advisor" anymore, I am extremely grateful to Diane Doran-Sheehy for being the first person at Stony Brook to take a chance on me. When I first came back from Argentina expressing an interest in studying multiple social groups, Diane was the one to point me towards the topic of functions of intergroup aggression. When my interest developed, and it became clear I was not going to pursue the course I'd plotted in my application statement, it was Diane who gently pushed me out of the nest. Her attitude then – and since – has been the definition of gracious, and I have never doubted that she has my best interest in mind.

Rounding out my committee is external member, David Watts. Since he joined my committee five years ago, I have disappeared for long periods of time, going to the field or my office without remembering to provide anyone with updates. David has accepted each of my reappearances with little more than a brief hesitation to switch his mental track before providing suggestions and a broader context to my capuchin-centric worldview. It is an impressive feat.

I am indebted to the Argentine National Park Administration (APN) for allowing me to work in Iguazú for such an extended period of time. I want especially to recognize Paula Cichero and Dalma Raymundi from the Delegacion Regional Tecnica, who worked with me to ensure my permit applications were successful. Thanks also to Justo Herrera and Monica Montero from the Centro de Investigaciones del Ecologicas Subtropicales for providing logistic support and access to the research station for myself and my team. Although he had moved on to more carnivorous pastures as head of the Proyecto Tigre, Mario Di Bitetti volunteered to serve as my host country collaborator, for which I am grateful.

I had help in the field from a fantastic crew of people without whom I would never have been able to complete this project. When I first arrived in Iguazú as Charlie's field assistant, Brandon Wheeler and Fermino da Silva were instrumental in teaching me to identify the monkeys and their behaviors. That Fermino continued to work with me later has been an incredible boon to the project. He has a lifetime of skills developed while working for the Proyecto Caí, which kept seemingly herculean tasks like establsihing provisioning sites or following new groups from turning into logistic nightmares. From the diverse array of people that collected data on this project, I owe an especially profound "thank you" to María Veronica Cifre, Ivana Ghione, and Taylor Rubin. But for these three women, this project could so easily have reached an early completion when my own heath issues interfered with fieldwork. I am grateful not only that they believed enough in the merit of the project to soldier on during my brief absence but that they continued to support me as I recovered. Because she was with me at the beginning of the project and at the end, Elizabeth Gonzáles Valentin belongs with this group although academic responsibilities kept her out of the field briefly. Lara Colleselli, Natalia Gomez de Olivera, Ximena Merelle Dherve, Jacqueline Kehoe, Luis Molina, Gillian Moritz, Carolina Páez, Amparo Perez Rueda, Jen Hudyma, and Sara Cortez also provided important data and companionship. For all of them, I say: *¡Gracias a los moneros de Iguazú…y sus espiritus "ayudables"!*

Although not actually working on my project, others in Argentina provided the laughter, collaboration, and mental stimulation that kept me going for three years. For their continued friendship, I thank María Paula Tujague, Barbara Tiddi, María Celia Baldovino and Martin Morales. I have to thank the rest of the Tujagues – Feny, Fernando and Zulma – as well; although I entered their home as a "Swine flu" Mary, they have become a family away from home, and I am grateful for their continued acceptance. *¡Que nos veamos pronto!*

During the portions of graduate school away from the monkeys and waterfalls, another incredible group of people has been instrumental in keeping me motivated. My fellow nestlings – Alice Elder and Liz St. Clair – have provided encouragement almost from the beginning and are the greatest "cohort" I could have imagined. Although they arrived on the scene later, James Herrera and Roberta Salmi have been critical in getting me through this last push, giving me a friendly outlet for frustration and mumbling before throwing me back into the fray. Paula Tujague has kept me connected to Iguazú, recounting updates about both monkeys and people and giving me the opportunity to address new questions through collaboration. Thanks also to Andrea Baden, Carola Borries, David Fernandez, Rachel Jacobs, Kerry Ossi-Lupo, Jonathan Perry, Mat Sisk, and Carrie Veilleux.

Finally, I would be remiss if I failed to acknowledge the incredible support that my family has provided while I pursued this degree. My parents offered encouragement, counseling, financial support, or just an outlet for conversation as the need arose. That love and support – combined with twenty-four years of zoo visits during which they saw nothing but primates – would have warranted my thanks, but I have been even luckier. Before even my advisors had seen a draft, each piece of this dissertation passed through the editorial board of John and Margaret Scarry and was improved for their reviews. Thanks also to the other board members of the "ScarryFelder Foundation for Primatological Research", especially Bob and Clara Mosenfelder, George and Joann Scarry, Bill and Sue Mosenfelder, and Becca Michener. Since the beginning, my education has been a family effort through examples set and support provided.

Financial support for fieldwork was provided by the Leakey Foundation, the National Science Foundation (DDIG: BCS-0752683), the National Geographic Society, and the Wenner-Gren Foundation (Grant 50350). Additional funding for the pilot portion of the study was provided by an NSF Research Grant to Charles Janson (BCS-0515007). This study was conducted in accordance with Stony Brook University's Institutional Animal Care and Use Committee guidelines (protocol numbers 2007-1580, 2008-1580, 2009-1560, and 2010-1560).

Chapter 1:
Background and introduction

While between-group competition over mates and resources is a pivotal factor in theoretical models of the evolution of social behavior (Emlen and Oring 1977; Wrangham 1980; Rubenstein 1986; van Schaik 1989; Packer et al. 1990; Isbell 1991; Sterck et al. 1997), systematic study of these interactions has been limited due to the relative rarity of intergroup encounters and the logistical difficulties of studying multiple social groups simultaneously. In addition, the nature of intergroup encounters is the collective expression of individual strategies, which may or may not be complementary. As a result, the functions and consequences of these interactions remains poorly understood for most primate species (Fashing 2001).

The current study examines the nature and consequences of between-group competition in tufted capuchin monkeys (*Cebus apella* [*Sapajus*] *nigritus*) in Iguazú National Park, Argentina. I observed multiple social groups, collecting explicit measures of the foraging and social contexts and consequences of intergroup aggression – through both naturalistic observations and experiments, which allow me to address a series of interrelated questions. First, what are the function(s) of intergroup aggression in this population? Second, what are the mechanisms through which fitness consequences arise? Third, what factors influence individual assessment of the costs and benefits of participation in intergroup aggression? Finally, do individuals vary in their contribution to collective defense, and do contingent strategies of participation exist?

Background

The function of intergroup aggression

In many social-living mammals, intergroup encounters are characterized by aggressive interactions (e.g., non-human primates: Cheney 1987; Fashing 2001; carnivores: Kruuk 1972; Packer 1986; Cant et al. 2002; humans: Manson and Wrangham 1991), yet the functions and consequences of these interactions are poorly understood (Fashing 2001). It has been hypothesized that aggressive behavior during intergroup encounters functions to defend access to limiting resources or mating opportunities. Individuals in dominant groups may aggressively defend access to food, which can increase their energetic intake and ultimately reproductive success (Wrangham 1980; Cheney and Seyfarth 1987; Dittus 1987; Robinson 1988; van Schaik 1989; Sterck et al. 1997; Suzuki et al. 1998). However, it has also been noted that aggressive encounters frequently occur in the absence of contestable food resources (Stanford 1991; Cowlishaw 1995), which may suggest that males are competing over reproductive access to females (Emlen and Oring 1977; van Schaik 1996).

1. Resource defense

Socioecological models of primate behavior suggest that among group-living species, female social relationships and dispersal patterns are determined by the relative strength of three modes of competition: within-group scramble competition, within-group contest competition, and between-group contest competition (Wrangham 1980; van Schaik 1989; Sterck et al. 1997). When high-quality food resources occur in defensible patches large enough to support an entire group, individuals in dominant groups may increase energetic intake, and ultimately reproductive success, by aggressively excluding members of subordinate groups.

However, due to the logistic difficulties of collecting detailed ecological and behavioral data for multiple social groups, few studies have attempted to directly measure the effects of between-group contest competition on individual energetic intake and reproductive success (Janson and van Schaik 1988; reviewed in Koenig 2002). The existing evidence has provided limited support for the resource defense hypothesis. Detailed studies of the effects of group membership on energetic intake and expenditure suggest that the relative importance of between-group contest competition is low compared to within-group contest competition (Janson 1985, 1988a; van Noordwijk and van Schaik 1987). Nevertheless, in some primates, large group size is correlated with increased energy gain (Hanuman langurs, *Semnopithecus entellus*: Koenig 2000) and increased fecundity (vervet monkeys, *Chlorocebus aethiops*: Cheney and Seyfarth 1987; toque macaques, *Macaca sinica*: Dittus 1987; Japanese macaques, *Macaca fuscata*: Suzuki et al. 1998; weeper capuchin monkeys, *Cebus olivaceus*: Robinson 1988).

In the absence of direct measures of energy gain or reproductive success, most studies of intergroup aggression have relied on proxy measures of between-group contest competition, including: 1) female participation in intergroup aggressive encounters and 2) the proximity of the location of the encounter to contestable food resources. Because female reproductive success is limited by access to food resources to a greater degree than is male reproductive success (Trivers 1972), females are expected to be the primary aggressors during intergroup encounters over food (Wrangham 1980; van Schaik 1989; Sterck et al. 1997). Yet, female participation in intergroup aggression is frequent only among territorial, monogamous species (Garber 1988; Lazaro-Perea 2001; Peres 1989; Bartlett 2003), female-dominant lemur species (Sauther et al. 1999; Nunn and Deaner 2004), and some cercopithecoids (Struhsaker, 1980; Kumar and Kurup, 1985; Cords 1987; Kinnaird, 1992; Borries 1993; Hill, 1994). In most other species, female participation is limited or absent (reviewed in Cheney 1987; Fashing 2001). Even among species with limited female participation, however, dominant females frequently assist males in making aggressive displays towards members of neighboring groups (Cheney 1981; Robinson 1986; Perry 1996; Kitchen 2006). For dominant females, the benefits of exclusive access to resources may be increased by their ability to exclude subordinates from group-utilized resources, promoting participation in intergroup encounters. Additionally, female participation may occur among members of numerically weaker groups (e.g., Cheney and Seyfarth 1987; Kitchen 2006), indicating that female resource defense is important, but may be reduced when male intrasexual competition is prominent (cf. Steenbeek 1999).

Nonetheless, the degree of female participation may not be a relevant or sufficient measure of the importance of between-group contest competition for individual reproductive success. Although males are expected to compete primarily for access to reproductive females (Trivers 1972), resource defense may also be used as a male reproductive strategy (Harrison 1983; Janson 1984; Borgerhoff Mulder 1990; Nievergelt et al. 1998; Mutschler et al. 2000; Fashing 2001; Williams et al. 2002, 2004; Harris 2006). When the spatiotemporal distribution of food resources permits monopolization by a single male, males can indirectly defend access to females by directly defending access to limiting food resources (Bradbury and Vehrencamp 1977; Emlen and Oring 1977). Resource defense polygyny – wherein males attract females to high-quality territories (Emlen and Oring 1977) – appears rare among primates (but see Borgerhoff Mulder 1990; Williams et al. 2002, 2004). Yet among species with female philopatry, males may use resource defense to influence female mating preferences (Janson 1984) or to reduce female interbirth intervals and increase infant survivorship, consequently increasing male reproductive success (cf. "hired guns": Rubenstein 1986).

The location of intergroup encounters and the proximity of high quality food patches have also been used to examine the importance of resource defense strategies, with mixed results (Lawes and Henzi 1995; Perry 1996; Steenbeek 1999; Fashing 2001; Harris 2006). Among some species, intergroup aggression appears to occur only over spatiotemporally clumped food resources, while neutral or affiliative interactions occur in other situations (e.g., Jolly 1972; Kavanagh 1981; Harrison 1983; Kinnaird 1992; Fashing 2001). However, in many non-territorial species, aggressive intergroup encounters frequently occur in the absence of contestable food resources, leading some researchers to conclude that resource defense is unimportant in these species (Stanford 1991; Cowlishaw 1995).

Finally, while displacement at important food resources may have important consequences for individual energetic intake, other subtle advantages may be conferred by large group size (Janson and van Schaik 1988). In species in which groups maintain exclusive access to part of their home range, differences in the quality of the core area may exist between groups (e.g., Cheney and Seyfarth 1987; Harris 2006). For instance, Harris (2006) found that dominant black-and-white colobus groups aggressively defend core areas that offer increased resource availability. Additionally, intergroup avoidance in areas of overlap may affect the quantity and quality of resources used by smaller groups. These other forms of competition may not be apparent when only the location of intergroup encounters is considered.

2. Mate defense

Female sociality has also been argued to decrease predation risk (van Schaik 1983, 1989; Sterck et al. 1997) and reduce the potential for sexual coercion and infanticide by males (Packer et al. 1990; Pusey and Packer 1994; van Schaik 1996; van Schaik and Kappeler 1997; Sterck et al. 1997). If these factors are the primary forces driving the evolution of group-living, females may form permanent social groups in the absence of intense between-group contest competition for food resources. As a result, males may be able to increase reproductive success by directly defending access to females (Emlen and Oring 1977), and aggression during intergroup encounters may reflect male intrasexual competition.

In a number of primate species, the context of intergroup aggression appears consistent with a direct male mate defense function (Stanford 1991; Kinnaird 1992; van Schaik et al. 1992; Sicotte 1993; Cowlishaw 1995; Perry 1996; Steenbeek 1999). Within the context of intergroup encounters, male tactics to increase reproductive success may include engaging in extragroup copulations (Packer 1979; Kinnaird 1992; Palombit 1994; Cowlishaw 1995; Reichard 1995; Reichard and Sommer 1997; Agoramoorthy and Hsu 2000; Kitchen et al. 2004a), taking over reproductive positions in neighboring social groups (Crockett and Sekulic 1984; Steenbeek 1999; Wich et al. 2002; Kitchen 2004), or influencing female transfer decisions (Watts 1989; Sicotte 1993; Steenbeek 1999). Accordingly, male response to intergroup encounters may be influenced by the reproductive state of females (Kinnaird 1992; Cowlishaw 1995), the probability of female transfer (Steenbeek 1999), and the intergroup difference in potential male mating opportunities (Packer 1979; Pusey and Packer 1987; Stanford 1991; Sicotte 1993; Gibson and Koenig 2012).

Although male mate defense is a form of intrasexual competition, females and infants are frequently the targets of male aggression during intergroup encounters. To prevent extragroup copulations, males may aggressively herd sexually receptive female group mates away from non-resident males (Packer 1979; Cowlishaw 1995; Steenbeek 1999). In species characterized by female dispersal, sexual coercion and infanticidal attacks by extragroup males may expose the relative weakness of the resident male, promoting female transfer (Sicotte 1993; Smuts and

Smuts 1993; Steenbeek 1999; Sicotte and Macintosh 2004; Korstjens et al. 2005). Similarly, in species with female philopatry, extragroup males may attack and kill young infants because premature loss of an infant can release females from lactational amenorrhea, thereby shortening interbirth intervals (Altmann et al. 1978; Bogges 1994; Crockett and Sekulic 1984; Packer and Pusey 1984; Borries 1997; Ramírez Llorens et al. 2008). This behavior is only expected, however, if attacking males have a reasonable expectation of siring future offspring within the group (e.g., during attempted takeovers) because the indirect benefits of increased genetic representation in the population are unlikely to offset the associated risk of injury by resident females and potential sires that defend the infant (Broom et al. 2004).

Untangling the factors influencing male behavior during intergroup encounters is further complicated because the proposed functions of intergroup aggression are not mutually exclusive; individual males may pursue multiple strategies. As a result, simultaneously examination of all of the various hypotheses is necessary to draw conclusions about the relationship between male reproductive strategies and the nature of intergroup encounters (Harris 2006).

Games of ownership: asymmetries and assessment

When limiting resources are economically defensible, individuals or groups are expected to compete for access (Nicholson 1954; Brown 1964; Stanford 1991). Game theoretic models suggest that the outcome of contests is determined by asymmetries in 1) the resource holding potential (RHP) of the competitors and/or 2) the marginal costs and benefits of exclusive access to the resource (relative to either shared access or exclusion from use of the resource) for each contestant (Maynard Smith and Parker 1976; Parker and Rubenstein 1981). In addition, the level of escalation is expected to be influenced by the value of the contested resource and the degree of asymmetries (Maynard Smith and Parker 1976), although other factors may mediate the aggressive response, including familiarity (Stanford 1991; Wich et al. 2002) and relatedness (Bradley et al. 2004).

1. Asymmetries in Resource Holding Potential

Frequently, the outcome of contests is determined by asymmetries in the RHP of competitors. When asymmetries in RHP allow some competitors to consistently win repeated contests against other competitors, a clear between-group dominance hierarchy may be detected (Drews 1993). In pairwise contests, the fighting ability of individuals may be affected by individual age, body size, personality or weaponry (Parker 1974). Among species in which a single individual – typically the dominant male – is the primary aggressor during intergroup encounters, the RHP of the group may be determined by individual quality (Ellefson 1974; Steenbeek 1999; Harris et al. 2006). Alternatively, if multiple individuals participate in intergroup aggression, the RHP of the group may be related to group size, which establishes the number of coalitionary partners available during aggressive intergroup encounters (Cheney 1987; Kinnaird 1992; McComb et al. 1994; Cowlishaw 1995; Heinsohn and Packer 1995). Individual strategies and the nature of the contested resource will determine whether the relevant measure of the group's RHP is total group size (e.g., Cheney 1987), male group size (e.g., Cowlishaw 1995), or female group size (e.g., Hill 1994).

In contrast to contests between single competitors, intergroup aggression in defense of limiting resources (e.g., territories, food patches or reproductive females) frequently produces benefits that are shared by multiple individuals, regardless of their contribution to the collective effort. Consequently, individuals may be tempted to free-ride on the aggressive behaviors of other group members (Heinsohn and Packer 1995; Nunn and Deaner 2004) to avoid the energetic costs (Garber 1988; Peres 1989) and potential for death (Goodall 1986; Palombit 1993; Heinsohn and Packer 1995; Gros-Louis et al. 2003; Watts et al. 2006) or injury (Cheney 1987; Nunn and Deaner 2004). When the fighting ability of groups is determined by the degree of individual participation, this tendency for individuals to defect must be overcome for cooperative defense to succeed (Nunn 2000; Nunn and Lewis 2001). Increased tolerance in within-group dominance relationships (Kitchen et al. 2004b), which decreases the asymmetry in payoffs derived by dominant and subordinate individuals (Nunn 2000), and philopatry among members of the defending sex (Nunn and Deaner 2004) have been suggested as evolutionary mechanisms to promote participation when between-group contest competition is strong (Wrangham 1980; Sterck et al. 1997; Nunn 2000).

Nevertheless, although maximum RHP increases with group size, the realized RHP is frequently lower than suggested by relative group size (Crofoot et al. 2008) due to the increased prevalence of free-riding in larger groups (Nunn 2000; Crofoot et al. 2012). With increasing group size, the marginal value of each additional defender decreases (van Schaik 1996; Nunn 2000; Nunn and Lewis 2001) and within-group scramble competition for the contested resource increases (van Schaik 1989; Sterck et al. 1997), reducing the payoff to participants. Unless individual costs are reduced through the presence of additional defenders, the diminishing returns on individual energy expenditure should promote reduced investment in intergroup aggression by individuals residing in larger groups (van Schaik 1996; Nunn 2000). In some cases, the total energy expended on between-group competition may be reduced in larger groups, leading to an inverse relationship between group size and intergroup dominance rank (e.g., Harris 2006; 2010).

Additionally, in large groups, increased within-group scramble and contest competition may promote reduced group cohesiveness – expressed as increased interindividual spacing and the formation of foraging subgroups (e.g., van Noordwijk and van Schaik 1987; Lynch Alfaro 2007). Studies of within-group competition have focused on the importance of reduced group cohesiveness as a tradeoff between the benefits of increased foraging success (van Noordwijk and van Schaik 1987; van Schaik 1989; Lynch Alfaro 2007) and energetic intake and the costs of increased predation risk and energetic expenditure for traveling (van Noordwijk and van Schaik 1987; Janson 1988b). A third consequence of reduced cohesiveness, however, is an effective reduction in the number of available coalitionary partners. As a result, intergroup encounters may involve only a fraction of the larger group (Manson and Wrangham 1991; Wilson et al. 2001; Pusey and Packer 1994), allowing smaller groups to win despite an apparent numerical disadvantage (Hausfater 1972; C.H. Janson personal communication).

2. Asymmetries in payoff value

When the payoffs gained by access to the contested resource are asymmetrical, groups are expected to differ in their willingness to escalate contests, which can affect the outcome of contests (cf. contests between individuals: Maynard Smith and Parker 1976). Both the location of the encounter and the current condition of the competitors can affect the assessment of the relative costs and benefits of ownership. In species that exhibit home range fidelity, familiarity increases the value of the contested location for the resident, but not the intruder (e.g., pied wagtails, *Motacilla alba*: Davies and Houston 1981). Within the boundaries of the home range or core area, groups may know the spatiotemporal distribution of resources, promoting efficient resource exploitation (Milton 1981; Garber 1989; Janson 1998). Consequently, the outcome of intergroup encounters may be determined by the role played by each group, which leads to site-dependent dominance relations (Cheney 1981; Kinnaird 1992; Kitchen et al. 2004a; Crofoot et al. 2008). Alternatively, asymmetries in the perceived value of the resource may be related to the current state of the competitors, determined by short- or long-term between-group differences in energetic intake (Janson and Vogel 2006). Groups may be less likely to contest over access to a food resource if they have recently fed in the area and individuals are currently satiated.

In contrast, although access to reproductive females is a high quality resource over which males are expected to compete (Trivers 1972), inequalities in the current number of potential mates do not necessarily correspond to asymmetries in payoff value among males. For example, in species in which mating opportunities are limited outside of social groups, the consequences of losing an aggressive encounter may be equally high for resident and intruder males. Solitary males and all-male bands may use intergroup encounters to take over reproductive positions (Hrdy 1977; Crockett and Janson 2000) or expose the weakness of resident males. Weak resident males risk female transfer (Stewart and Harcourt 1987; Sicotte 1993) or losing the support of group females, which may be influential in preventing male take-overs (Hausfater 1984; Steenbeek 2000).

Because participation in escalated aggression is affected not only by the objective resource value (e.g., total energy available, potential reproductive output of mates), but also by the perceived asymmetry among competitors – the assessment of which can vary widely among group members – an approach focused on individual assessment is crucial to understand the function and expression of intergroup aggression (Kitchen and Beehner 2007).

Outline of the dissertation

This dissertation addresses a series of interrelated questions related to between-group competition among tufted capuchin monkeys (*Cebus apella* [*Sapajus*] *nigritus*) in Iguazú National Park, Argentina: 1) What is the function of aggressive behavior during intergroup encounters? 2) What are the mechanisms of intergroup dominance? Is the outcome of intergroup encounters related to properties of the competing group or the location of the encounter? What are the long-term consequences of intergroup dominance? 3) What factors influence individual willingness to participate in intergroup aggression? 4) How concordant are the strategies of individuals of differing age-sex classes, rank and reproductive status?

Previous studies of the socioecology of tufted capuchin monkeys conducted in tropical forests have found only limited effects of between-group contest competition relative to intense within-group contest competition (Janson 1985, 1988, 1990). Among Peruvian tufted capuchin monkeys (*Cebus apella* [*Sapajus*] *macrocephalus*), intergroup aggression is associated with encounters at high quality food patches, while neutral or affiliative encounters occur in other contexts (Terborgh 1983). However, the quantitative effects of displacement on average individual energetic intake are negligible (4% variation between groups, relative to 36% variation within groups: Janson 1985).

In contrast, among Argentine capuchins, the ability of dominant individuals to monopolize resources is reduced (Janson 1994), intergroup aggression occurs outside of fruit patches, and critical food resources are heterogeneously distributed across habitats (Di Bitetti 2001). Consequently, between-group competition may have significantly greater effects on individual energetic intake and reproductive success due to differences in habitat; unlike previously studied populations, Iguazú is a semi-deciduous subtropical forest with marked seasonality in resource availability situated near the southern border of the species' geographical range.

In Chapter 2, I attempt to disentangle the relative importance of mate defense and resource defense strategies on the occurrence of aggressive behavior by males during intergroup encounters. Through provisioning experiments I show that male aggression during intergroup encounters in Argentine tufted capuchin monkeys is directly related to the presence of a high-quality food resource. Capuchin monkeys appear unusual in this pattern, given that, previously, male resource defense as a mating strategy has been demonstrated primarily in uni-male social systems. In contrast, males in multi-male groups generally directly defend access to mates, which provide the greatest fitness returns, although indirect benefits may arise through defending access to resources. Within this population, male capuchin monkeys act as "hired guns" (Rubenstein 1986), cooperating among each other and with resident females to defend food resources that may directly increase female fitness, yet only indirectly influence male reproductive success (Trivers 1972).

In Chapter 3, I investigate the consequences of this male-male cooperation for intergroup dominance relationships and home range quality. I use the outcome of naturally occurring intergroup encounters to assess the relative importance of male group size and encounter location on the outcome. Relative male group size is the most important factor in determining the winner of encounters, outweighing the competitive advantage of ownership. I then compare the availability of food resources within core areas as a function of male group size. Although resource density is not increased in the core areas of dominant groups, groups with more males are better able to defend their core area against other groups. As a result of reduced home range overlap, dominant groups may have higher *per capita* access to food. These results suggest that male-male cooperation could ultimately increase female reproductive success.

In Chapter 4, I return to the experimental analyses to examine how variation in resource value and relative competitive ability influence individual assessment of costs and benefits of participation. Although defense is a cooperative action, individuals differ in their motivations, which can lead to variation both between groups and between contests in the identity of participating individuals. Yet among tufted capuchin monkeys, males and females demonstrate concordant strategies, responding aggressively only in the presence of a high-quality food resource. Although male responses are significantly stronger than those of females, no differences are observed between dominant and subordinate individuals. As a result, intercontest variation in the resource holding potential of groups is minimal. Yet individuals appear to have adopted a strategy of probing the tolerance of dominant neighboring groups, likely due to rapid fluctuations in the opponent's subjective resource valuation as a function of hunger levels.

In Chapter 5, I examine whether these initial responses by individuals translate into participation in escalated conflicts by examining individual responses to naturally occurring intergroup encounters. Dominant males, subordinate males and females appear to employ variations of similar strategies during intergroup encounter, demonstrating sensitivity to the asymmetry in relative competitive ability. Dominant males, which monopolize the majority of mating, engaged in the highest-risk behaviors. In contrast, participating subordinate males have higher opportunity costs, pursuing neighboring groups farther and remaining longer at the site of the interaction. Overall, females are less likely to behave aggressively during intergroup encounters than males. When their group is at a competitive disadvantage, however, participating females take a more active role in defense of resources, especially if they have a young infant, suggesting that energetic costs rather than risks from intersexual aggression determine female behavior.

Finally, in Chapter 6, I summarize the major findings, synthesizing how ecological conditions such as high habitat homogeneity and low predator density create the potential for intense between-group contest competition over exclusive access to individual food resources and home ranges. That intergroup dominance in defense of food resources is mediated by high levels of cooperation amongs male “hired guns” remains an open question, and I suggest that future studies focusing on both short-term and long-term benefits for subordinate are necessary.

References

Agoramoorthy G, Hsu MJ (2000) Extragroup copulation among wild red howler monkeys in Venezuela. Folia Primatologica 71:147-151

Altmann J, Altmann SA, Hausfater G (1978) Primate infant's effects on mother's future reproduction. Science 201:1028-1030

Bartlett T (2003) Intragroup and intergroup social interactions in white-handed gibbons. International Journal of Primatology 24:239-259

Boggess J (1984) Infant killing and male reproductive strategies in langurs (*Presbytis entellus*). In: Hausfater G, Hrdy SB (eds) Infanticide: Comparative and Evolutionary Perspectives, Aldine Publishing Company, New York, pp 283-310

Borgerhoff Mulder M (1990) Kipsigis womens preferences for wealthy men - evidence for female choice in mammals. Behavioral Ecology and Sociobiology 27:255-264

Borries C (1993) Ecology of female social relationships: Hanuman langurs (*Presbytis entellus*) and the van Schaik model. Folia Primatologica 61:21-30

Borries C (1997) Infanticide in seasonally breeding multimale groups of Hanuman langurs (*Presbytis entellus*) in Ramnagar (South Nepal). Behavioral Ecology and Sociobiology 41:139-150

Bradbury JW, Vehrencamp SL (1977) Social-organization and foraging in emballonurid bats, III: mating systems. Behavioral Ecology and Sociobiology 2:1-17

Bradley BJ, Doran-Sheehy DM, Lukas D, Boesch C, Vigilant L (2004) Dispersed male networks in western gorillas. Current Biology 14:510-513

Broom M, Borries C, Koenig A (2004) Infanticide and infant defence by males - modelling the conditions in primate multi-male groups. Journal of Theoretical Biology 231:261-270

Brown JL (1964) Social regulatory mechanisms in bird populations - territoriality. American Zoologist 4:270-270

Cant MA, Otali E, Mwanguhya F (2002) Fighting and mating between groups in a cooperatively breeding mammal, the banded mongoose. Ethology 108:541-555

Cheney DL (1981) Intergroup encounters among free-ranging vervet monkeys. Folia Primatologica 35:124-146

Cheney DL (1987) Interactions and relationships between groups. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate Societies. University of Chicago Press, Chicago, pp 267-281

Cheney DL, Seyfarth RM (1987) The influence of intergroup competition on the survival and reproduction of female vervet monkeys. Behavioral Ecology and Sociobiology 21:375-386

Cords M (1987) Forest guenons and patas monkeys: male-male competition in one-male groups. In: Smuts BB, Cheney D, Seyfarth R, Wrangham R, Struhsaker T (eds) Primate Societies. University of Chicago Press, Chicago, pp 98-111

Cowlishaw G (1995) Behavioural patterns in baboon group encounters: the role of resource competition and male reproductive strategies. Behaviour 132:75-86

Crockett CM, Janson CH (2000) Infanticide in red howlers: female group size, male membership, and a possible link to folivory. In: van Schaik CP, Janson CH (eds) Infanticide By Males and Its Implications. Cambridge Univ Press, Cambridge, pp 75-98

Crockett CM, Sekulic R (1984) Infanticide in red howler monkeys (*Alouatta seniculus*). In: Hausfater G, Hrdy SB (eds) Infanticide: Comparative and Evolutionary Perspectives, Aldine Publishing Company, New York, pp 173-191

Crofoot MC, Gilby IC, Wikelski MC, Kays RW (2008) Interaction location outweighs the competitive advantage of numerical superiority in *Cebus capucinus* intergroup contests. Proceedings of the National Academy of Sciences of the United States of America 105:577-581

Crofoot MC, Gilby IC (2012) Cheating monkeys undermine group strength in enemy territory. Proceedings of the National Academy of Sciences of the United States of America 109:501-505

Davies NB, Houston AI (1981) . Owners and satellites: the economics of territory defence in the pied wagtail, *Motacilla alba*. Journal of Animal Ecology 50:157-180

Di Bitetti MS (2001) Home-range use by the tufted capuchin monkey (*Cebus apella nigritus*) in a subtropical rainforest of Argentina. Journal of Zoology 253:33-45

Dittus WPJ (1987) Group fusion among wild toque macaques - an extreme case of intergroup resource competition. Behaviour 100:247-291

Drews C (1993) The concept and definition of dominance in animal behaviour. Behaviour 125:283-31.

Ellefson JO (1974) A natural history of white-handed gibbons in the Malayan peninsula. Gibbon and Siamang 3:1-136

Emlen ST, Oring LW (1977) Ecology, sexual selection, and evolution of mating systems. Science 197:215-223

Fashing PJ (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 50:219-230

Garber PA (1988) Diet, foraging patterns, and resource defense in a mixed species troop of *Saguinus mystax* and *Saguinus fuscicollis* in Amazonian Peru. Behaviour 105:18-34

Garber PA (1989) Role of spatial memory in primate foraging patterns: *Saguinus mystax* and *Saguinus fuscicollis*. American Journal of Primatology 19:203-216

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 66:633-643

Goodall J (1986) The Chimpanzees of Gombe: Patterns of Behavior. Harvard University Press, Cambridge

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

Harris TR (2006) Between-group contest competition for food in a highly folivorous population of black and white colobus monkeys (*Colobus guereza*). Behavioral Ecology and Sociobiology 61:317-329

Harris TR, Fitch WT, Goldstein LM, Fashing PJ (2006) Black and white colobus monkey (*Colobus guereza*) roars as a source of both honest and exaggerated information about body mass. Ethology 112:911-920

Harris TR (2010) Multiple resource values and fighting ability measures influence intergroup conflict in guerezas (*Colobus guereza*). Animal Behaviour 79:89-98

Harrison MJS (1983) Territorial behaviour in the green monkey, *Cercopithecus sabaeus*: seasonal defense of local food supplies. Behavioral Ecology and Sociobiology 12:85-94

Hausfater G (1972) Intergroup behavior of free-ranging rhesus monkeys (*Macaca mulatta*). Folia Primatologica 18:78-107

Hausfater G (1984) Infanticide in langurs: strategies, counterstrategies, and parameter values. In: Hausfater G, Hrdy SB (eds) Infanticide: Comparative and Evolutionary Perspectives, Aldine Publishing Company, New York, pp 257-281

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

Hill C (1994) The role of the female diana monkeys, *Cercopithecus diana*, in territorial defence. Animal Behaviour 47:425-431

Hrdy SB (1977) Infanticide as a primate reproductive strategy. American Scientist 65:40-49

Isbell LA (1991) Contest and scramble competition: patterns of female aggression and ranging behavior among primates. Behavioral Ecology 2:143-155

Janson CH (1985) Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). Behavioral Ecology and Sociobiology 18:125-138

Janson CH (1988a) Food competition in brown capuchin monkeys (*Cebus apella*): Quantitative effects of group size and tree productivity. Behaviour 105:53-76

Janson, CH (1988b) Intra-specific food competition and primate social structure: A synthesis. Behaviour 105: 1-17

Janson CH (1990) Ecological consequences of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. Animal Behaviour 40:922-934

Janson CH (1994) Comparison of mating system across two populations of brown capuchin monkeys. American Journal of Primatology 33:217

Janson CH (1998) Experimental evidence for spatial memory in foraging wild capuchin monkeys, *Cebus apella*. Animal Behaviour 55:1229-1243

Janson CH, van Schaik CP (1988) Recognizing the many faces of primate food competition: Methods. Behaviour 105:165-186

Janson CH, Vogel ER (2006) Hunger and aggression in capuchin monkeys. In: Hohmann G, Robbins MM, Boesch C (eds) Feeding Ecology in Apes and Other Primates: Ecological, Physical and Behavioral Aspects. Cambridge Univ Press, Cambridge, pp 285-311

Jolly A (1972) Troop continuity and troop spacing in *Propithecus verreauxi* and *Lemur catta* at Berenty (Madagascar). Folia Primatologica 17:335-362

Kavanagh M (1981) Variable territoriality among tantalus monkeys in Cameroon. Folia Primatologica 36:76-98

Kinnaird MF (1992) Variable resource defense by the Tana River crested mangabey. Behavioral Ecology and Sociobiology 31:115-122

Kitchen DM (2004) Alpha male black howler monkey responses to loud calls: effect of numeric odds, male companion behaviour and reproductive investment. Animal Behaviour 67:125-139

Kitchen DM (2006) Experimental test of female black howler monkey (*Alouatta pigra*) responses to loud calls from potentially infanticidal males: effects of numeric odds, vulnerable offspring, and companion behavior. American Journal of Physical Anthropology 131:73-83

Kitchen DM, Beehner JC (2007) Factors affecting individual participation in group-level aggression among non-human primates. Behaviour 144, 1551-1581

Kitchen DM, Cheney DL, Seyfarth RM (2004a) Factors mediating inter-group encounters in savannah baboons (*Papio cynocephalus ursinus*). Behaviour 141:197-218

Kitchen DM, Horwich RH, James RA (2004b) Subordinate male black howler monkey (*Alouatta pigra*) responses to loud calls: experimental evidence for the effects of intra-group male relationships and age. Behaviour 141:703-723

Koenig A (2002) Competition for resources and its behavioral consequences among female primates. International Journal of Primatology 23:759-783

Korstjens AH, Nijssen EC, Noe R (2005) Intergroup relationships in western black-and-white colobus, *Colobus polykomos polykomos*. International Journal of Primatology 26:1267-1289

Kruuk H (1972) The Spotted Hyena: A Study of Predation and Social Behavior. University of Chicago Press, Chicago

Kumar A, Kurup GU (1985) Inter-troop interactions in the lion-tailed macaque, *Macaca silenus*. In: Heltne PG (ed). The Lion-Tailed Macaque: Status and Conservation. Liss, New York, pp 91-107

Lawes M, Henzi S (1995) Inter-group encounters in blue monkeys: How territorial must a territorial species be? Animal Behaviour 49:240-243

Lazaro-Perea C (2001) Intergroup interactions in wild common marmosets, *Callithrix jacchus*: Territorial defence and assessment of neighbours. Animal Behaviour 62:11-21

Lynch Alfaro JW (2007) Subgrouping patterns in a group of wild *Cebus apella nigritus*. International Journal of Primatology 28:271-289

Manson JH, Wrangham RW (1991) Intergroup aggression in chimpanzees and humans. Current Anthropology 32:369-377

Maynard Smith J, Parker GA (1976) Logic of asymmetric contests. Animal Behaviour 24:159-175

McComb K, Packer C, Pusey A (1994) Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. Animal Behaviour 47:379-387

Milton K (1981) Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental-development. American Anthropologist 83:534-548

Mutschler T, Nievergelt CM, Feistner ATC (2000) Social organization of the Alaotran gentle lemur (*Hapalemur griseus alaotrensis*). American Journal of Primatology 50:9-24

Nicholson AJ (1954) An outline of the dynamics of animal populations. Australian Journal of Zoology 2:9-65

Nievergelt CM, Mutschler T, Feistner ATC (1998) Group encounters and territoriality in wild Alaotran gentle lemurs (*Hapalemur griseus alaotrensis*). American Journal of Primatology 46:251-258

Nunn CL (2000) Collective benefits, free-riders, and male extra-group conflict. In: Kappeler PM (ed) Primate Males: Causes and Consequences of Variation in Group Composition. Cambridge Univ Press, Cambridge, pp 192-204

Nunn CL, Deaner RO (2004) Patterns of participation and free riding in territorial conflicts among ringtailed lemurs (*Lemur catta*). Behavioral Ecology and Sociobiology 57:50-61

Nunn CL, Lewis RJ (2001) Cooperation and collective action in animal behaviour. In: Noe R, Van Hooff JA, Hammerstein P (eds) Economics in Nature: Social Dilemmas, Mate Choice and Biological Markets. Cambridge Univ Press, Cambridge, pp 42-66

Packer C (1979) Inter-troop transfer and inbreeding avoidance in *Papio anubis*. Animal Behaviour 27:1-36

Packer C (1986) The ecology of sociality in felids. In: Rubenstein D, Wrangham R (eds) Ecological Aspects of Social Evolution: Birds and Mammals. Princeton University Press, Princeton, pp 282-302

Packer C, Pusey AE (1984) Infanticide in carnivores. In: Hausfater G, Hrdy SB (eds) Infanticide: Comparative and Evolutionary Perspectives, Aldine Publishing Company, New York, pp 31-42

Packer C, Scheel D, Pusey AE (1990) Why lions form groups: food is not enough. American Naturalist 136:1-19

Palombit R (1993) Lethal territorial aggression in a white-handed gibbon. American Journal of Physical Anthropology 31:311-318

Palombit R (1994) Extra-pair copulations in a monogamous ape. Animal Behaviour 47:721-723

Parker GA (1974) Assessment strategy and evolution of fighting behavior. Journal of Theoretical Biology 47:223-243

Parker GA, Rubenstein DI (1981) Role assessment, reserve strategy, and acquisition of information in asymmetric animal conflicts. Animal Behaviour 29:221-240

Peres CA (1989) Costs and benefits of territorial defense in wild golden lion tamarins, *Leontopithecus rosalia*. Behavioral Ecology and Sociobiology 25:227-233

Perry S (1996) Intergroup encounters in wild white-faced capuchins (*Cebus capucinus*). International Journal of Primatology 17:309-330

Pusey AE, Packer C (1987) Dispersal and philopatry. In: Smuts BB, Cheney DL, Seyfarth RM, Struhsaker TT, Wrangham RW (eds) Primate Societies. University of Chicago Press, Chicago, pp 250-266

Pusey AE, Packer C (1994) Infanticide in lions: consequences and counterstrategies. In: Parmigiani S, vom Saal FS (eds) Infanticide and Parental Care. Harwood Academic Publishers, Chur, Switzerland, pp 277-299

Ramírez-Llorens P, Di Bitetti MS, Baldovino MC, Janson CH (2008) Infanticide in black capuchins (*Cebus apella nigritus*) in Iguazú National Park, Argentina. American Journal of Primatology 70:473-484

Reichard U (1995) Extra-pair copulation in a monogamous gibbons (*Hylobates lar*). Ethology 100:99-112

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

Robinson JG (1986) Seasonal variation in use of time and space by the wedge-capped capuchin monkey, *Cebus olivaceus*: Implications for foraging theory. Smithsonian Contributions to Zoology 431:1-60

Robinson JG (1988) Group size in wedge-capped capuchin monkeys *Cebus olivaceus* and the reproductive success of males and females. Behavioral Ecology and Sociobiology 23:187-197

Rubenstein DI (1986) Ecology and sociality in horses and zebras. In: Rubenstein D, Wrangham R (eds) Ecological Aspects of Social Evolution: Birds and Mammals. Princeton University Press, Princeton, pp 282-302

Sauther ML, Sussman RW, Gould L (1999) The socioecology of the ringtailed lemur: Thirty-five years of research. Evolutionary Anthropology 8:120-132

Sicotte P (1993) Inter-group encounters and female transfer in mountain gorillas: influence of group composition on male behavior. American Journal of Primatology 30:21-36

Sicotte P, Macintosh AJ (2004) Inter-group encounters and male incursions in *Colobus vellerosus* in central Ghana. Behaviour 141:533-553

Smuts BB, Smuts RW (1993) Male aggression and sexual coercion of females in nonhuman primates and other animals: evidence and theoretical implications. Advances in the Study of Behavior 22

Stanford CB (1991) The capped langur in Bangladesh: Behavioral ecology and reproductive tactics. Contributions to Primatology:1-179

Steenbeek R (1999) Tenure related changes in wild Thomas's langurs. I: Between-group interactions. Behaviour 136:595-625

Steenbeek R (2000) Infanticide by male and female choice in wild Thomas's langurs. In: Van Schaik CP, Janson CH (eds) Infanticide by Males and its Implications. Cambridge Univ Press, Cambridge, pp 153-177

Sterck EHM, Watts DP, van Schaik CP (1997) The evolution of female social relationships in nonhuman primates. Behavioral Ecology and Sociobiology 41:291-309

Stewart KJ, Harcourt AH (1987) Gorillas: Variation in female relationships. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate Societies. University of Chicago Press, Chicago, pp 155-164

Struhsaker T (1980) Comparison of the behavior and ecology of red colobus and redtail monkeys in the Kibale Forest, Uganda. African Journal of Ecology 18:33-51

Suzuki S, Noma N, Izawa K (1998) Inter-annual variation of reproductive parameters and fruit availability in two populations of Japanese macaques. Primates 39:313-324

Terborgh J (1983) Five New World Primates: A Study in Comparative Ecology. Princeton University Press, Princeton

Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual Selection and the Descent of Man. Aldine, Chicago, pp 136-179

van Noordwijk MA, van Schaik CP (1987) Competition among female long-tailed macaques, *Macaca fascicularis*. Animal Behaviour 35:577-589

van Schaik CP (1983) Why are diurnal primates living in groups? Behaviour 87:120-144

van Schaik CP (1989) The ecology of social relationships amongst female primates. In: Standen V, Foley RA (eds) Comparative Socioecology: The Behavioral Ecology of Humans and Other Mammals. Blackwell Scientific Publications, Oxford, pp 195-218

van Schaik CP (1996) Social evolution in primates: The role of ecological factors and male behaviour. Proceedings of the British Academy 88:9-3

van Schaik CP, Assink PR, Salafsky N (1992) Territorial behavior in southeast Asian langurs: Resource defense or mate defense? American Journal of Primatology 26:233-242

van Schaik CP, Kappeler PM (1997) Infanticide risk and the evolution of male-female associations in primates. Proceedings of the Royal Society B-Biological Sciences 264:1687-1694

Watts DP (1989) Infanticide in mountain gorillas: New cases and a reconsideration of the evidence. Ethology 81:1-18

Watts DP, Muller M, Amsler SJ, Mbabazi G, Mitani JC (2006) Lethal intergroup aggression by chimpanzees in Kibale National Park, Uganda. American Journal of Primatology 68:161-180

Wich SA, Assink PR, Becher F, Sterck EHM (2002) Playbacks of loud calls to wild thomas langurs (Primates; *Presbytis thomasi*): The effect of familiarity. Behaviour 139:79-87

Williams J, Pusey A, Carlis J, Farm B, Goodall J (2002) Female competition and male territorial behaviour influence female chimpanzees' ranging patterns. Animal Behaviour 63:347-360

Williams JM, Oehlert GW, Carlis JV, Pusey AE (2004) Why do male chimpanzees defend a group range? Animal Behaviour 68:523-532

Wilson ML, Hauser MD, Wrangham RW (2001) Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? Animal Behaviour 61:1203-1216

Wrangham RW (1980) An ecological model of female-bonded primate groups. Behaviour 75:262-300

Chapter 2:
Male tufted capuchin monkeys cooperate to defend access to valuable food resources

Abstract

Intergroup encounters provide dramatic examples of cooperative behavior, in which unrelated individuals may coordinate aggression when mutual benefits arise from defending access to resources. For males, the spatiotemporal distribution of resources should determine whether they engage in food or mate defense. Yet resource defense as a male mating strategy has been demonstrated primarily in uni-male social systems, while males in multi-male groups generally directly defend access to females. Through provisioning experiments I show that male aggression during intergroup encounters in Argentine tufted capuchin monkeys (*Cebus* [*apella*] *nigritus*) is directly related to the presence of a high-quality food resource. Within this population, male capuchin monkeys act as "hired guns", cooperating with each other and resident females to defend the food resources critical for female fitness.

Introduction

Among group-living species, neighboring social groups compete for access to resources, and encounters between groups are frequently aggressive, even in the absence of strict territoriality. Interactions may involve chases, threat displays and occasionally lethal attacks (Mitani et al. 2010). In addition to the direct risk due to fighting, intergroup aggression may exhaust energy reserves and directly interfere with an individual's ability to rebuild these reserves (Peres 1989). Consequently, individuals are expected to participate only if the rewards directly benefit reproductive success. Sex differences in potential reproductive rates and parental investment cause males and females to differ in the relative benefits to reproductive success provided separately by food and mates (Trivers 1972). Thus female participation is more likely in defense of food resources, whereas males are expected to compete primarily for access to fertile females (Trivers 1972). In many species, male aggression during encounters serves to defend mating opportunities directly by discouraging potential male immigrants (Cheney and Seyfarth 1977) or preventing takeovers (Grinnell et al. 1995; Fedigan and Jack 2004) and extragroup copulations (Cheney and Seyfarth 1977; Palombit 1994). Among species that live in multimale groups, resident males may cooperate to defend access to a group of females (Cowlishaw 1995; Grinnell et al. 1995; Perry 1996). Unless mating is monopolized by a single male (Janson 1984), reproductive opportunities lost to extragroup males potentially affect the lifetime reproductive success of several individuals. Under these conditions, however, males may be tempted to free-ride upon the defensive actions of others to avoid incurring the costs of participation, which can result in suboptimal returns on cooperative defense (Nunn 2000; Harris 2010).

Resource defense can also serve as a male tactic to influence female mate choice (Emlen and Oring 1977), commonly-found among birds and harem-living mammals. Even among multi-male species, resource defense has been proposed as a male strategy to gain female support during intrasexual conflict over group membership (Wrangham 1980), and may indirectly benefit male reproductive success if resident females are able to reproduce more frequently (Rubenstein 1986). Despite this prediction, male participation in defense of food resources appears relatively uncommon among species with multi-male groups (Janson 1986; Williams et al. 2004; Crofoot

2007), and is generally found in combination with direct male mate defense (Kinnaird 1992; Crofoot 2007). Because the benefits of resource ownership only indirectly increase male reproductive success (Trivers 1972), male should be less likely to participate in intergroup aggression over food resources (van Schaik 1996; Nunn 2000). Here, I examined the strategies pursued by males and females during intergroup encounters in tufted capuchin monkeys (*Cebus apella* [*Sapajus*] *nigritus*) and found that male aggression is directly related to the presence of a high-quality food resource.

In Iguazú National Park, Argentina, tufted capuchin monkeys live in bisexual groups ranging in size from 5-44 individuals, and females typically remain in their natal group while males disperse before reaching sexual maturity (Janson et al. 2012). Interactions between neighboring groups are uniformly aggressive (Di Bitetti 2001), varying primarily in the degree of escalation, and both sexes participate in directing aggressive behaviors towards extragroup individuals (Di Bitetti 2001). The long-distance chases (≤400 m) associated with encounters (Di Bitetti 2001) make it difficult to correlate the intensity of aggressive response with resource presence – the method with which previous studies have tested the function of intergroup aggression (Kinnaird 1992; Crofoot 2007; Harris 2010) – because it is very likely that some food resources would be present in the neighborhood of any encounter. Therefore, I conducted playback experiments in combination with artificial manipulation of the resource base (Janson 1998b) of three habituated groups (Figure 4.1) to examine the independent effects of the presence of receptive females and available energy on the intensity of intergroup aggression, without introducing spatial or seasonal variation. I assessed individual response using three measures: whether the focal individual began to approach the speaker, acceleration, and change in neighbor density following the playback. If the experimental treatment increases the payoff to the winner, then individuals should be willing to invest more in intergroup aggression (Parker 1974), being either more likely to participate or increasing the strength of their responses.

Methods

Experimental design and data collection

Iguazú National Park is a semi-deciduous, subtropical forest near the southern limit of the Atlantic forest. I conducted all experiments during the austral winters of 2009 and 2010. This season is both a naturally occurring nadir in resource availability and the period in which most conceptive matings occur (Di Bitetti and Janson 2001a). Control conditions for each factor included natural levels of food availability (N = 27 trials) and days on which no sexually receptive female was present (N = 48 trials); experimental treatments included periods of provisioning (N = 34 trials) and/or when a sexually receptive female was present within the group (N = 13 trials). By established provisioning sites (Janson 1998b) in areas of home range overlap for three groups (see Figure 4.1), I could temporarily elevate local resource availability in the absence of concurrent changes in resource availability in the surrounding area. Similarly, the staggered occurrence of female proceptive and receptive sexual behaviors creates variation in the risk of extragroup copulations that both resident and extragroup males can easily assess. Because both the location and the season were held constant, any difference in individual response can be attributed to the experimental treatment.

I simulated encounters by presenting long-distance whistle series given during intergroup encounters to rally group members. I recorded the calls from adult and subadult males in neighboring groups using a Marantz PMD670 or PMD660 solid-state audio recorder with a

Sennheiser ME 67 or ME 66 shotgun microphone. I only presented vocalizations from groups that had been previously encountered in the area surrounding the provisioning site, so that individual response did not reflect a violation of expectation (Cheney and Seyfarth 1982). The speaker was positioned approximately 50 to 150 m from the edge of the group (observed distance at which individuals become aware of neighboring groups: C.J. Scarry, unpublished data). I conducted all playbacks in the vicinity of the provisioning sites (≤ 50 m), whether or not active provisioning was occurring. Although the order of presentation of the two contexts varied across the three groups, all groups became accustomed to the resource distribution before conducting the experiments. To avoid habituation to the playback vocalizations, I waited at least two days between experiments and did not conduct experiments on days on which natural encounters had already occurred.

One minute prior to the stimulus presentation, I established baseline measures by recording general behavior, current velocity (horizontal and vertical displacement in one minute, measured in ten-meter intervals) and neighbor density for the focal individual. I compared these data to matched samples recorded one minute following the playback to determine the strength of the individual's response. I also recorded whether or not the focal individual began to approach the speaker within one minute of the stimulus playback (similar to the latency to movement measure used in other studies). I considered only immediate responses because, during provisioning periods, the playback distance fell well within that at which the group had already begun directed movement toward the site (Janson 1998b), which interfered with my ability to determine whether arrival at the speaker was an indication of interest in the neighboring group or the food resource. To avoid artificially inflating the importance of the high-quality resource on approach behavior, I only counted cases in which the focal animal altered its general behavior to begin travelling.

Statistical analyses

I performed generalized linear mixed-effects modeling in R (R Development Core Team 2010) using the function "lmer" in the lme4 package (Bates et al. 2011) to identify factors that influence the probability of individual approach (N = 42), individual acceleration (N = 35) and group cohesion (N = 34). I calculated individual acceleration as the difference in velocity post- and pre-stimulus presentation, and then log-transformed the raw values to conform to the assumption of a normal distribution of residuals. I included focal animal identity as a random effect; fixed effects included focal sex, focal dominance status, presence of a defendable food resource, presence of a receptive female, and the relative rank of the caller. For individual approach, I used a logit-link function because the dependent variable (approach/non-approach) was binomially-distributed. I tested the overall significance of the full models against null models which included only focal identity as a random effect before selecting variables for the best-fit model. I tested for the significance of individual factors by removing single factors and using a likelihood-ratio test comparing the fit of the reduced model to the model including the factor of interest. For the analysis of individual approach, results of the likelihood ratio test are presented, rather than Wald's test statistic (Hauck and Donner 1977).

Results

Female sexual behavior did not significantly affect the behavioral response of resident males. The presence of one or more receptive females in the focal group affected neither the probability that a male approached the speaker (Figure 2.1) nor the rate at which a male approached ($\bar{x}_{\text{Present}}$ = 7.00 ± 16.01 m/min (± s.d.) vs. $\bar{x}_{\text{Absent}}$ = 6.25 ± 15.84 m/min (± s.d.); Generalized Linear

Mixed Effects Model (GLMM), receptive female presence: t = -0.192, P = 0.850, N = 24 trials). Furthermore, males were never observed to herd resident females away from extragroup males or otherwise discourage their participation in intergroup encounters.

Potential immigrants, which could increase the future costs of within-group competition for mates, may elicit higher levels of aggression from resident males. Because dominant males have never been observed to surrender a top breeding position in their current group to transfer to another group (Janson et al. 2012), I explored the possibility that the rank of the calling individual affected responses by focal males. Yet, males responded did not respond more strongly to recordings from smaller subordinate males ($P_{\text{Approach}} = 0.78$) in neighboring groups than they did to those from dominant males ($P_{\text{Approach}} = 0.69$; GLMM, male caller rank: X21 = 0.0018, P = 0.967, N = 24 trials). In the absence of a defendable food resource, resident males were more likely to approach a subordinate male caller (N = 4 out of 8 trials) than a dominant male (N = 1 out of 5 trials); however, the difference was not significant (GLMM, male caller rank: X21 = 0.459, P = 0.498, N = 13). Moreover, these approaches lacked the agitation observed in the presence of a defendable food resource, and no acceleration occurred ($\bar{x}$ = -1.67 ± 2.89 m/min (± s.d.), N = 3).

The presence of a defendable food resource significantly increased the probability of approach by both males and females (GLMM, resource presence: $X^2_1 = 16.156$, $P < 0.001$, N = 42 trials). Similarly, individuals accelerated more following the presentation of the playback stimulus during periods of active provisioning (Figure 2.2; GLMM, resource presence: t = 5.08, $P < 0.001$, N = 42 trials). During provisioning periods individuals increased their travel speed by nearly an order of magnitude after hearing the vocalization ($\bar{x}_{\text{Present}} = 18.65 \pm 14.25$ m/min (± s.d.), N = 26) relative to encounters when resource levels were at their natural low ($\bar{x}_{\text{Absent}} = 2.19 \pm 7.30$ m/min (± s.d.), N = 16), including cases in which they were already approaching the food source. Males accelerated significantly more than females during provisioning periods (GLMM, focal sex: t = 2.38, P = 0.032, N = 26 trials), but no sex difference was observed in the absence of a defendable resource (GLMM, focal sex: t = -0.083, P = 0.938, N = 16 trials). Furthermore, males, but not females, increased their density of neighbors within 5 m (Figure 2.3; GLMM, focal animal sex: t = 2.520, P = 0.021, N = 34 trials), regardless of the context. Dominant and subordinate males demonstrated no difference in their willingness to defend high-quality food resources, as measured by either their probability of approach ($P_{\text{Dominant}} = 1.00 \pm 0.00$ (± s.d.), $P_{\text{Subordinate}} = 1.00 \pm 0.00$ (± s.d.); GLM, focal rank: t = -0.379, P = 0.704, N = 17 individuals) or their acceleration upon hearing the playback vocalization ($\bar{x}_{\text{Dominant}} = 27.50 \pm 16.48$ m/min (± s.d.), $\bar{x}_{\text{Subordinate}} = 20.00 \pm 8.94$ m/min (±s.d.); GLMM, focal rank: t = -0.626, P = 0.551, N = 24 trials).

Discussion

The results suggest that males do not employ aggressive behavior during intergroup encounters as a tactic to defend short-term access to reproductive opportunities. Although females were never observed to either solicit or engage in copulations with extragroup males during naturally-occurring intergroup encounters (C.J. Scarry, unpublished data), this absence of extragroup copulations does not appear to be due to interference by resident males. The degree of male aggression towards extragroup individuals varied independently of female sexual behavior. Among tufted capuchin monkeys, males may not need to use aggressive behavior to separate extragroup males from resident females (Cheney and Seyfarth 1977; Kinnaird 1992; Palombit

1994; Agoramoorthy and Hsu 2000) due to strong female preference for resident males that can provide direct benefits (Janson 1984).

Similarly, there is no support for intergroup aggression as a response to the threat posed by neighboring males to long-term male reproductive success – through either aggressive takeovers (Grinnell et al. 1995; Steenbeek 1999; Kitchen 2004) or increased male immigrations (Cheney and Seyfarth 1977). In contrast to dominant males, subordinate males in neighboring groups occasionally use intergroup encounters as an opportunity to transfer directly between groups (C.J. Scarry, unpublished data); yet the rank of the calling individual had no effect on the response of resident males. This undifferentiated response may occur because male tufted capuchin monkeys do not regularly form coalitions to gain entry into bisexual groups (Janson et al. 2012), as is found in other species (Pope 1990; Grinnell et al. 1995; Steenbeek 1999; Kitchen 2004). Without coalitionary support, immigrant males, being generally younger and smaller-bodied than resident males, enter low in the hierarchy and typically need several years before being able to successfully challenge the alpha male (Janson et al. 2012). Furthermore, females generally avoid soliciting copulations with subadult males (Janson 1998a); consequently, these immigrants pose little threat to the current reproductive success of resident males.

Instead, male aggression during intergroup encounters appears to serve primarily to defend access to high-quality food resources. During provisioning periods, males invariably responded aggressively to the presence of a neighboring group, increasing travel speed and approaching the speaker. In contrast, although they occasionally approached the speaker during periods of natural resource availability, these approaches lacked the velocity and degree of agitation observed when high-quality resources were at stake, suggesting that they serve to assess neighboring groups rather than as active defense. Males may benefit from investigating the reproductive opportunities presented by neighboring groups, which can influence future transfer decisions (Packer 1979; Cheney 1981; Cheney and Seyfarth 1983; van Noordwijk and van Schaik 1985; Lazaro-Perea 2001).

Strikingly, although affiliative interactions among resident males are infrequent (Di Bitetti 1997), aggression towards extragroup individuals appears to be a semi-coordinated action. Following the playback presentation, males actively recruited aid in coalitionary defense, glancing over their shoulder to solicit support before proceeding jointly, which resulted in an increased neighbor density for males, but not females. This difference is striking, given that subordinate males typically occupy isolated positions on the periphery of the group to avoid aggression from the dominant male (Di Bitetti and Janson 2001b). By forming dispersed coalitions, males may be able to reduce the costs of intergroup aggression.

These coalitions, however, are not mutual endeavors to maintain control of groups as occur in some species (Pope 1990; Grinnell et al. 1995; Fedigan and Jack 2004). Thus, presumably subordinate males receive some form of reproductive benefits, either through direct or indirect fitness, to ensure their cooperation during intergroup encounters. The potential for indirect fitness benefits seems limited in this population, given the patterns of male dispersal noted above. Instead it seems likely that subordinate males benefit directly via individual mating success, perhaps using defense of group resources during intergroup encounters to influence female mate choice. How effective this tactic is remains unknown because paternity assessments have not yet been conducted. However, it is noteworthy that females in this population show reduced preference for the dominant male, and the dominant male's investment in maintaining consortships with receptive females is significantly greater than in other populations with less frequent and collaborative between-group aggression (Janson 1998a).

Although it has become clear that resource defense by males, in combination with direct mate defense (Trivers 1972), plays an important role in determining patterns of intergroup aggression (Wrangham 1980; Williams et al. 2004; Crofoot 2007), male resource defense as a primary strategy has been limited to species with harem groups (Emlen and Oring 1977; Rubenstein 1986). In multi-male groups, by leaving a receptive female in order to engage in intergroup aggression, males risk losing mating opportunities to other resident males. Thus, diminishing returns on investment in male resource defense may lead to a collective action problem in the absence of private returns (e.g., mating access: Nunn 2000; Harris 2010). Even within multi-male groups, however, resident males that sire infants may derive benefits from group defense, such as provisioning offspring, increasing the frequency of mating opportunities (Di Bitetti and Janson 2001b), and solidifying female support, which allows males to retain their rank beyond their physical prime (Janson et al. 2012).

Because female tufted capuchin monkeys are active participants in contests over food, however, males in this population may benefit more from resource defense. By mirroring patterns of female engagement, males may be able to successfully combine the benefits of mate guarding and resource defense. Thus, females appear able to manipulate male-male competition within groups so as to increase infant survivorship and decrease interbirth intervals (Di Bitetti and Janson 2001a), using males as “hired guns” (Rubenstein 1986) to increase resident females’ access to food resources. Simultaneously, females appear to be taking advantage of the additional support, adopting a laggard strategy of participation (Heinsohn and Packer 1995) and allowing the physically larger males to take positions at the forward edge of the group where the risk of injury is greater. In this population, intersexual conflict – often associated with infanticide (Hrdy 1977) and sexual coercion (Smuts and Smuts 1993) in non-human primates – has promoted cooperation between the sexes.

References

Agoramoorthy G, Hsu MJ (2000) Extragroup copulation among wild red howler monkeys in Venezuela. Folia Primatologica 71:147-151

Bates D, Maechler M, Bolker B (2011) lme4 - Linear mixed-effects models using S4 classes. R package version 0.999375-42, URL http://lme4.r-forge.r-project.org/

Cheney DL (1981) Intergroup encounters among free-ranging vervet monkeys. Folia Primatologica 35:124-146

Cheney DL, Seyfarth RM (1977) Behaviour of adult and immature male baboons during inter-group encounters. Nature 269:404-406

Cheney DL, Seyfarth RM (1982) Recognition of individuals within and between groups of free-ranging vervet monkeys. American Zoologist 22:519-529

Cheney D, Seyfarth RM (1983) Nonrandom dispersal in free-ranging vervet monkeys: social and genetic consequences. American Naturalist 122:392-412

Cowlishaw G (1995) Behavioural patterns in baboon group encounters: the role of resource competition and male reproductive strategies. Behaviour 132:75-86

Crofoot MC (2007) Mating and feeding competition in white-faced capuchins (*Cebus capucinus*): the importance of short- and long-term strategies. Behaviour 144:1473-1495

Di Bitetti MS (1997) Evidence for an important social role of allogrooming in a platyrrhine primate. Animal Behaviour 54:199-211

Di Bitetti MS (2001) Home-range use by the tufted capuchin monkey (*Cebus apella nigritus*) in a subtropical rainforest of Argentina. Journal of Zoology 253:33-45

Di Bitetti MS, Janson CH (2001a) Reproductive socioecology of tufted capuchins (*Cebus apella nigritus*) in northeastern Argentina. International Journal of Primatology 22:127-142

Di Bitetti MS, Janson CH (2001b) Social foraging and the finder's share in capuchin monkeys, *Cebus apella*. Animal Behaviour 62:47-56

Emlen ST, Oring LW (1977) Ecology, sexual selection, and evolution of mating systems. Science 197:215-223

Fedigan LM, Jack KM (2004) The demographic and reproductive context of male replacements in *Cebus capucinus*. Behaviour 141:755-775

Grinnell J, Packer C, Pusey AE (1995) Cooperation in male lions - kinship, reciprocity or mutualism. Animal Behaviour 49:95-105

Harris TR (2010) Multiple resource values and fighting ability measures influence intergroup conflict in guerezas (*Colobus guereza*). Animal Behaviour 79:89-98

Hauck WW, Donner A (1977) Wald's test as applied to hypotheses in logit analysis. Journal of the American Statistical Association 72:851-853

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

Hrdy SB (1977) Infanticide as a primate reproductive strategy. American Scientist 65:40-49

Janson CH (1984) Female choice and mating system of the brown capuchin monkey *Cebus apella* (Primates: Cebidae). Zeitschrift für Tierpsychologie 65:177-200

Janson CH (1986) The mating system as a determinant of social evolution in capuchin monkeys (*Cebus*). In: Else JG, Lee PC (eds) Primate Ecology and Conservation. Cambridge University Press, New York, pp 169-179

Janson CH (1998a) Capuchin counterpoint. In: Ciochon RL, Nisbett RA (eds) The Primate Anthology: Essays on Primate Behavior, Ecology and Conservation from Natural History. Prentice Hall, Upper Saddle River, NJ

Janson CH (1998b) Experimental evidence for spatial memory in foraging wild capuchin monkeys, *Cebus apella*. Animal Behaviour 55:1229-1243

Janson CH, Baldovino MC, Di Bitetti MS (2012) The group life cycle and demography of brown capuchin monkeys (*Cebus [apella] nigritus*) in Iguazú National Park, Argentina. In: Kappeler PM, Watts DP (eds) Long-Term Field Studies of Primates. Springer, Heidelberg, pp 185-212

Kinnaird MF (1992) Variable resource defense by the Tana River crested mangabey. Behavioral Ecology and Sociobiology 31:115-122

Kitchen DM (2004) Alpha male black howler monkey responses to loud calls: effect of numeric odds, male companion behaviour and reproductive investment. Animal Behaviour 67:125-139

Lazaro-Perea C (2001) Intergroup interactions in wild common marmosets, *Callithrix jacchus*: Territorial defence and assessment of neighbours. Animal Behaviour 62:11-21

Mitani JC, Watts DP, Amsler S (2010) Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. Current Biology 20:R507-R508

Nunn CL (2000) Collective benefits, free-riders, and male extra-group conflict. In: Kappeler PM (ed) Primate Males: Causes and Consequences of Variation in Group Composition. Cambridge Univ Press, Cambridge, pp 192-204

Packer C (1979) Inter-troop transfer and inbreeding avoidance in *Papio anubis*. Animal Behaviour 27:1-36

Palombit R (1994) Extra-pair copulations in a monogamous ape. Animal Behaviour 47:721-723

Parker GA (1974) Assessment strategy and evolution of fighting behavior. Journal of Theoretical Biology 47:223-243

Peres CA (1989) Costs and benefits of territorial defense in wild golden lion tamarins, *Leontopithecus rosalia*. Behavioral Ecology and Sociobiology 25:227-233

Perry S (1996) Intergroup encounters in wild white-faced capuchins (*Cebus capucinus*). International Journal of Primatology 17:309-330

Pope T (1990) The reproductive consequences of male cooperation in the red howler monkey: Paternity exclusion in multi-male and single-male troops using genetic markers. Behavioral Ecology and Sociobiology 27:439-446

R Development Core Team (2010) R: A language and environment for statistical computing. In: R Foundation for Statistical Computing, Vienna, Austria, URL http://www.R-project.org/.

Rubenstein DI (1986) Ecology and sociality in horses and zebras. In: Rubenstein DI, Wrangham RW (eds) Ecological Aspects of Social Evolution: Birds and Mammals. Princeton University Press, Princeton, NJ, pp 282-302

Smuts BB, Smuts RW (1993) Male aggression and sexual coercion of females in nonhuman primates and other animals: evidence and theoretical implications. Advances in the Study of Behavior 22

Steenbeek R (1999) Tenure related changes in wild Thomas's langurs. I: Between-group interactions. Behaviour 136:595-625

Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual Selection and the Descent of Man. Aldine, Chicago, pp 136-179

van Noordwijk MA, van Schaik CP (1985) Male migration and rank acquisition in wild long-tailed macaques (*Macaca fascicularis*). Animal Behaviour 33:849-861

van Schaik CP (1996) Social evolution in primates: The role of ecological factors and male behaviour. Proceedings of the British Academy 88:9-3

Williams JM, Oehlert GW, Carlis JV, Pusey AE (2004) Why do male chimpanzees defend a group range? Animal Behaviour 68:523-532

Wrangham RW (1980) An ecological model of female-bonded primate groups. Behaviour 75:262-300

Figure 2.1 Fitted values of the probability of male approach depending on the presence (block) or absence (gray) of a defendable resource. The presence of a defendable food resource increased the probability that the male approached the speaker (GLMM, resource presence: $X^2{}_1 = 13.506$, $P < 0.001$, $N = 24$ trials). The presence of a receptive female did not have a significant effect on the probability of male approach (GLMM, receptive female presence: $X^2{}_1 = 2.657$, $P = 0.104$), and the difference was in the opposite direction than predicted by the mate defense hypothesis. Reliable estimates of the standard error could not be determined (Hauck and Donner 1977).

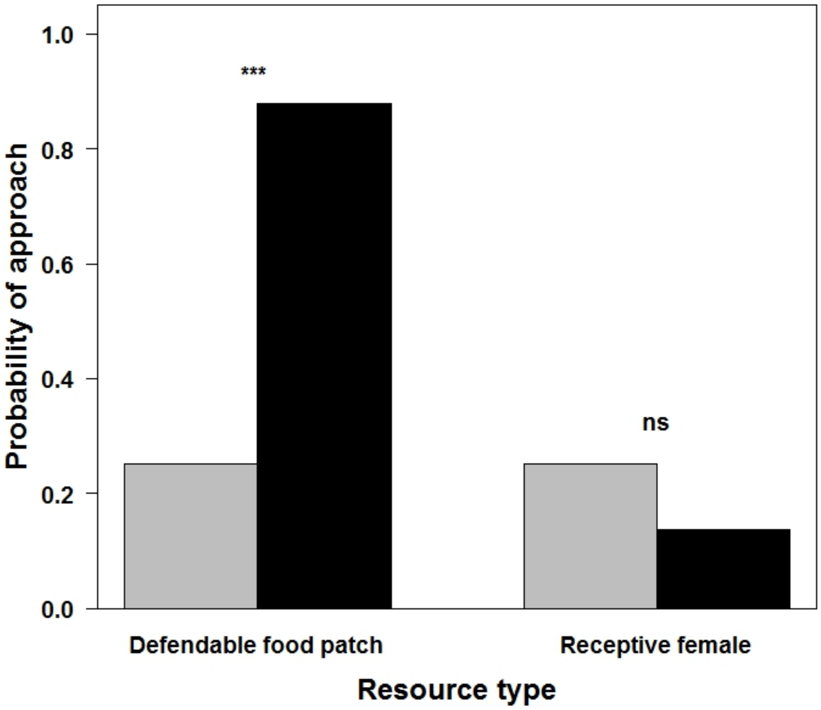


Figure 2.2 Fitted values for males (solid) and females (striped) of the effect of resource presence on acceleration. In the presence of a food resource, males accelerated more than females, but no difference occurred in the absence of a defendable food resource.

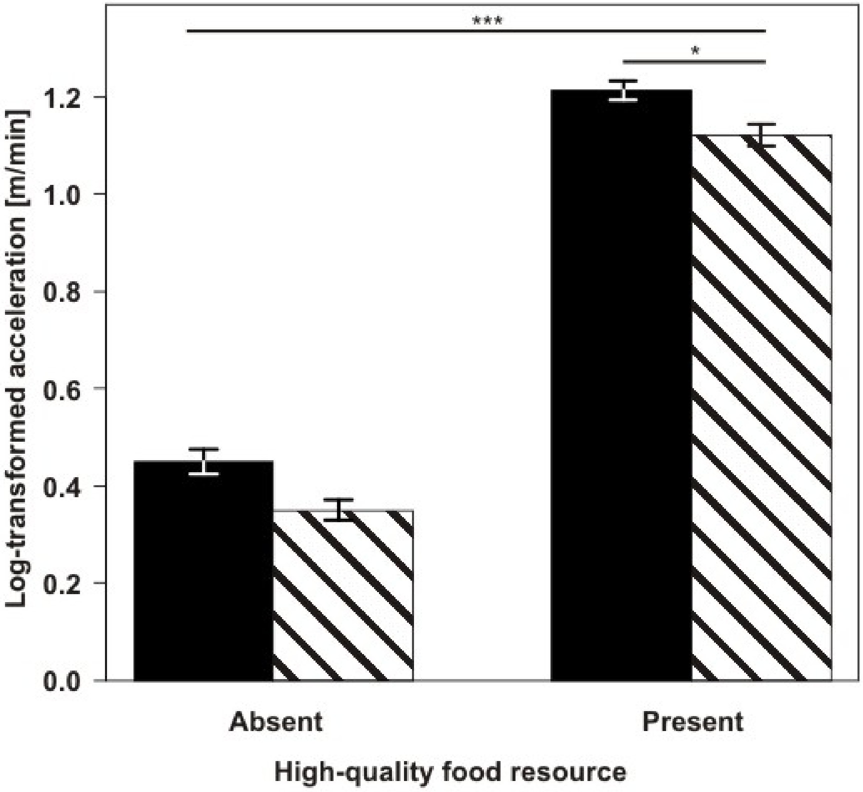
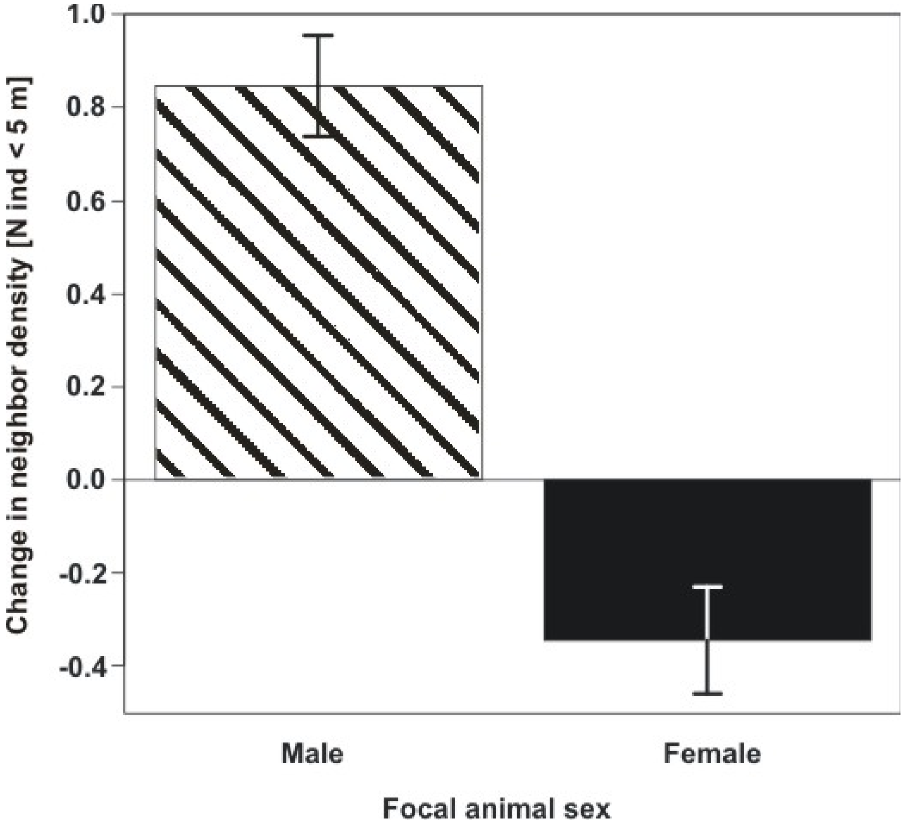


Figure 2.3 Fitted values for males (striped) and females (solid) for changes in neighbor density following the presentation of the playback stimulus. Error bars indicate values within one standard error of the mean. Males significantly increased their neighbor density relative to females following the presentation of the playback stimulus



Chapter 3:
Between-group contest competition among Argentine tufted capuchin monkeys (*Cebus apella* [*Sapajus*] *nigritus*) and the importance of male "hired guns"

Abstract

Between-group contest competition and the relative importance of male resource defense have recently been suggested to have been previously underestimated among nonhuman primates. When males contribute to the defense of group-controlled resources, the quality of the area utilized may depend on the resource holding potential of a group's males. Among Argentine tufted capuchin monkeys (*Cebus apella* [*Sapajus*] *nigritus*), dominant and subordinate males cooperate to defend immediate access to high-quality food resources. Here I investigate consequences of this male-male cooperation for intergroup dominance relationships and home range quality. I recorded ranging behavior for four habituated groups in Iguazú National Park, for 23 months to identify home ranges and core areas. I measured the availability of food species within botanical plots placed in each group's core area, using a stratified random sampling. I recorded the location and outcome of intergroup encounters and fitted predictive models using generalized estimating equations to assess the relative importance of male group size and location on the outcome encounters, before performing linear mixed-effects modeling to address the long-term benefits of winning encounters. Relative male group size was the most important factor in determining the winner of encounters, outweighing the competitive advantage of ownership. Average core area size was positively correlated with male group size, but neither the density of food species nor the total availability of food resources within the core area was influenced by the group's competitive ability. Dominant groups are better able to defend their core area, however, and adjusting for the degree of home range overlap revealed that dominant groups may have higher *per capita* access to food. These results suggest that male-male cooperation in defense of food resources could ultimately increase female reproductive success.

Introduction

Reduced risk of predation is frequently considered to be the primary benefit of sociality, while competition for food resources limits maximum group size (van Schaik 1983; van Schaik 1989; Sterck et al. 1997). Recently, however, it has been suggested that benefits obtained through between-group contest competition – wherein, by cooperating to defend access to food resources, individuals in dominant groups have relatively higher energy gain and, consequently, increased reproductive success (Wrangham 1980) – may have been previously underestimated (Fashing 2001).

Because group defense of food resources produces a public good, it is vulnerable to the collective action problem (Olson 1965). Through cooperation, individuals in large groups could benefit from the greater resource holding potential (RHP) of their group in order to win contests over access to resources (cf. larger body size or greater physical strength in contests between individuals: Parker 1974). Yet group members share the benefits of access regardless of their contribution to obtaining the resources, which may lead individuals to defect during aggressive intergroup encounters (Heinsohn and Packer 1995), avoiding both the energetic costs and risk of injury incurred by participants. The increased costs of within-group competition for resources in larger groups lead to diminishing returns of collective action to the individual as group size increases. Simultaneously, the marginal value of each additional competitor decreases, increasing the probability of free-riding within large groups. Consequently although maximum RHP increases with group size, the realized RHP is frequently lower than suggested by relative group size (Crofoot et al. 2008), and can even be inversely correlated with group size (Harris 2010).

Mechanisms to promote successful group defense proposed by theoretical model of the evolution of within-group social relationships – female philopatry (Wrangham 1980) and increased social tolerance (Sterck et al. 1997) – assume that resident females are the primary aggressors during these encounters. Although female reproductive success benefits more directly from increased access to food resources than does male reproductive success (Trivers 1972), defense of monopolizable food resource has also been demonstrated as a male strategy to attract mates among species with uni-male groups (resource defense polygyny: Emlen and Oring 1977; "hired guns": Rubenstein 1986). Moreover, recent analyses of individual participation suggest that resource defense can be a key component of male intergroup aggression in multi-male groups, as well (Fashing 2001; Harris 2006; Crofoot 2007). Yet, the role of male cooperation in mediating access to food resources in such multi-male groups has received little attention.

Among Argentine tufted capuchin monkeys (*Cebus apella* [*Sapajus*] *nigritus*), dominant and subordinate individuals of both sexes participate in aggressive intergroup encounters (Di Bitetti 2001b; Chapter 5), but the factors affecting the outcome of aggressive intergroup encounters within this population are unclear (Di Bitetti 2001b). Thus, the first goal of this study is to identify the factors allowing groups to win an intergroup encounter. In addition to the relative contribution of individuals from various age and sex classes, the outcome of contests may be influenced by the location of the encounter (Crofoot et al. 2008). Familiarity with an area allows individuals to utilize resources more efficiently and may create differing returns to owners versus intruders (Davies and Houston 1981). As a result, subjective resource valuation by individuals can vary depending on where the encounter occurs relative to the home range, affecting their willingness to escalate aggressive conflicts (Giraldeau and Ydenberg 1987). These differences in perceived value of a location may exacerbate patterns of individual defection (Crofoot and Gilby 2012), especially by subordinate individuals that gain less due to within-group contest competition, creating location-dependent dominance among groups.

In the absence of the demographic or energetic data needed to fully assess the between-group contest component of the competitive regime (Janson and van Schaik 1988), many studies have used the context of intergroup aggression as a proxy for the energetic consequences of intergroup dominance (e.g., Jolly 1972; Kavanagh 1981; Harrison 1983; Stanford 1991; Kinnaird 1992; Cowlishaw 1995; Fashing 2001). Willingness to participate in aggressive intergroup encounters should reflect the individual's perception of the relative benefits of gaining or maintaining access to the resource (including both individual fruit trees and larger areas such as territories or home ranges). Therefore, a pattern in which intergroup aggression occurs primarily at food resources, and affiliative or neutral interactions occur in other contexts, is indicative of contest competition for a high quality resource. Through playback experiments, I have demonstrated elsewhere that individuals respond strongly to the simulated presence of a neighboring group – even when it occurs within the core area – only during periods in which food is available at a location (Chapters 2 and 4). A similar response was observed among Peruvian tufted capuchin monkeys (*Cebus apella* [*Sapajus*] *macrocephalus*: Janson 1986), but in this population the cumulative effects for individual energy gain were negligible, relative to the costs of intragroup feeding competition (Janson 1985, 1988a). Moreover, because individual willingness to behave aggressively is driven by the immediate energetic returns provided by a resource, not merely proximity of another group, the consequences of these interactions for home range quality may be limited. Losing encounters may impose immediate costs through lost feeding opportunities (Janson and van Schaik 1988), yet these losses do not necessarily affect future access.

Other subtle advantages conferred by intergroup dominance (Janson and van Schaik 1988) may not be apparent if only the location of intergroup encounters is considered. In species in which groups maintain exclusive access to part of their home range, the density of food species within the core area may be greater for dominant groups (e.g., Cheney and Seyfarth 1987; Harris 2006; VanderWaal et al. 2009), or areas of exclusive access may increase with intergroup dominance, reducing the consequences of between-group scramble competition. If competitive ability is correlated with group size, however, simply increasing food availability may not outweigh the additional costs of within-group scramble competition. For example, increasing home range size with group size is a common pattern among mammals (Clutton-Brock and Harvey 1977; Grant et al. 1992), but it does not automatically increase the absolute quantity of food resources available per individual (Janson and van Schaik 1988). The second goal of this study, therefore, is to quantify long-term consequences of male intergroup aggression, by examining the relationship between intergroup dominance and home range quality. First, I examine whether their increased competitive ability during aggressive intergroup encounters allows dominant groups to have access to higher quality core areas (i.e., core areas with higher total food availability). Second, I test the hypothesis that through between-group contest competition, groups are able to offset the associated costs of group size, increasing *per capita* food availability within their home range.

Methods

Study site and population

Iguazú National Park is a 60,000 ha preserve in the Misiones province of northeastern Argentina, located at the southern border of the Atlantic forest biome. The Area Cataratas study site (25° 40’ S, 54° 30’ W) is composed of semi-deciduous forest and characterized by a humid, subtropical climate. Annual rainfall varies between 1500 and 2000mm, with no clear distinctions between wet and dry seasons (Brown and Zunino 1990). In contrast, marked seasonality in temperature and daylight exists with corresponding variation in the availability of both fleshy fruits and arthropods. Average availability of resources reaches its lowest point during the austral winter (May-Aug: Di Bitteti 1997). I collected all data over a 20-month period, which was divided across two sampling periods (Jun – Dec 2007, Jun 2008 – Aug 2009).

Within the study site, the only primate species present is the tufted or black-capped capuchin monkey (*Cebus apella* [*Sapajus*] *nigritus*), which occurs at a density of approximately 16 individuals/km^2 (Di Bitetti 2001b). Widely distributed throughout South America (Lynch Alfaro et al. 2012), tufted capuchin monkeys are small-bodied omnivores (Fragaszy et al. 2004). At Iguazú, capuchin monkeys live in permanent multi-male, multi-female groups of 5-44 individuals (Janson et al. 2012), which are characterized by male dispersal and female philopatry (Di Bitetti 1997). The site also hosts a nearly complete set of suspected and actual capuchin predators (Janson et al. 2012), although many of these species are found at low densities relative to other Neotropical sites (Di Bitetti et al. 2008; Paviolo et al. 2009).

All ranging and focal animal data were collected from four fully-habituated groups with overlapping home ranges (Figure 3.1), which have been the subjects of intermittent study since

1991 (e.g., Janson and Di Bitetti 1997). In addition, I identified seven groups residing within the study area that had occasional contact with the focal groups. For these non-focal groups, I obtained accurate counts of adult male group size and approximate total group size (Table 3.1). Although some males transfer from their natal groups as juveniles (Janson et al. 2012), I did not include these individuals in the count of male group size because I could only reliably identify non-natal juvenile males within the focal groups. Furthermore, due to large group spread, I was only able estimate relative female and juvenile group size for some of these non-focal groups. Other groups were also present; however, they were observed so infrequently so as to prevent reliable identification of any individuals.

Ranging data and identification of core areas and contestable resources

While following focal groups, I recorded the location of the group's center – defined as the point at which the observer is evenly surrounded by monkeys on all sides (Janson 1985) – at 15-minute intervals (Altmann 1974) using a Garmin GPSMAP 60Cx unit and/or the location relative to the geo-referenced trail system. In addition, if the group was traveling or foraging, I recorded the approximate direction of movement with ten degree precision.

I also collected ten-minute instantaneous focal animal samples (Altmann 1974) of adult group members, recording individual behavior at one-minute intervals. For a subsample of these data (N = 325.5 hrs), I was able to correlate the sample with the group's location, and I used these data to identify feeding locations within the home range. For each month, I overlaid a raster layer composed of 50 x 50 m cells on the study site, summing total feeding minutes occurring within each quadrat. I identified quadrates in which greater than 5% of monthly feeding minutes occurred as "important" feeding locations.

I entered all ranging data into an ArcGIS 9.3 (ESRI) database, and using the Hawth's Analysis Tools extension (Beyer 2004), I identified the home range and core area of each focal group from the 95% and 50% kernel density estimates (Worton 1989), respectively, analyzing ranging data from the two study periods separately for each group. To assess home range overlap with non-focal groups, I created minimum-convex polygons using all known locations that were recorded prior to the initiation of an intergroup encounter.

Intergroup encounter data

I defined intergroup encounters behaviorally (vs. spatially: Crofoot et al. 2008; Harris 2010) as occurring when the proximity of a neighboring group elicited reactions from one or more individuals in each group (including vocal exchanges in the absence of direct visual contact). I chose this more conservative definition because when following larger groups, I was not always aware of the proximity of neighboring groups. Low group cohesion limited our ability to detect subtle indicators of individual awareness (e.g., heightened vigilance in response to movements from the periphery of the group) that accompany interactions wherein one group alters its direction of movement to prevent direct interactions. Therefore, by defining encounters behaviorally, I avoid biasing the dataset towards avoidance by small groups, which could artificially inflate the importance of measures of group size on the outcome of encounters.

For all encounters, I recorded the starting location, as well as the direction of travel by the focal group following initial contact. I used two criteria to define the starting location of the encounter. First, if the majority of individuals in one group immediately fled the area without aggression, I used the location of that group prior to the encounter as the starting location (cf. Harris 2010). Otherwise, if both groups approached, I used the location where the leading edges of the groups met. Although in this population encounters are universally aggressive initially (Di Bitetti 2001b), they can terminate in long periods of co-feeding among neighboring groups. Therefore, I also recorded the location at which intergroup hostilities ceased; however, this was not always possible because I was occasionally unable to follow groups during the rapid chase that followed the initial aggressive behavior. Even on these occasions, it was easy to determine the identity of the winning group from the relative displacement of competing groups that occurred during the encounter (cf. Perry 1996) because losing groups generally retreat further into their core area (Di Bitetti 2001b). Undecided encounters – in which an extended face-off followed by mutual retreat prohibited identification of a winner – were infrequent (N = 8), but I included these events as ties in the analyses.

For encounters involving non-focal groups, if the identity of the group encountered could not immediately be determined, I recorded distinguishing characteristics of individuals and the minimum number of individuals in each age-sex class to permit identification of the group at a later date. If eventual identification of the group was not possible, data from the problematic encounter were excluded from all analyses (N = 17 encounters).

Home range quality and vegetation sampling

I used stratified random sampling to establish 80 botanical plots (20 x 50 m) such that (a) a minimum of twenty plots were located within each focal group's home range and (b) the number of core versus non-core plots per group was relatively even. Following Ganzhorn (1995), within each plot, we recorded the species, diameter at breast height (cm; DBH), height (m), crown diameter along two perpendicular axes (m), crown depth (m), and crown shape (i.e., sphere, hemisphere, cylinder, cone) for all stems greater than 10 cm DBH, which I used to calculate the basal area (m^2) and crown volume (m^3) of each stem.

To assess spatial heterogeneity of resource availability, I first calculated Lloyd's index of patchiness (Lloyd 1967) for each species using the frequency of stems within each plot. I then performed Kruskal-Wallis's *H*-tests to examine whether the average availability of each species within plots differed significant among groups.

Statistical analysis

Both males and females participate in intergroup aggression; therefore, I began by examining the importance of male group size relative to other measures of group size (i.e., number of adult females and total number of individuals) in deciding the outcome of intergroup encounters. For this analysis, I included only encounters that occurred between groups for which I had all three relevant measures of group size (N = 6 groups, 42 encounters). I fit predictive models using generalized estimating equations (GEE) with the function "geeglm" in the geepack package (Højsgaard et al. 2006) for R (R Development Core Team 2010) to identify the factors influencing whether or not the focal group won an encounter. Prior experience with a neighboring group (e.g., winner-loser effects: Chase et al. 1994) or differentiated individual responses based on the identity of the encountered group (e.g., due to prior history of male transfers: Cheney and Seyfarth 1987; or due to variation in the degree of male relatedness between groups: Bradley et al. 2004) could affect the nature and outcome of the current encounter. These factors could cause autocorrelation in successive encounters by interacting dyads – rather than the focal group, so I included the identity of the competing dyad as a random factor with an exchangeable correlation structure. I created a saturated model that included male group size, female group size and total group size as predictive variables relative to the null model, before removing terms that did not significantly increase the fit of the model, as assessed using the Wald's test via the 'anova' function.

I then compared the relative importance of subjective resource valuation (i.e., distance from home range center and distance from frequently-utilized resources) *versus* a group's competitive ability for determining the outcome of an intergroup encounter. For these analyses, I included only male group size as a measure of competitive ability, so that I could use the complete dataset (N = 105 encounters), including encounters with non-focal groups for which I was unable to obtain a complete census (N = 5 groups). I tested two separate definitions of home range center: 1) by averaging all recorded locations for the focal group and 2) by averaging only the group's location at midday, to avoid temporal autocorrelation. I calculated proximity to a contestable resource as the straight-line distance between the encounter location and the center of the closest raster cell that accounted for >5% of monthly feeding records.

As a second measure of competitive ability, I adapted R functions developed by Neumann et al. (2011) to calculate Elo-ratings for each group over the 2008-2009 field season, during which I detected no changes in adult male group size. The Elo-rating of a group is calculated from the outcomes of a sequence of dyadic interactions, which provides a measure of both cardinal rank and the relative power of non-interacting players that share a joint opponent (Albers and de Vries 2001). I performed linear regression to examine the effect of male group size on the final Elo-rating of the group, including ranks only for groups that had either a) interactions against both competitively stronger and weaker opposing groups (Albers and de Vries 2001) or b) at least nine straight winning or losing interactions by the end of the sampling period (N = 7 groups; Glickman and Doan 2010).

To estimate the total food available within plots, I summed basal areas and crown volume separately for all stems belonging to 32 tree species identified by Di Bitetti (2001a) as being seasonally important components of the capuchin diet. I also created a second, more conservative dataset, including only species that constituted >1% of monthly feeding records during focal animal samples. Analyses using these four measures of resource availability produced similar results, so I present only the results of the analysis of basal area of all known important food species (Di Bitetti 2001a). To determine whether core areas differed significantly from other parts of the home range, I randomly selected five core and five non-core plots for each group, ensuring that individual plots were not included twice. I performed generalized-linear mixed effect modeling (GLMM) with an identity-link function using the "lme" function in the nlme package for R (Pinheiro et al. 2012), including plot location (core vs. non-core) as a fixed factor and group identity as a random factor.

Finally, to assess the benefits of increasing male group size, I performed a series of sequential GLMMs, examining multiple pathways to increased resource access while correcting the significance level for the increased false-discovery rate due to multiple testing (Benjamini and Hochberg 1995). Dependent variables included: 1) core area size (ha); 2) total home range size (ha); 3) average resource density within the core area (basal area: m^2/hectare; crown volume: m^3/hectare); 4) total resource availability within the core area (basal area: m^2; crown volume: m^3); 5) *per capita* resource availability within the core area (basal area: m^2/individual; crown volume: m^3/individual) including only members of the focal group; and 6) *per capita* resource availability within the core area (basal area: m^2/individual; crown volume: m^3/individual) including individuals in overlapping groups. To calculate this last measure of resource availability, I first subdivided the core area based on the identity of groups utilizing each piece of the space (i.e., some portions of the core area overlapped with one or more other groups, while others were used exclusively; Table 3.2). For each subsection, I then calculated *per capita* availability from the estimated total number of individuals across all groups using that area. By summing these adjusted measures of *per capita* resource availability across the entire core area, I obtained the total basal area of food resources per individual.

Results

Male group size and competitive ability

The majority of the 105 intergroup encounters (92.4%) included in these analyses were decided in favor of one of the competing groups. The asymmetry in total group size, which includes both adults and juvenile group members, was not correlated with the probability of the focal group winning the encounter (GEE logistic regression: OR = 1.08, $X^2_1 = 3.63$, $p = 0.057$, repeated measure = dyad). Yet the competitive ability of the group increased with both relative female group size (GEE logistic regression: OR = 1.57, $X^2_1 = 6.26$, $p = 0.012$, repeated measure = dyad) and relative male group size (Figure 3.2; GEE logistic regression: OR = 3.56, $X^2_1 = 11.2$, $p < 0.001$, repeated measure = dyad) even after accounting for multiple testing; however, these two measures of group size are correlated ($r^2 = 0.835$, $p < 0.001$). Including both variables in a multiple regression reveals that only the asymmetry in male group sizes significantly affects the probability that the focal group will win the encounter (Table 3.3). Of the 93 encounters in which an asymmetry in male group size occurred between the competitors, 87.1% ($N = 81$) were decided in favor of the group with more males, while only 5.3% ($N = 5$) were won by the group with fewer males.

Consistent with the competitive advantage provided by each additional male, the final Elo-rating of the group increased with male group size (linear regression: $F_{1,5} = 37.16$, $p = 0.002$, $r^2 = 0.858$). Moreover, the low stability index ($S = 0.009$) indicates that group ranks were relatively unchanging (Neumann et al. 2011), suggesting that in the absence of demographic changes, clear dominance relationships exist among differently-sized groups (directional inconsistency index (DII) = 0.151; Noë et al. 1980), although undecided relationships were apparent (Figure 3.3).

Neither measure of proximity to the home range center directly affected the outcome of encounters (Table 3.4); however, the interaction of group size and relative location was significant in both models, even after correcting for multiple testing (Figure 3.4; Table 3.4). As groups with more males move away from the center of their home range, they are less likely to win encounters, whereas groups are more likely to win near the periphery of their home range when they are outnumbered. When the asymmetry is large, the cumulative effect of distance on the outcome of the encounter is minimal within one kilometer of the home range center.

Distance to a high-quality food resource had no effect on the probability of the focal group winning an encounter either as a main effect (GEE logistic regression: $X^2_1 = 1.04$, $p = 0.31$, repeated measure = dyad) or through an interaction with male group size (GEE logistic regression: $X^2_1 = 2.27$, $p = 0.13$, repeated measure = dyad).

Benefits of intergroup dominance

Average (± SD) core area size during the 2008-2009 field season was 39.3 ± 17.1 ha (N = 4 groups), which comprised 27.1 ± 5.8% of the total home range size (141.0 ± 52.4 ha). As expected, both core area (GLMM: $X^2_1 = 7.53$, $p = 0.006$, repeated measure = group) and total home range size (GLMM: $X^2_1 = 6.95$, $p = 0.008$, repeated measure = group) increase with increasing male group size. Although the core areas are defined based on high degrees of utilization, they do not differ from other portions of the home range in their average density of food resources (Figure 3.5; GLMM: $X^2_1 = 0.018$, $p = 0.89$, repeated measure = group).

Contrary to predictions, male group size had no effect on the average density of food tree species in the core area (Figure 3.6; GLMM, basal area: $X^2_1 = 0.006$, $p = 0.94$, repeated measure = group; GLMM, crown volume: $X^2_1 = 0.18$, $p = 0.67$, repeated measure = group). The extremely low density of food species within the home range of the most dominant group corresponds with synchronous masting of the tacuarazú bamboo (*Guadua chacoensis*) for the first time in approximately 30 years (Areta et al. 2009). While this unusual food resource was present, the Macuco group (but not the other focal groups) demonstrated a novel pattern of home range use (vs. Di Bitetti et al. 2000). Only nine stands occurred within the entire study area, and none of these patches was located within a botanical plot; however, removing this atypical data point from the analysis did not affect the results (GLMM, basal area: $X^2_1 = 0.21$, $p = 0.65$). Moreover, while the majority of food tree species (77.4%, N = 24 species) exhibit a clumped distribution, only one species (laurel blanco, *Ocotea diopsyrifolia*) differed significantly in its availability (basal m^2/ha) across the core areas of the four groups (Table 3.4). Although Di Bitetti (2001a) previously identified the species as being a seasonally important component of the capuchin diet, during this study, individuals were never observed feeding on *O. diospyrifolia*.

Despite the general homogeneity of core area quality, total basal area of food tree species within the home range increased with male group size (GLMM: $X^2_1 = 7.12$, $p = 0.008$, repeated measure = group) due to the observed relationship between male group size and core area size. Total crown volume, however, did not vary with male group size (GLMM: $X^2_1 = 0.72$, $p = 0.40$, repeated measure = group). Because male group size is correlated with increasing total group size ($r^2 = 0.77$, $p = 0.04$), more individuals are utilizing these resources, and the increased total availability does not translate into increased *per capita* food availability (GLMM, basal area: $X^2_1 = 0.05$, $p = 0.82$, repeated measure = group; GLMM, crown volume: $X^2_1 = 3.62$, $p = 0.06$, repeated measure = group).

This calculation assumes that groups maintain exclusive access to the resources within their core areas, yet tufted capuchin monkeys exhibit significant home range overlap (Terborgh 1983; Di Bitetti 2001b). On average, 60.6% of the core area (range: 8.6 – 93.6%) was utilized by at least one neighboring group. As a result, some portions of the core areas were used by 10 – 50 extragroup individuals, in addition to the members of the focal group. Although neither the percentage (GLMM: $t = 5.64$, $p = 0.018$) nor total area of exclusive access (GLMM, area: $t = 3.62$, $p = 0.068$) correlated with male group size, after correcting *per capita* availability for shared use by neighboring groups, a positive correlation with male group size was apparent (Figure 3.7; GLMM: $X^2_1 = 6.05$, $p = 0.014$, repeated measure = group; ; GLMM, crown volume: $X^2_1 = 8.42$, $p = 0.004$, repeated measure = group). This is not a small effect: per-capita food available to members of a group in its core area more than doubled as male group size increased from 1 to 5.

Discussion

The role of males in winning intergroup encounters

Across a wide range of taxa, group size correlates with resource holding potential (RHP) and is critical in determining the outcome of contests between groups (lions: Packer et al. 1990; primates: reviewed in Cheney 1987). Although group size establishes the maximum number of potential coalitionary partners available, the realized RHP of the group is frequently lower than this maximum due to defection by group members. Among species in which both sexes participate in intergroup aggression, for example, males and females may differ in their relative contribution to the collective effort (e.g., *Alouatta pigra*: Kitchen 2004, 2006; *Cercopithecus mitis*: Cords 2007). Disentangling these two measures of fighting ability can be difficult (e.g., Crofoot et al. 2008), because male group size frequently correlates with female group size (e.g., primates: Mitani et al. 1996). Although decided between-group dominance relationships (vs. location-dependent dominance: Cheney 1981; Kinnaird 1992; Kitchen et al. 2004a) within this capuchin population had been detected previously (Di Bitetti 2001b), no clear relationship with either total group size or female group size was apparent. The large sample size available for this study makes it clear that both of these measures are imperfect proxies for the true competitive ability of the group: tufted capuchin groups are more likely to win intergroup encounters when they have an advantage in relative number of males (Bygott et al. 1979; Robinson 1988; Cowlishaw 1995; Grinnell et al. 1995), which supports recent findings that established dominance relationships may shift following a change in relative male group sizes (Scarry and Tujague 2012).

That each additional male enhances the competitive ability of the group (cf. lions, *Panthera leo*: Grinnell et al. 1995) indicates that tufted capuchin monkeys are able to overcome the potential collective action problem while engaging in intergroup aggression (Nunn 2000; Nunn and Lewis 2001). In contrast to two previously studied species (Harris 2010; Crofoot and Gilby 2012), the collective strength of groups with more males is not disproportionately reduced by defectors, although free-riding may still occur. One possible explanation for this successful collective defense is that males cannot use lagging during intergroup encounters as a strategy to bypass intragroup mating competition (vs. Harris 2010). Frequent participation by adult females (Di Bitetti 2001b; Chapter 5) eliminates the possibility for subordinate males to engage in sneak copulations while the dominant male is occupied.

The presence of bystanders may even promote willingness to participate by males, as has recently been suggested to occur among white-faced capuchin males (*Cebus capucinus*: Meunier et al. 2012). Although females could presumably benefit by avoiding the potential costs and free-riding on the defensive behavior of males (Nunn and Lewis 2001; Kitchen 2006), they not only approach neighboring groups (Di Bitetti 2001b) but also assist resident males in directing coalitionary threats towards extragroup individuals (Chapter 5). If male behavior during intergroup encounters is influenced by an “audience effect” (reviewed in Earley 2010), female participation may serve primarily to monitor the aggressive response of resident males, so that the competitive advantage provided by numerical superiority is maintained throughout the encounter. Audience effects have previously been described in the production of food-associated calls within this species (Di Bitetti 2005), and individuals exhibit high rates of social vigilance during normal group activities (Hirsch 2002); however, increased monitoring may be insufficient to ensure cooperation during intergroup encounters because males may be tempted to participate initially but then defect during the long chase that follows initial contact (Di Bitetti 2001b), unless accompanied by other group members.

Nonetheless, the competitive advantage provided by increased male group size is insufficient to entirely overcome asymmetries in perceived resource ownership or increased familiarity with an area (Fig. 4). Groups with more males are more likely to lose encounters that occur farther from the center of their home range, which suggests that increasing peripherality may affect individual assessment of the relative costs and benefits of engagement (birds: Giraldeau and Ydenberg 1987; primates: Crofoot and Gilby 2012). Yet in contrast to several previously studied primate species (Cheney 1981; Kinnaird 1992; Kitchen et al. 2004a; Crofoot et al. 2008), proximity to the home range center does not increase the probability that the numerically weaker group will win. Instead, there is a slight tendency for groups with fewer males to win encounters occurring near the periphery of their home ranges. This seemingly paradoxical result most likely emerges due to the circumscribed position of relatively small groups within areas of overlap between large groups (Fig. 1), such that increasing proximity to the home range center for the subordinate group generally coincides with increasing centrality for one of the larger neighbors. Instead, for the majority of intergroup encounters, the asymmetry in male group size strongly predicts the outcome of the encounter. An asymmetry in perceived resource ownership only allows smaller groups to win when the relative difference in male group size equals one, indicating that a general pattern of home-field advantage does not occur.

The benefits of collective male resource defense

These results add to the growing body of literature indicating that defending access to limiting food resources can be an important component of male aggression towards extragroup individuals (Fashing 2001; Harris 2006; Crofoot 2007). Earlier experimental analyses at Iguazú linked willingness to participate in intergroup encounters by both dominant and subordinate male capuchin monkeys to immediate energetic gains (Chapter 2), but it was not possible to determine whether participation by multiple males increases returns, or simply reduces individual costs of defense. The current analyses suggest that – due to collective defense by resident males – both immediate and long-term access to food resources increase with male group size. Groups with more males are able to win encounters, allowing them to displace neighboring groups from individual food resources and maintain exclusive access to larger areas. By sharing fewer of the food resources available within their core area with neighboring groups, individuals may incur reduced costs of between-group scramble competition (Janson and van Schaik 1988). The absence of a group size effect in *per capita* reproductive rates (Janson et al. 2012), however, suggests that the increase in absolute quantity of food resources available per individual increases in dominant groups serves only to compensate for the increased costs of within-group scramble competition in larger groups (Stacey 1986; Janson 1988b; Koenig 2000; Koenig 2002).

The alternate possibility – that access to higher quality areas permits increased female group size, thereby attracting more male immigrants and promoting intergroup dominance (Janson and van Schaik 1988) – was not supported; the density of fruit tree species within the core area does not vary among groups (vs. black-and-white colobus monkeys, *Colobus guereza*: Harris 2006). Furthermore, a significant decrease in relative male group size resulted in decreased exclusivity of the home range (Scarry and Tujague 2012), although the resulting group may continue to utilize most or all of the original home range (Di Bitetti 2001b).

Critically, the current results provide no support for the recent suggestion that location-dependent patterns of free-riding are necessary to promote stable coexistence by variably sized groups within a single population (Crofoot and Gilby 2012). In the absence of a home-field advantage, smaller groups appear confined to areas of overlap between the home ranges of larger groups, yet there is no evidence of frequent group extinctions or fusions (Janson et al. 2012). Indeed, although groups are occasionally displaced from their home range, even relatively small groups can exhibit long-term range stability (Di Bitetti 2001b). If the constant growth rate of groups during periods of demographic stability (Janson et al. 2012) is an indication that the capuchin monkey population at Iguazú is not energy-limited, then the objective value of contested locations may be insufficient to warrant escalated conflicts (Maynard Smith and

Parker, 1976). In keeping with this hypothesis, aggressive physical contact between adult individuals from opposing groups was observed in less than 1% of intergroup encounters (N = 1), and no injuries could be attributed to intergroup aggression. The absence of lethal intergroup aggression sets up the possibility for subordinate groups to establish and maintain home ranges by repeatedly "nagging" at their dominant neighbors (Stamps and Krishnan 2001), which increases the opportunity costs of maintaining exclusive access. Through persistence in the face of defeat, subordinate groups can force larger neighbors to tolerate their presence rather than exerting the effort necessary to totally exclude them. Thus, long-term coexistence appears may be promoted through tradeoffs between the costs and benefits of exclusive access, which vary according to group size.

The role of males as "hired guns"

While it is not currently evident whether dominant and subordinate males contribute equally to the collective effort (Kitchen 2004; Kitchen et al. 2004b), agonistic support from subordinate males is a critical factor in determining the outcome of intergroup aggression. Thus, overall, these results suggest that resident females derive clear benefits from the presence of additional subordinate males within the group (cf. Wrangham 1980). Among birds and harem-living mammals, defense of feeding territories or individual contestable resources has been established as a common male strategy to attract mates (resource defense polygyny: Emlen and Oring 1977) or to improve offspring survival and reduce female interbirth intervals (cf. "hired guns": Rubenstein 1986). Yet within multi-male groups, both theoretical (van Schaik 1996; Nunn 2000) and empirical studies (Harris 2010; Crofoot and Gilby 2012) suggest that male collective action is difficult to maintain in this context, especially when mating access is highly skewed (e.g., Janson 1986). Due to the more indirect nature of benefits to male reproductive success accrued through access to food relative to additional mating opportunities (Trivers 1972), subordinate males will likely be tempted to defect during intergroup encounters over food resources (Nunn 2000), unless the costs of participation are offset by inclusive fitness benefits (Hamilton 1964, Vehrencamp 1983b) or private incentives (e.g., mating opportunities: Nunn 2000).

Female mate choice among tufted capuchins is influenced by within-group resource monopolization (Janson 1984), but the potential for males to use aggression towards extragroup individuals as a tactic to influence female mate choice appears limited. At Iguazú, tufted capuchin monkeys have seasonal mating and reproduction (Di Bitetti and Janson 2001a). Thus despite absorbing immediate costs of intergroup aggression, males would not receive copulations in exchange for participation for several months out of the year. To balance this transaction, adult females could direct other affiliative behaviors (e.g., grooming) towards males to provide a "shadow of the future" (Axelrod 1984, p. 124); yet during non-mating seasons, the dominant male is the preferred socio-spatial partner of adult females, regardless of rank (Di Bitetti 1997; Tiddi et al. 2011b), whereas subordinate adult males have affiliative contacts primarily with juvenile males (Di Bitetti 1997). Moreover, while tufted capuchins have well-developed cognitive abilities (Fragaszy et al. 2004), they demonstrate a high degree of temporal discounting (foraging tasks: Ramseyer et al. 2006), and it is not clear the degree to which partner choice reflects the long-term potential for providing benefits versus immediate reciprocity (but see Tiddi et al. 2011a). The delayed nature of reciprocity, therefore, increases the chances that males will undervalue the possibility of eventual repayment (Kagel et al. 1986), making collective action difficult to maintain.

This problem could be resolved if males are directly defending access to food resources critical to their own reproductive success. In this context, benefits to females are simply a byproduct of male mating competition, rather than the basis of female mate choice (cf. Rubenstein 1986). Tufted capuchin males transfer prior to attaining adult body size, and typically wait several years before they are able to successfully challenge the dominant male (Janson et al. 2012). Although they occupy relatively high positions in within-group dominance hierarchies (Di Bitetti 1997), subordinate males continue to receive high rates of aggression from the dominant male and resident females (Janson 1985), which negatively impacts their daily energy intake (Janson 1985) and may increase physiological indicators of stress (Abbott et al. 2003; Sapolsky 2005). Depending on the strength of this within-group contest competition, subordinate males may exhibit suboptimal body condition (Setchell et al. 2010) or delayed physical maturation. Thus, although parental investment theory suggests that males should compete primarily over access to mating opportunities (Trivers 1972), intolerance at food resources could also serve as a form of intrasexual competition (Janson 1985), whereby the dominant male is able to prolong his tenure as alpha and increase his lifetime reproductive success (Muniz et al. 2010). Because their aggressive behavior increases *per capita* food availability for the group, the overall magnitude of within-group competition may be reduced (Janson and van Schaik 1988), attenuating these effects of intrasexual competition. In addition, subordinate males may benefit through trading participation during intergroup encounters for increased tolerance at contestable food resources by other group members (cf. grooming for tolerance: Tiddi et al. 2011a). Understanding the degree to which females – or other group members – are manipulating this competition, therefore, requires further analyses examining the relationship between co-feeding and male behavior during intergroup encounters.

Conclusion

While these results are suggestive of a competitive regime with strong between-group contest competition, further analyses are needed to assess the tradeoff that occurs between increasing competitive ability of the group and costs of within-group competition (van Schaik 1989). Tufted capuchin monkeys exhibit high rates of intragroup aggression, and – at least in other subspecies – strong effects of within-group contest competition on individual energy intake (Janson 1985; Janson 1988a). Yet despite the low density of capuchin monkey predators (Vargas et al. 2006; Di Bitetti et al. 2008; Paviolo et al. 2009), relative group sizes at Iguazú are large compared with other populations (reviewed in Di Bitetti 2001b). The subtropical habitat at Iguazú, which is comprised of relatively small but abundant patches, reduces the ability of dominant individuals to monopolize individual resources (Janson 1994), while reduced group cohesion may further decrease within-group competition (Janson et al. 2012). The willingness of subordinate individuals – both males and females – to participate in defense of group-controlled resources (Chapter 2, 4 and 5) strongly suggests they derive fitness benefits. If true, these fundamental differences in the resource base appear to alter the competitive regime experienced (van Schaik 1989); yet the predicted increased tolerance in female dominance relationships (Sterck et al. 1997) does not occur (e.g., Di Bitteti and Janson 2001b). The importance of resident males in determining the outcome of intergroup aggression suggests the need to expand existing models to include the potential for ecological variation to affect male-female social relationships, as well.

References

Abbott DH, Keverne EB, Bercovitch FB, Shively CA, Mendoza SP, Saltzman W, Snowdon CT, Ziegler TE, Banjevic M, Garland Jr T, Sapolsky RM (2003) Are subordinates always stressed? a comparative analysis of rank differences in cortisol levels among primates. Hormones and Behavior 43:67-82

Albers PCH, de Vries H (2001) Elo-rating as a tool in the sequential estimation of dominance strengths. Animal Behaviour 61:489-495

Altmann J (1974) Observational study of behavior - sampling methods. Behaviour 49:227-267

Areta JI, Bodrati A, Cockle K (2009) Specialization on *Guadua* bamboo seeds by three bird species in the Atlantic Forest of Argentina. Biotropica 41:66-73

Axelrod R (1984) The Evolution of Cooperation. Basic Books, New York

Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society Series B (Methodological) 57:289-300

Beyer HL (2004) Hawth's Analysis Tools for ArcGIS. URL http://www.spatialecology.com/htools

Bradley BJ, Doran-Sheehy DM, Lukas D, Boesch C, Vigilant L (2004) Dispersed male networks in western gorillas. Current Biology 14:510-513

Brown AD, Zunino GE (1990) Dietary variability in *Cebus apella* in extreme habitats: evidence for adaptability. Folia Primatologica 54:187-195

Bygott JD, Bertram BCR, Hanby JP (1979) Male lions in large coalitions gain reproductive advantages. Nature 282:839-841

Chase ID, Bartolomeo C, Dugatkin LA (1994) Aggressive interactions and inter-contest interval: how long do winners keep winning? Animal Behaviour 48:393-400

Cheney DL (1981) Intergroup encounters among free-ranging vervet monkeys. Folia Primatologica 35:124-146

Cheney DL, Seyfarth RM (1987) The influence of intergroup competition on the survival and reproduction of female vervet monkeys. Behavioral Ecology and Sociobiology 21:375-386

Clutton-Brock TH, Harvey PH (1977) Primate ecology and social organization. Journal of Zoology 183: 1-39

Cords M (2007) Variable participation in the defense of communal feeding territories by blue monkeys in the Kakamega Forest, Kenya. Behaviour 144:1537-1550

Cowlishaw G (1995) Behavioural patterns in baboon group encounters: the role of resource competition and male reproductive strategies. Behaviour 132:75-86

Crofoot MC (2007) Mating and feeding competition in white-faced capuchins (*Cebus capucinus*): the importance of short- and long-term strategies. Behaviour 144:1473-1495

Crofoot MC, Gilby IC (2012) Cheating monkeys undermine group strength in enemy territory. Proceedings of the National Academy of Sciences of the United States of America 109:501-505

Crofoot MC, Gilby IC, Wikelski MC, Kays RW (2008) Interaction location outweighs the competitive advantage of numerical superiority in *Cebus capucinus* intergroup contests. Proceedings of the National Academy of Sciences of the United States of America 105:577-581

Davies NB, Houston AI (1981) Owners and satellites - the economics of territory defense in the Pied Wagtail, *Motacilla alba*. Journal of Animal Ecology 50:157-180

Di Bitetti MS (1997) Evidence for an important social role of allogrooming in a platyrrhine primate. Animal Behaviour 54:199-211

Di Bitetti MS (2001a) Food Associated Calls in the Tufted Capuchin Monkey (*Cebus apella*). In: Ecology and Evolution. Stony Brook University, Stony Brook

Di Bitetti MS (2001b) Home-range use by the tufted capuchin monkey (*Cebus apella nigritus*) in a subtropical rainforest of Argentina. Journal of Zoology 253:33-45

Di Bitetti MS (2005) Food-associated calls and audience effects in tufted capuchin monkeys, *Cebus apella nigritus*. Animal Behaviour 69:911-919

Di Bitetti MS, Janson CH (2001a) Reproductive socioecology of tufted capuchins (*Cebus apella nigritus*) in northeastern Argentina. International Journal of Primatology 22:127-142

Di Bitetti MS, Janson CH (2001b) Social foraging and the finder's share in capuchin monkeys, *Cebus apella*. Animal Behaviour 62:47-56

Di Bitetti MS, Paviolo A, De Angelo CD, Di Blanco YE (2008) Local and continental correlates of the abundance of a neotropical cat, the ocelot (*Leopardus pardalis*). Journal of Tropical Ecology 24:189-200

Di Bitetti MS, Vidal EML, Baldovino MC, Benesovsky V (2000) Sleeping site preferences in tufted capuchin monkeys (*Cebus apella nigritus*). American Journal of Primatology 50:257-274

Earley RL (2010) Social eavesdropping and the evolution of conditional cooperation and cheating strategies. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2675-2686

Emlen ST, Oring LW (1977) Ecology, sexual selection, and evolution of mating systems. Science 197:215-223

Fashing PJ (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 50:219-230

Fragaszy DM, Visalberghi E, Fedigan LM (2004) The Complete Capuchin: Biology of the Genus *Cebus*. Cambridge University Press, Cambridge

Ganzhorn JU (1995) Low-level forest disturbance effects on primary production, leaf chemistry, and lemur populations. Ecology 76:2084-2096

Giraldeau LA, Ydenberg R (1987) The center-edge effect: the result of a war of attrition between territorial contestants? Auk 104:535-538

Glickman ME, Doan T (2010) The UCSF Rating System. URL http://www.glicko.net/ratings/rating.system.pdf

Grant JWA, Chapman CA, Richardson KS (1992) Defended versus undefended home range size of carnivores, ungulates and primates. Behavioral Ecology and Sociobiology 31: 149-161

Grinnell J, Packer C, Pusey AE (1995) Cooperation in male lions - kinship, reciprocity or mutualism. Animal Behaviour 49:95-105

Hamilton WD (1964) Genetical evolution of social behaviour I. Journal of Theoretical Biology 7:1-16

Harris TR (2006) Between-group contest competition for food in a highly folivorous population of black and white colobus monkeys (*Colobus guereza*). Behavioral Ecology and Sociobiology 61:317-329

Harris TR (2010) Multiple resource values and fighting ability measures influence intergroup conflict in guerezas (*Colobus guereza*). Animal Behaviour 79:89-98

Harrison MJS (1983) Territorial behaviour in the green monkey, *Cercopithecus sabaeus*: seasonal defense of local food supplies. Behavioral Ecology and Sociobiology 12:85-94

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

Hirsch BT (2002) Social monitoring and vigilance behavior in brown capuchin monkeys (*Cebus apella*). Behavioral Ecology and Sociobiology 52:458-464

Højsgaard S, Halekoh U, Yan J (2006) The R Package geepack for generalized estimating equations. Journal of Statistical Software 15:1-11

Janson CH (1984) Female choice and mating system of the brown capuchin monkey *Cebus apella* (Primates: Cebidae). Zeitschrift Fuer Tierpsychologie 65:177-200

Janson CH (1985) Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). Behavioral Ecology and Sociobiology 18:125-138

Janson CH (1986) The mating system as a determinant of social evolution in capuchin monkeys (*Cebus*). In: Else JG, Lee PC (eds) Primate Ecology and Conservation. Cambridge University Press, New York, pp 169-179

Janson CH (1988a) Food competition in brown capuchin monkeys (*Cebus apella*): Quantitative effects of group size and tree productivity. Behaviour 105:53-76

Janson CH (1988b) Intra-specific food competition and primate social structure: A synthesis. Behaviour 105:1-17

Janson CH (1994) Comparison of mating system across two populations of brown capuchin monkeys. American Journal of Primatology 33:217

Janson CH, Baldovino MC, Di Bitetti MS (2012) The group life cycle and demography of brown capuchin monkeys (*Cebus [apella] nigritus*) in Iguazú National Park, Argentina. In: Kappeler PM, Watts DP (eds) Long-Term Field Studies of Primates. Springer, Heidelberg, pp 185-212

Janson CH, Di Bitetti MS (1997) Experimental analysis of food detection in capuchin monkeys: Effects of distance, travel speed, and resource size. Behavioral Ecology and Sociobiology 41:17-24

Janson CH, van Schaik CP (1988) Recognizing the many faces of primate food competition: Methods. Behaviour 105:165-186

Jolly A (1972) Troop continuity and troop spacing in *Propithecus verreauxi* and *Lemur catta* at Berenty (Madagascar). Folia Primatologica 17:335-362

Kagel JH, Green L, Caraco T (1986) When foragers discount the future: constraint or adaptation? Animal Behaviour 34:271-283

Kavanagh M (1981) Variable territoriality among tantalus monkeys in Cameroon. Folia Primatologica 36:76-98

Kinnaird MF (1992) Variable resource defense by the Tana River crested mangabey. Behavioral Ecology and Sociobiology 31:115-122

Kitchen DM (2004) Alpha male black howler monkey responses to loud calls: effect of numeric odds, male companion behaviour and reproductive investment. Animal Behaviour 67:125-139

Kitchen DM (2006) Experimental test of female black howler monkey (*Alouatta pigra*) responses to loud calls from potentially infanticidal males: Effects of numeric odds, vulnerable offspring, and companion behavior. American Journal of Physical Anthropology 131:73-83

Kitchen DM, Cheney DL, Seyfarth RM (2004a) Factors mediating inter-group encounters in savannah baboons (*Papio cynocephalus ursinus*). Behaviour 141:197-218

Kitchen DM, Horwich RH, James RA (2004b) Subordinate male black howler monkey (*Alouatta pigra*) responses to loud calls: Experimental evidence for the effects of intra-group male relationships and age. Behaviour 141:703-723

Koenig A (2000) Competitive regimes in forest-dwelling Hanuman langur females (*Semnopithecus entellus*). Behavioral Ecology and Sociobiology 48:93-109

Koenig A (2002) Competition for resources and its behavioral consequences among female primates. International Journal of Primatology 23:759-783

Lloyd M (1967) `Mean Crowding'. Journal of Animal Ecology 36:1-30

Lynch Alfaro JW, Boubli JP, Olson LE, Di Fiore A, Wilson B, Gutiérrez-Espeleta GA, Chiou KL, Schulte M, Neitzel S, Ross V, Schwochow D, Nguyen MTT, Farias I, Janson CH, Alfaro ME (2012) Explosive Pleistocene range expansion leads to widespread Amazonian sympatry between robust and gracile capuchin monkeys. Journal of Biogeography 39:272-288

Maynard Smith J, Parker GA (1976) Logic of asymmetric contests. Animal Behaviour 24:159-175

Meunier H, Molina-Vila P, Perry S (2012) Participation in group defence: proximate factors affecting male behaviour in wild white-faced capuchins. Animal Behaviour 83:621-628

Mitani JC, Gros-Louis J, Manson JH (1996) Number of males in primate groups: comparative tests of competing hypotheses. American Journal of Primatology 38:315-332

Muniz L, Perry S, Manson JH, Gilkenson H, Gros-Louis J, Vigilant L (2010) Male dominance and reproductive success in wild white-faced capuchins (*Cebus capucinus*) at Lomas Barbudal, Costa Rica. American Journal of Primatology 72:1118-1130

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

Noë R, de Waal FBM, van Hooff JARAM (1980) Types of dominance in a chimpanzee colony. Folia Primatologica 34:90-110

Nunn CL (2000) Collective benefits, free-riders, and male extra-group conflict. In: Kappeler PM (ed) Primate Males: Causes and Consequences of Variation in Group Composition. Cambridge Univ Press, Cambridge, pp 192-204

Nunn CL, Lewis RJ (2001) Cooperation and collective action in animal behaviour. In: Noe R, Van Hooff JA, Hammerstein P (eds) Economics in Nature: Social Dilemmas, Mate Choice and Biological Markets. Cambridge Univ Press, Cambridge, pp 42-66

Olson M (1965) The Logic of Collective Action. Harvard University Press, Cambidge, MA

Parker GA (1974) Assessment strategy and evolution of fighting behavior. Journal of Theoretical Biology 47:223-243

Paviolo A, Di Blanco YE, De Angelo CD, Di Bitetti MS (2009) Protection affects the abundance and activity patterns of pumas in the Atlantic Forest. Journal of Mammalogy 90:926-934

Perry S (1996) Intergroup encounters in wild white-faced capuchins (*Cebus capucinus*). International Journal of Primatology 17:309-330

Pinheiro J, Bates D, DebRoy S, Sarkar D, Team RDC (2012) nlme: Linear and nonlinear mixed effects models. In, R package version 3.1-103 edn

R Development Core Team (2010) R: A language and environment for statistical computing. In: R Foundation for Statistical Computing, Vienna, Austria, URL http://www.R-project.org/.

Ramseyer A, Pele M, Dufour V, Chauvin C, Thierry B (2006) Accepting loss: the temporal limits of reciprocity in brown capuchin monkeys. Proceedings of the Royal Society B-Biological Sciences 273:179-184

Robinson JG (1988) Group size in wedge-capped capuchin monkeys *Cebus olivaceus* and the reproductive success of males and females. Behavioral Ecology and Sociobiology 23:187-197

Rubenstein DI (1986) Ecology and sociality in horses and zebras. In: Rubenstein D, Wrangham R (eds) Ecological Aspects of Social Evolution: Birds and Mammals. Princeton University Press, Princeton, NJ, pp 282-302

Sapolsky RM (2005) The influence of social hierarchy on primate health. Science 308:648-652

Scarry CJ, Tujague MP (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 74:804-810

Setchell JM, Smith T, Wickings EJ, Knapp LA (2010) Stress, social behaviour, and secondary sexual traits in a male primate. Hormones and Behavior 58:720-728

Stacey PB (1986) Group size and foraging efficiency in yellow baboons. Behavioral Ecology and Sociobiology 18:175-187

Stamps JA, Krishnan VV (2001) How territorial animals compete for divisible space: a learning-based model with unequal competitors. American Naturalist 157:154-169

Stanford C (1991) The capped langur in Bangladesh: behavioral ecology and reproductive tactics, vol 26

Sterck EHM, Watts DP, van Schaik CP (1997) The evolution of female social relationships in nonhuman primates. Behavioral Ecology and Sociobiology 41:291-309

Terborgh J (1983) Five New World Primates: A Study in Comparative Ecology. Princeton University Press, Princeton, New Jersey

Tiddi B, Aureli F, di Sorrentino EP, Janson CH, Schino G (2011a) Grooming for tolerance? Two mechanisms of exchange in wild tufted capuchin monkeys. Behavioral Ecology 22:663-669

Tiddi B, Aureli F, Schino G, Voelkl B (2011b) Social relationships between adult females and the alpha male in wild tufted capuchin monkeys. American Journal of Primatology 73:812-820

Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual Selection and the Descent of Man. Aldine, Chicago, pp 136-179

VanderWaal KL, Mosser M, Packer C (2009) Optimal group size, dispersal decisions and postdispersal relationships in female African lions. Animal Behaviour 77:949-954.

van Schaik CP (1983) Why are diurnal primates living in groups? Behaviour 87:120-144

van Schaik CP (1989) The ecology of social relationships amongst female primates. In: Standen V, Foley RA (eds) Comparative Socioecology: The Behavioral Ecology of Humans and Other Mammals. Blackwell Scientific Publications, Oxford, pp 195-218

van Schaik CP (1996) Social evolution in primates: The role of ecological factors and male behaviour. Proceedings of the British Academy 88:9-3

Vargas JdJ, Whitacre D, Mosquera R, Albuquerque J, Piana R, Thiollay J-M, Márquez C, Sánchez JE, Lezama-López M, Midence S, Matola S, Aguilar S, Rettig N, Sanaiotti T (2006) Estado y distribución actual del águila arpía (*Harpia harpyja*) en Centro y Sur América. Ornitologia Neotropical 17:39-55

Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164-168

Wrangham RW (1980) An ecological model of female-bonded primate groups. Behaviour 75:262-300

Figure 3.1 Relative home range positions of the four study groups during the 2008-2009 study period. Open polygons represent minimum convex polygons depicting the known extent of the ranges of non-focal groups encountered during the study (1 – Tufty; 2 – Bizzarros; 3 – Yacaratiá; 4 – Tanque; 5 – Cantera; 6 – Laboratorio).

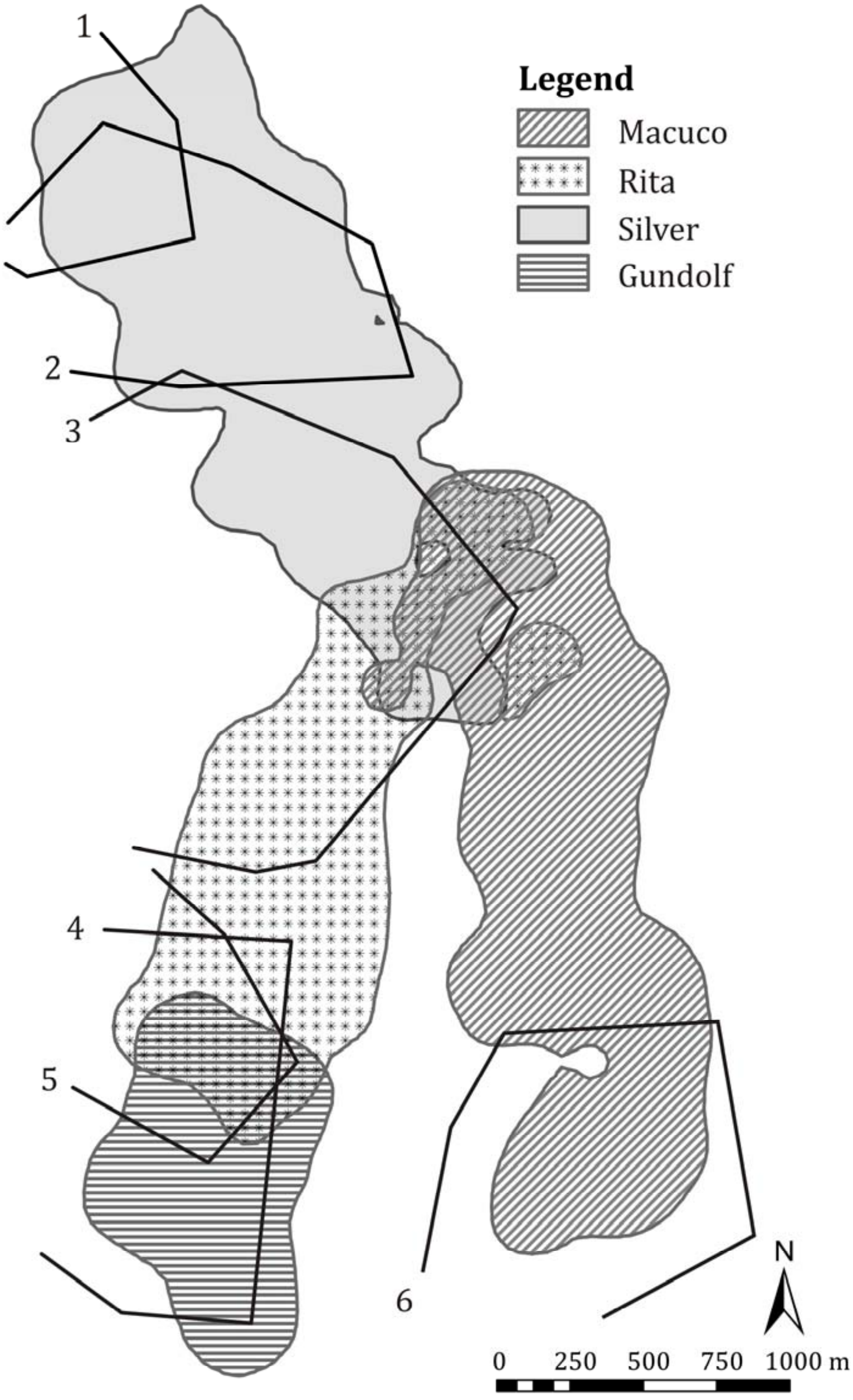


Figure 3.2 Probability of winning an encounter as a function of relative male group size.

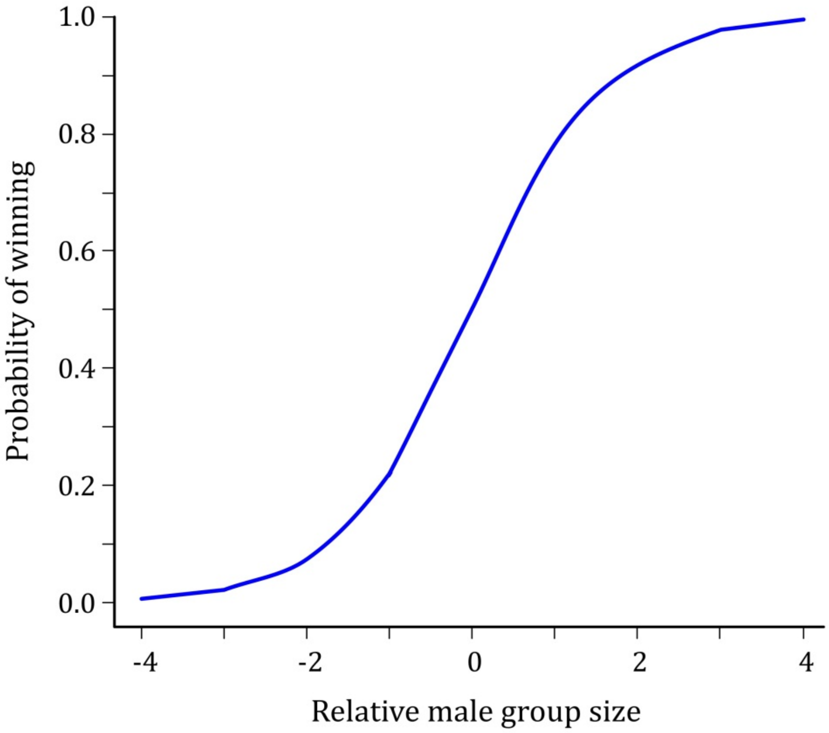


Figure 3.3 Outcome of intergroup encounters among groups. Focal groups are indicated in blue. Line thickness corresponds to the relative number of interactions within each dyad.

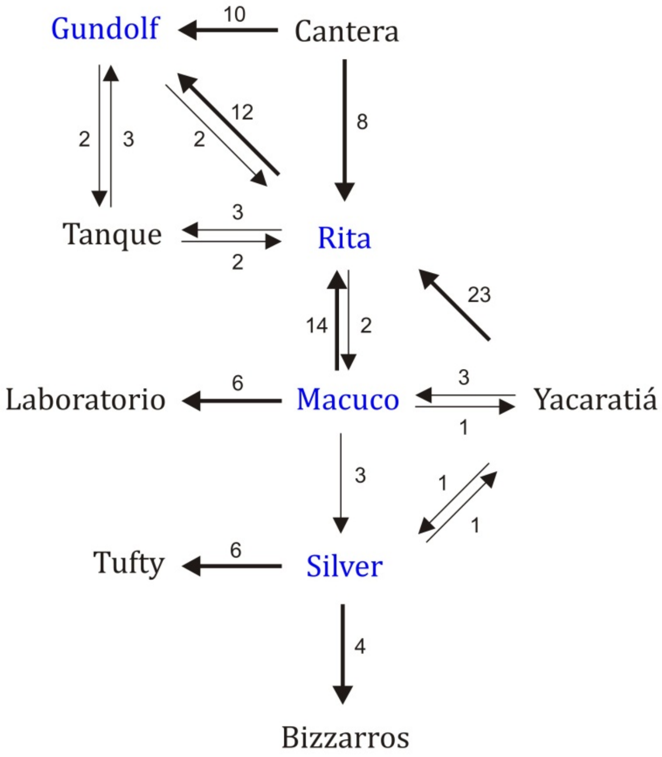


Figure 3.4 Predicted probability of winning an encounter as a function of distance from the center of the home range (calculated by averaging all locations). Encounters in which the focal group is relatively larger are shown in blue, while the reverse is shown in red. The dashed line indicates encounters between evenly matched groups. Line weights and values shown in the left margin indicate the degree of asymmetry. Because small focal groups were never observed to have an encounter beyond 1250 m of their home range center, extrapolated probabilities are indicated with the grey box.

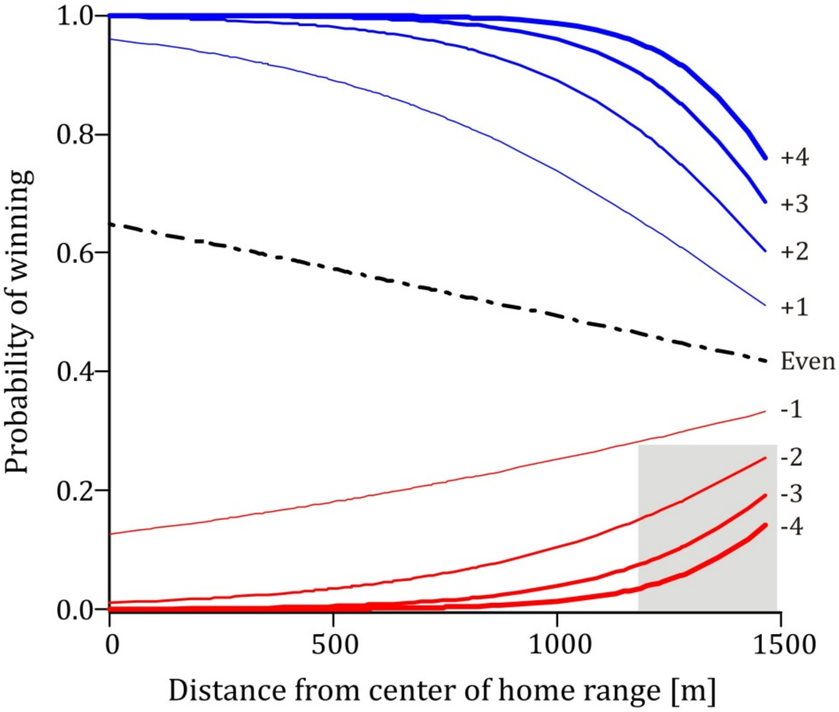


Figure 3.5 Resource density as a function of location within the home range.

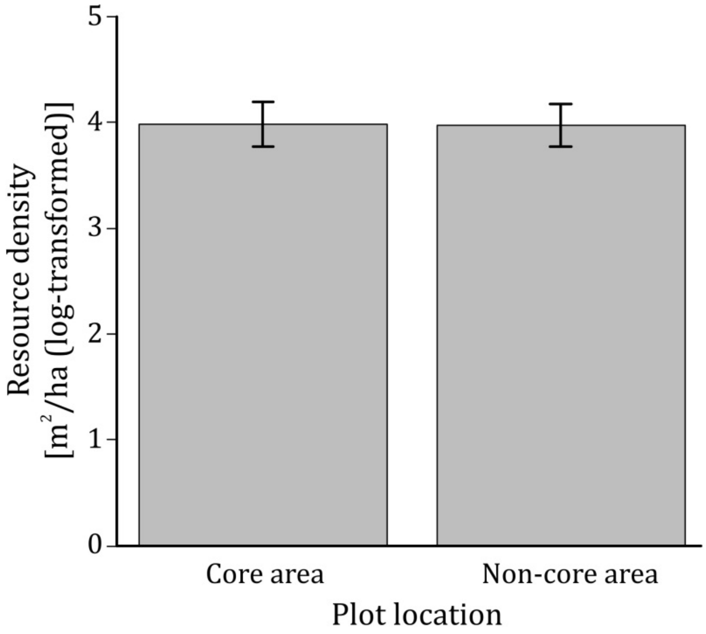


Figure 3.6 Total basal area of food resources within the core area as a function of male group size.

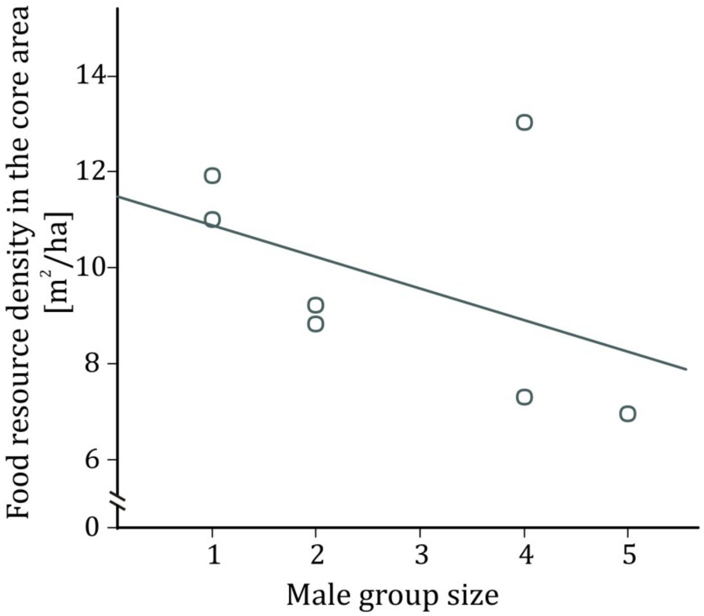


Figure 3.7 *Per capita* resource availability within the core area after correcting for overlap with neighboring groups as a function of male group size.

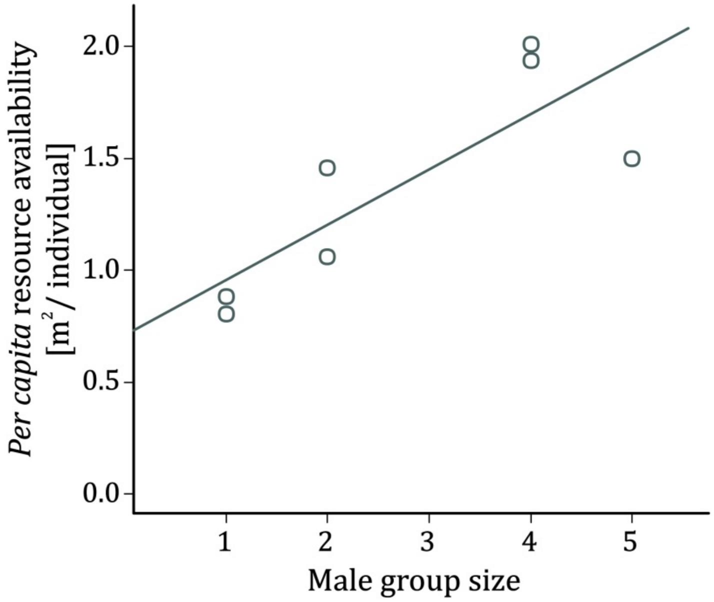


Table 3.1 Composition of focal (bold) and non-focal groups, excluding infants (<1 yr).

Group	Year	Males	Females	Total
Yacaratiá	2007-2009	5	≥6	~35
Macuco	2007	5	8	22-23
	2008-2009	4	9	25-27
Silver	2008-2009	4	6	20
Cantera	2007-2009	3	≥4	~20
Laboratorio	2007-2009	2	4	19
Rita	2007	2	4	11
	2008-2009	2	4	11
Bizzarros	2008-2009	2	≥3	~15
Tufty	2008-2009	2	2	7
Tanque	2007-2009	2	≥2	~10
Gundolf	2007	1	4	12
	2008-2009	1	5	15-16
Spot[1]	2010	1	2	5

[1] The Spot group formed from a matriline in the Macuco group in 2010, following a change in the male dominance hierarchy.

Table 3.2 Percentage of core area overlapped by neighboring groups.

	Year	# Males	Yac	Mac	Sil	Can	Lab	Rita	Biz	Tuf	Tan	Gun	Total[1]
Macuco	2007	4	3.4	-	7.1	-	0.9	0.6	-	-	-	-	8.6
	2008-2009	5	5.3	-	10.0	-	7.0	13.8	-	-	-	-	29.5
Silver	2008-2009	4	2.0	0.0	-	-	-	-	57.0	18.2	-	-	65.4
Rita	2007	2	48.7	29.4	-	15.0	-	-	-	-	11.2	30.3	90.3
	2008-2009	2	23.0	0.0	-	30.0	-	-	-	-	22.0	11.3	54.9
Gundolf	2007	1	-	-	-	76.6	-	60.2	-	-	33.0	-	93.6
	2008-2009	1	-	-	-	82.1	-	0.5	-	-	4.3	-	82.1

[1] Total overlap is the percentage of the core area shared with any group, and therefore differs from the summed values of individual overlaps because some areas are overlapped by more than one group.

Table 3.3 Multivariate model of the effect of multiple measures of group size on the probability that the focal group wins an encounter (N = 42 encounters).

	Parameter estimate	**SE**	X^2_1	***p***
Relative male group size	1.27	0.38	11.2	**<0.001**
Relative female group size	0.08	0.18	0.21	0.65
Relative total group size	-0.02	0.05	0.20	0.66
Intercept	0.00	0.37	0	0.99

Table 3.4 Best fit models of the combined effects of male group size and encounter location on the probability that the focal group wins an encounter after controlling for the group dyad.

	Parameter estimate	**SE**	X^2_1	***p***
Center calculated by averaging midday locations				
Relative male group size	2.57	0.54	22.48	**<0.001**
Location	-0.07	0.08	0.80	0.37
Group size by location	-0.15	0.05	9.69	**0.002**
Intercept	0.64	0.72	0.78	0.38
Center calculated by averaging all locations				
Relative male group size	2.44	0.54	20.59	**<0.001**
Location	-0.09	0.08	1.35	0.24
Group size by location	-0.14	0.05	7.99	**0.005**
Intercept	0.82	0.76	1.18	0.27

Table 3.5 Average basal area (m^2) per botanical plot within the core area of each group during the 2008-2009 field season.

Species	Gun	Mac	Rit	Sil	X^2	*p*	Lloyd's Index
Allophyllus edulis	2.51	0.96	0.47	2.85	3.09	0.38	**7.12**
Arecastrum romanzoffianum	7.42	3.63	3.28	4.06	3.63	0.3	**1.60**
Cabralea canjerana	8.14	1.00	13.13	7.23	1.7	0.64	**2.30**
Campomanesia guazumaefolia	0.00	0.21	0.00	0.30	2.62	0.45	**4.66**
Campomanesia xanthocarpa	0.28	0.66	1.90	5.60	2.57	0.46	**3.06**
Casearia decandra	0.56	0.93	0.12	1.27	4.31	0.23	**3.90**
Casearia sylvestris	0.87	0.00	0.00	0.00	6.66	0.08	**6.67**
Cecropia pachystachia	1.50	1.18	3.25	2.08	2.71	0.44	1.33
Chrysophyllum gonocarpum	18.29	9.06	21.79	14.89	1.62	0.66	1.48
Erythrina falcate	0.00	1.39	0.40	0.00	3.86	0.28	**5.18**
Eugenia pyriformis	3.29	1.76	0.00	3.03	6.79	0.08	**4.89**
Ficus sp.	1.30	0.00	0.00	2.56	3.83	0.28	**4.95**
Hovenia dulcis	7.77	1.02	0.00	1.16	0.88	0.83	**34.05**
Inga marginata	0.12	0.45	0.00	0.21	4.58	0.2	**4.66**
Inga uruguensis	4.42	1.79	0.00	0.00	4.32	0.23	**1.71**
Luehea divaricata	12.58	14.60	12.93	14.02	2.7	0.44	**3.03**
Maclura tinctorea	3.07	3.71	0.86	10.07	3.45	0.33	**2.36**
Matayba eleagnoides	0.13	5.81	0.00	1.45	2.94	0.4	**4.08**
Miconia sp.	0.00	1.37	0.00	0.00	2.09	0.55	**13.25**
Nectandra lanceolata	7.71	1.95	0.18	11.70	1.38	0.71	**3.56**
Nectandra megapotamica	15.61	5.15	17.29	17.49	0.37	0.94	**2.36**
Ocotea diospyrifolia	12.91	1.84	3.78	14.09	8.04	**0.04**	**2.69**
Ocotea puberula	6.62	3.10	3.31	1.73	5.8	0.12	1.16
Plinia rivularis	0.00	0.69	0.55	4.71	5.38	0.15	**8.35**
Prunus subcoriacea	0.99	0.69	4.75	3.01	4.02	0.26	**2.08**
Psidium guajaba	0.00	0.00	0.00	0.00	2.09	0.55	1.00
Rapanea lorentziana	0.31	0.00	0.00	0.00	2.09	0.55	**18.33**
Rapanea umbelata	0.65	0.00	0.18	0.00	0.07	0.99	0.13
Sebastiana brasiliensis	1.06	0.80	2.10	0.42	3.95	0.27	**3.31**
Sorocea bonplandii	0.79	1.11	0.20	0.94	5.61	0.13	1.11
Trichilia catigua	0.00	0.60	0.45	0.86	5.78	0.12	1.44

Chapter 4:
Resource quality outweighs relative competitive ability in decisions to participate in intergroup aggression among tufted capuchin monkeys

Abstract

In group-living species, conflicts between groups frequently involve multiple individuals participating in aggression towards the opposing group. Although defence is a cooperative action, individuals differ in their motivations, which can lead to variation both between groups and between contests in the identity of participating individuals. I examined the factors affecting individual assessment of the costs and benefits of participation in aggressive intergroup encounters among tufted capuchin monkeys (*Cebus apella* [*Sapajus*] *nigritus*) at Iguazú National Park, Argentina. I created high-quality food resources using provisioning platforms, which allowed me to test separately the effects of two resource types (food and mates). To simulate the presence of a neighboring group, I presented playbacks of vocalizations from known adult males, recording approach behaviors of individuals within the study groups. Males and females demonstrated concordant strategies, responding aggressively only in the presence of a high-quality food resource. Male responses were significantly stronger than those of females, but no differences were observed between dominant and subordinate individuals. As a result, the sex-rank profile of participants was consistent across contests, suggesting that intercontest variation in the resource holding potential of groups is minimal. Yet the ability of a focal group to win an encounter had only limited effects on the willingness of individuals to approach the speaker to gain or maintain ownership of a high-quality food resource. Instead, individuals appear to have adopted a strategy of probing the tolerance of dominant neighboring groups, likely due to rapid fluctuations in the opponent's subjective resource valuation as a function of hunger levels.

Introduction

In many social mammals, interactions between neighboring groups are primarily aggressive (Cheney 1987; Packer et al. 1990). These contests between groups – like those between single competitors – are expected to be influenced by asymmetries in both the competitive ability and the motivation of the opponents (Maynard Smith and Parker 1976; Parker and Rubenstein 1981). When multiple individuals participate in aggressive behavior, the competitive ability of the group may be tied to group size (Cheney 1987; Packer et al. 1990). The resource holding potential (RHP) of the group, however, depends on the willingness of individuals to cooperate (van Schaik 1996; Nunn 2000). Sex differences (Trivers 1972), within-group social relationships (Pope 1990; Kitchen et al. 2004; Mares et al. 2011), and current condition (Cant et al. 2002) can all influence an individual's decision to participate. Hence, to fully understand the relationship between group-level properties and the pattern of intergroup conflicts, an approach focused on individual strategies is necessary (Cheney 1987; Kitchen and Beehner 2007).

By participating in aggressive intergroup encounters, cooperating individuals must bear the associated costs. In some species, participants risk severe injury or death (Palombit 1993; Watts and Mitani 2001; Gros-Louis et al. 2003; Wilson and Wrangham 2003; Watts et al. 2006), and even in the absence of direct attacks, intergroup aggression may involve displays and chases, which can exhaust energetic reserves and directly interfere with an individual's ability to rebuild them (Garber 1988; Peres 1989; Peres 1992). Moreover, in an arboreal setting, these chases are associated with rapid and potentially risky movements (Broom et al. 2009). Consequently, when the payoff to the winner is low, individuals and groups should invest little in intergroup aggression. Furthermore, if individuals can assess the relative costs prior to interacting, through previous experience (Ydenberg et al. 1988; Getty 1989; Temeles 1994; Wich et al. 2002; Wich and Sterck 2007; Rosell et al. 2008) or an assessment of the current competitive asymmetry (McComb et al. 1994; Grinnell et al. 1995; Wilson et al. 2001; Kitchen et al. 2004; Furrer et al. 2011), they may be able to refrain from engaging in escalated encounters when the probability of winning is low (Parker 1974; Maynard Smith and Parker 1976; Parker and Rubenstein 1981). Escalated aggression, therefore, is expected primarily between closely matched competitors that cannot easily assess the eventual outcome (Parker 1974; Maynard Smith and Parker 1976; Parker and Rubenstein 1981).

Among species that exhibit long-term site fidelity, prior experience may allow individuals from competing groups to more accurately predict the outcome of the encounter, eliminating the need for escalated conflicts (Ydenberg et al. 1988; Wich et al. 2002). Although members of dominant groups may benefit from initiating aggressive encounters that result in home range expansion (*Chlorocebus aethiops*: Cheney and Seyfarth 1987; *Panthera leo*: Heinsohn 1997; *Pan troglodytes*: Williams et al. 2004) or reinforce existing dominance relationships (Manson and Wrangham 1991; Mosser and Packer 2009), individuals in subordinate or numerically weaker groups should retreat immediately, rather than expending energy in escalated aggression (Parker 1974; Maynard Smith and Parker 1976; Parker and Rubenstein 1981). Yet, even during periods of demographic stability, neighboring groups may exhibit highly aggressive relationships in some species (primates, reviewed in Cheney 1987). This suggests that despite familiarity, uncertainty remains regarding either the RHP or the resource valuation of the opposing group.

By establishing an upper limit on the number of coalitionary partners available, group size sets the maximum possible RHP, which can remain relatively constant over long periods of time; however, the realized RHP of a group is determined by the number of individuals participating in the current contest. Despite frequent contact between neighboring groups, therefore, the asymmetry in RHP may fluctuate between encounters if groups either subdivide into flexibly-sized parties (*Panthera leo*: McComb et al. 1994; *Pan troglodytes*: Watts and Mitani 2001; Wilson et al. 2001) or individuals vary in their choice to defect or participate (Heinsohn and Packer 1995; Kitchen 2004; Kitchen et al. 2004).

In addition to assessing the potential for winning, individuals must simultaneously assess the value of the resource and whether the benefits of ownership offset any costs that winning might entail (Maynard Smith 1974). Although cooperative defence is a public good, benefits are frequently distributed unequally across classes of individuals (Nunn 2000; Nunn and Lewis 2001). Within-group social relationships frequently affect access to resources and reproductive opportunities, whereby dominant individuals receive greater benefits through ownership of resources. Individual participation, therefore, may be affected by the degree of tolerance in dominance relations (Sterck et al. 1997) or intragroup relatedness (Pope 1990). Whereas these properties of the group change over long time scales, when classes of individuals compete for different types of resources, significant variation in patterns of participation may occur from contest to contest (e.g., *Alouatta pigra*: Kitchen et al. 2004; Kitchen 2006). For example, due to sex differences in parental investment, improved nutrition generally provides greater fitness returns for females than it does for males (Trivers 1972), thus males and females may exhibit disparate strategies during intergroup encounters. In contests primarily over access to food resources female participation is expected, whereas males should compete primarily during contests for reproductive access to females – although these suggestions may depend on the mating system and spatiotemporal distribution of resources (e.g., male resource defense polygyny: Emlen and Oring 1977).

Individual assessment of resource value may also be influenced by internal physiological state (e.g., hunger: Janson and Vogel 2006), previous knowledge of the resource (Enquist and Leimar 1987), and the availability of alternative sources of the same resource type (Heinsohn 1997; Vogel and Janson 2007). These properties of the individual and the environment can cause fluctuations in the subjective resource valuation in the absence of measurable differences in the ecological properties of the contested resource (e.g., fruit crop production). In contrast to resource ownership, however, where benefits vary in a predictable manner as a function of spatially-defined roles (Davies and Houston 1981; Crofoot et al. 2008), state-dependent fitness returns are not predictable through prior experience, making it difficult to accurately assess an opponent's willingness to engage in aggressive competition (Parker and Rubenstein 1981). Despite being capable of inflicting greater costs, individuals in dominant groups do not benefit from escalating aggression to the point that their own costs outweigh the current value of the resource. Accordingly, the level of observable escalation and even the identity of the winner and loser may vary from encounter to encounter, in the absence of a significant change in the contested resource or RHP of the contestants (Maynard Smith and Parker 1976). Individuals in subordinate groups, therefore, may benefit from initiating encounters to probe the aggressive response of dominant groups, especially to gain access to high-quality resources.

In the current study, I examined the effects of resource value and relative competitive ability on individual participation in free-ranging tufted capuchin monkeys (*Cebus* [*apella*] *nigritus*) at Iguazú National Park, Argentina, using experimental manipulation of the resource base and playback experiments. Within this population, both sexes participate during natural intergroup encounters (Di Bitetti 2001b), so I first tested the hypothesis that multiple resource types (food and potential mates) lead to unpredictable variation in participation in intergroup aggression, interfering with the ability to gauge the asymmetry in RHP between groups. If this hypothesis were correct, I predicted sex-based differences in patterns of participation depending on the nature of the resource(s) at stake in the current contest. Increased energy gain increases female reproductive success (Trivers 1972) and may indirectly benefit the reproductive success of resident males that have mating access (Rubenstein 1986). Therefore, I predicted that either or both sexes would participate in encounters over access to food resources. In contrast, access to reproductive females is a resource that is uniquely beneficial to males, and I did not expect that female participation would occur.

I did not consider infant defense or infanticidal attacks as a potential explanation for aggression towards neighboring groups (Wich et al. 2002; Korstjens et al. 2005; Harris 2006; Wich and Sterck 2007; Harris 2010), in part due to logistic constraints. No vulnerable infants (<6 months: Ramírez Llorens et al. 2008) were present during the period in which provisioning was most viable, as a result of strong birth seasonality (Di Bitetti and Janson 2001a). Nevertheless this limitation is unlikely to have affected the results; while multiple infanticides by resident individuals have been documented (Ramírez-Llorens et al. 2008; B. Tiddi and C.Jpersonal communication. Scarry, unpublished data), no evidence for infanticide by extragroup males has been observed in this population. Moreover, tufted capuchin monkeys at Iguazú do not demonstrate the behavioral patterns expected to promote intergroup infanticide; females do not transfer among groups (Di Bitetti 1997), takeovers are exceedingly rare (Janson et al. 2012), and immigrating males have limited reproductive access in their new groups (Janson et al. 2012; B.

Tiddi, personal communication). Therefore, extragroup males are unlikely to gain direct reproductive benefits through infanticide, and the indirect benefits of increased genetic representation in the population are unlikely to offset the associated costs of an infanticidal attack (Broom et al. 2004).

I further tested the hypothesis that, for a given resource type, individuals differ in their assessment of the relative costs and benefits of participation. Within-group dominance directly affects individual access to food resources (Janson 1985) and mates (Janson 1984); therefore, I predicted that subordinate individuals would exhibit higher thresholds for participation than do dominant individuals. In addition, females are significantly smaller than males (♀ = 2.5 kg, ♂ = 3.6 kg: Smith and Jungers 1997); thus, I predicted that females would be more likely to defect (e.g., Kitchen 2006). Finally, groups vary in size and, presumably, competitive ability, and, thus, I predicted that individuals would choose not to participate when the probability of winning an encounter is low and benefits are unlikely to be accrued.

Methods

Study site and subjects

The study was conducted in Iguazú National Park, Argentina (25°40’ S, 54°30’ W), a 60,000 ha preserve near the southern limit of the Atlantic forest composed of a semi-deciduous, subtropical forest. Although there is no discernible dry season, marked seasonality in temperature and day length exists, with corresponding variation in the availability of fleshy fruits and arthropods (Brown and Zunino 1990). Experimental testing was divided between two separate periods, totalling six months (Jul-Sep 2009, Jun-Aug 2010). Prior to beginning the experimental study, I spent 17 months (Sep-Dec 2007, Jun 2008-Jun 2009) collecting observational data on behavior during naturally-occurring intergroup encounters for all adult individuals in four study groups.

Tufted capuchin monkeys (*Cebus apella* [*Sapajus*] *nigritus*) are small-bodied Neotropical primates (Janson 1985). Although the majority of their time is dedicated to foraging for arthropods, fruit resources account for the majority of an individual’s energy consumption (Janson 1985). At Iguazú, the average availability of capuchin food resources reaches its lowest point during the austral winter (Jun-Aug). Access to resources during this period appears to affect infant survival and female interbirth interval (Di Bitetti and Janson 2001a). All experiments were conducted during this naturally occurring nadir of resource availability, when competition for food is presumably strongest.

Capuchin monkeys live in multi-male, multi-female groups ranging from 5 – 44 individuals (Janson et al. 2012), characterized by habitual male dispersal and predominant female philopatry (Di Bitetti 1997). Within-group dominance relationships are strongly hierarchical (Janson 1985; Di Bitetti 1997) and predictably influence individual access to food resources (Janson 1985; Janson 1988). Moreover, male dominance status appears to determine mating access during the periovulatory period (Janson 1984; Janson 1998a); however all males included in this study were observed mating at least once.

I collected data on adult males and females in three, fully-habituated study groups: Macuco (3 males, 7 females, 25 individuals total), Rita (2 males, 4 females, 11 individuals total), and Silver (4 males, 6 females, 22 individuals total). All three groups were accustomed to experimental provisioning as part of the long-term research program at the site (e.g., Janson 1998b; Di Bitetti and Janson 2001b; Wheeler 2009). Within the experimental periods, the groups' compositions remained stable; however, in the interim between the two study periods, one group (Macuco) experienced a shift in the male dominance hierarchy that resulted in the death or dispersal of four adult males (Scarry & Tujague 2012). Following the dramatic change in the group composition, dominance relations with the neighboring groups became unstable, and were still in transition in August, 2010, when the study ended.

Outcome of natural intergroup encounters

During both the observational and experimental phases of the study, I recorded intergroup encounters involving the focal group *ad libitum* (Altmann 1974). Most intergroup encounters involved clear cases of one group vigorously chasing another from the area (Di Bitetti 2001b), so I used the relative displacement of the groups to determine the winner. If neither group was successful in expelling the other, that is both groups eventually retreated from the area, I considered the outcome of the encounter to be undecided (cf. Perry 1996).

Experimental design

To simulate the presence of a neighboring group, I presented recordings of long-distance whistles given during intergroup encounters (Di Bitetti 2001a). I recorded calls by adult males residing in neighboring groups using a Marantz PMD670 or PMD660 solid-state audio recorder with a Sennheiser ME 67 or ME 66 shotgun microphone. This family of calls has individually-distinct acoustic properties (Di Bitetti 2001a), and groups respond strongly to presentations of calls from groups that are frequently encountered, but do not utilize the experimental range. Whereas similar calls presented from the appropriate location elicited no response, in the trials in which expectations were violated (i.e., playbacks were presented from locations in which the calling individual would not normally be encountered, cf. Cheney and Seyfarth 1982), individuals rapidly approached the speaker, giving aggressive vocalizations in the absence of a contested resource. This pattern is suggestive of an ability to hierarchically classify extra-group individuals on the basis of their calls (Cheney and Seyfarth 1982); thus, I took care to only present vocalizations from groups that had been previously encountered in the area, so that individual response did not reflect a violation of expectation. I presented groups with vocalizations from groups to which they had previously lost encounters, so that an individual's estimation of the probability of winning the encounter was <1. I conducted playback trials from 50 to 150 m from the edge of the group, the observed distance at which individuals typically detect the presence of a neighboring group (C.J. Scarry, unpublished data). In addition, this is the distance at which groups begin accelerating during their approach to both provisioning platforms (Janson and Di Bitetti 1997) and naturally-occurring fruit resources (M.P. Tujague, personal communication).

I considered two potentially contestable resource types – food and mating opportunities – that could each be of either high or low value for a playback context. Through the use of provisioning platforms, I was able to hold the location of encounters constant with regards to the group's home range, while independently manipulating resource quality or the apparent resource holding potential of the neighboring group. I positioned platforms at sites within the area of home range overlap at which I provisioned the focal group daily with pieces of banana (Figure 4.1). This allowed me to conduct all trials during the same season, so that changes in resource availability in the surrounding area were minimized, strongly reducing variation in individual experience with resource availability. As a result, provisioning directly increased individual energy gain at a location relative to environmental availability, providing a high-quality food resource. The total number of bananas provided depended on the number of individuals in the group, so that per capita availability at the site was consistent across groups (~175 kJ/individual), maintaining a constant objective resource value. To limit the effects of satiation on the aggressive response of individuals (Janson and Vogel 2006), I conducted experiments early in the day, when the group typically is focused on fruit feeding (Terborgh 1983). Whether or not the group was currently being provisioned, I conducted all playbacks from the area surrounding the provisioning sites. The order of presentation of the two contexts varied across the three groups; however, I allowed groups to become accustomed to the resource distribution before conducting the experiments. I waited at least two days between experiments and did not conduct experiments on days on which natural encounters had already occurred to avoid habituation to the playback vocalizations.

During daily group follows, I recorded female sexual behavior to categorize the reproductive context for each experiment. Female capuchin monkeys exhibit proceptive and receptive sexual behavior that are hormonally-linked to the timing of ovulation (Carosi et al. 1999). Thus, copulations occurring during intergroup encounters could potentially result in fertilization. In addition, these behavioral cues may permit extragroup males to rapidly identify females from neighboring groups that are likely to conceive and target them for extragroup copulations. I also recorded the outcome of intragroup dyadic aggression *ad libitum* (Altmann 1974) in order to determine within-group dominance relationships; however, due to the high-frequency of polyadic aggression, I could not record sufficient dyadic interactions to assign ordinal ranks to individuals. Instead, I separated individuals into three dominance classes – dominant males and females (N = 8 individuals); mid-ranked females (N = 4); and subordinate males and females (N = 12) – based on whether or not aggression was received from and/or directed to same-sex individuals (i.e., dominant females were observed directing aggression toward other females but were not observed to receive aggression, whereas mid-ranked females both gave and received aggression). These categories correspond to distinct socio-spatial subgroups which differ in their access to both food resources (Di Bitetti and Janson 2001b) and mates (Janson 1984).

Whenever possible, my assistants and I collected data simultaneously on the behavioral response of one adult male and one adult female during each playback presentation. To establish baseline measures, one minute prior to the presentation of the stimulus, we recorded the general behavior (i.e., foraging, feeding, travelling, resting, other) and current velocity (horizontal and vertical displacement during one minute, measured in ten-meter intervals) for the focal individual. These data were compared to a matched sample recorded one minute following the playback. In addition, at the moment of the presentation of the vocalization, we recorded the immediate response (gazing in the direction of the speaker, giving vocalizations in response, and approach towards the speaker). Latency to movement could not be reliably recorded because, during periods of active provisioning at the platform site, the individual was frequently already approaching the site when the vocalization was presented. To avoid artificially inflating the importance of the high-quality resource on the probability that the focal individual approached the speaker, I only counted cases in which the focal animal altered its general behavior to begin travelling, although arrival in the vicinity of the speaker was not required. This restriction was not necessary for the analysis of individual acceleration because I measured the change in velocity, and not the approach speed *per se*, which controlled for the directed movement towards the provisioning platforms.

Statistical analyses

To determine the relative strengths of groups, which influence an individual's assessment of the asymmetry in competitive ability, I used the proportion of natural intergroup encounters with the group from which the playback vocalization was recorded that were won by focal group. I selected this method rather than the difference in group ranks or differences in normalized David's scores, because non-interactions between groups without overlapping home ranges created structural zeros in the dominance interactions matrix (De Vries 1995; De Vries et al. 2006). In addition, by using the proportion of wins by each group, I was able to update the relative strength of the neighboring group following sequential interactions during the period of instability, beginning with an unknown relationship following the male replacement event.

In addition to whether or not an individual approached a playback site, I measured the strength of individual response by calculating acceleration as the difference in velocity pre- and post-stimulus presentation. I performed generalized linear mixed models in R (R Development Core Team 2010) using the function 'lmer' in the lme4 package (Bates et al. 2011) to examine the factors that influence the probability of individual approach and individual acceleration, including individual focal animal identity as a random effect. As predictor variable, I used the probability of the focal group being able to win the encounter as derived from the natural intergroup encounters and the fixed effects included focal animal sex, focal animal dominance status, the presence of a high-quality food resource, and the presence of a sexually receptive female. I tested the overall significance of the full model against a null model including only focal identity as a random effect before selecting variables for the best-fit model.

<u>Results</u>

Natural intergroup encounters

In total, 116 natural intergroup encounters occurred involving the three focal groups, including 93 encounters with decided outcomes. Four groups utilized the area where the provisioning sites were located (Figure 4.1). Each of the focal groups lost encounters to at least two of its neighbors (Table 4.1), and I selected vocalizations from these groups to use in playback presentations.

Effect of food resource or female presence

Following the presentation of the playback stimulus, a focal individual approached the speaker on 35 occasions. Of these approaches, 30 occurred while the group was being actively provisioned at the platform site, significantly more than in the absence of provisioning (Figure 4.2, Table 4.2). Similarly, during provisioning periods, individuals increased their travel speed significantly after hearing the vocalization, including cases in which they were already approaching the food source (Figure 4.3, Table 4.3). Detecting a neighboring group in the vicinity of a high-quality resource resulted in an approximately ten-fold increase in travel speed relative to simulated encounters when resource levels were at their natural low ($\bar{x}$ Present ± SE = 18.65 ± 7.81 m/min, $\bar{x}$ Absent ± SE = 2.19 ± 3.33 m/min).

No effect of the reproductive context of the playback was observable on the probability of approach in either sex (Table 4.2). Similarly, the presence of a receptive female did not significantly affect individual acceleration, and the difference was in the opposite direction than predicted by the male mate defense hypothesis ($\bar{x}_{\text{Present}} \pm \text{SE} = 4.17 \pm 29.03$ m/min, $\bar{x}_{\text{Absent}} \pm \text{SE} = 13.75 \pm 5.73$ m/min, Table 4.3).

Individual differences in behavior

Including the sex of the individual significantly improved the fit of the model predicting individual approach behavior (Table 4.2) but not the speed of approach – although a staistical trend towards increased acceleration by males is present (Table 4.3). The strong effect of provisioning, however, led to unreliable estimates of the standard error (Hauck and Donner 1977). Therefore, I subdivided the dataset based on the presence or absence of the high-quality food resource (Venables and Ripley 2002). Males were not significantly more likely than females to approach the speaker in the presence of a high quality resource (although there is a trend in that direction: Figure 4, GLM, individual sex: $t = 2.06$, $P = 0.058$), but males were much more likely than females to approach the speaker in the absence of a resource (Figure 4.4, GLM, individual sex: $t = 4.86$, $P < 0.001$). No approaches by females were observed in the absence of a defendable food resource.

Dominant and subordinate individuals demonstrated no difference in their willingness to participate, as measured by either their probability of approach (Table 4.2) or the speed at which they approached the speaker (Table 4.3).

Relative competitive ability of the focal group

The interaction of individual sex and the probability of winning the encounter, as measured from the outcome of the natural intergroup encounters (Table 4.1), had a significant effect on willingness to participate, although the main effect was not significant (Table 4.2). In the presence of a high-quality food resource, females were less likely to approach the speaker as the competitive ability of the opposing group increased (Figure 4.5a), but male approaches were unaffected (Figure 4.5b). In the absence of a food resource, however, males were less likely to approach stronger groups (Figure 4.5b). Yet even individuals from the smallest group, which only won encounters against subgroups involving subordinate individuals from its larger neighbors, approached the speaker on numerous occasions (83%, N = 6).

The probability of winning the encounter had a significant effect on the speed at which individuals approached the speaker (Figure 4.6, Table 4.3). Individuals approached a neighboring group more rapidly if prior experience suggested an eventual win, both in the presence and absence of a defendable food resource.

<u>Discussion</u>

Individual factors influencing participation

In some species, patterns of intergroup aggression are influenced by multiple resource values (Harris 2010) in part because individuals pursue disparate strategies during encounters (reviewed in Kitchen and Beehner 2007). In the current study, however, a single high-quality resource (food) appears to drive participation in intergroup aggression by tufted capuchin monkeys. Despite the fact that improved nutrition more directly benefits female reproductive success than that of males (Trivers 1972), both males and females defend access to food resources. Furthermore, the presence of a sexually receptive female did not affect the probability of male engagement, although access to mates is critical to male reproductive success (Trivers 1972). One consequence of this convergence of individual strategies is that the demographic profile of participating individuals is relatively consistent across encounters. Upon hearing a vocalization from a neighboring group in proximity to the provisioning platform, most group members, regardless of sex or rank, begin a rapid approach to the speaker. Accordingly, the group's realized RHP is unlikely to fluctuate depending on the nature of the contested resource.

Yet the relative costs of participation do appear to have an effect on willingness to participate. During periods of provisioning, males always approached the speaker, whereas females occasionally defected. Significant sexual dimorphism exists in both body size (Smith and Jungers 1997) and canine tooth size (Plavcan and van Schaik 1992), suggesting that the risks of physical injury may be higher for females than for males. Furthermore, energetic losses are expected to have a greater effect on female reproductive success (Trivers 1972). Consequently, females may benefit from defecting either when they can gain access to resources by free-riding on successful defense by males or when the probability of eventually winning the encounter is low (e.g., Kitchen 2006). The degree of free-riding is relatively low, however, and females participated in approximately 75% of contests over food resources.

Whether the initial response demonstrated here would translate into participation in escalated conflicts is unclear because such conflicts cannot be simulated through playbacks. Overall, the intensity of aggression during naturally-occurring intergroup encounters is relatively low. Lethal intergroup aggression has never been observed in this population, and contact aggression is virtually absent (C.J. Scarry, unpublished data). Instead, the majority of encounters are characterized by rapid, long-distance chases (≤500 m in 10 minutes: C.J. Scarry, unpublished data) with infrequent occurrences of direct face-offs between groups (Di Bitetti 2001b). Although complete defection (e.g., immediately fleeing or abstaining from participation: Robinson 1986; Perry 1996) is uncommon, individuals may drop out or lag behind during extended conflicts, similar to the behaviors observed during intergroup encounters in both lions and dogs (Heinsohn and Packer 1995; Bonanni et al. 2010). During naturally-occurring intergroup encounters, for example, subordinate females approach the neighboring group, but only behind the front line of males and dominant females (C.J. Scarry, unpublished data). In contrast to lions, in which female participatory strategies reflect differences in personality (Heinsohn and Packer 1995), female investment in intergroup encounters among tufted capuchin monkeys may be influenced by their rank (Di Bitetti 2001b), although effects of reproductive state (Cant et al. 2002) and intragroup relatedness (Nunn and Deaner 2004) cannot be excluded.

Economic theory suggests that when collective benefits are derived from individual actions, free-riding should be common (Nunn 2000), especially when asymmetrical access to public goods results in privileged groups (i.e., dominant individuals). Among tufted capuchin monkeys, strong within-group contest competition allows dominant individuals to have greater energetic intake in medium-sized fruit patches (Janson 1988; Janson 1996). At Iguazú, however, group cohesion is relaxed as a result of the relatively low predator density (Vargas et al. 2006; Di Bitetti et al. 2008; Paviolo et al. 2009; Janson et al. 2012). Accordingly, subordinate individuals are able to forage farther away from the group (Di Bitetti and Janson 2001b) – spatial positions that would otherwise be associated with high predation risk (Janson 1990) – and frequently arrive at the provisioning platforms several minutes in advance of the centre of the group. On most occasions, early arriving individuals are eventually supplanted by dominant individuals; however, subordinate females may be willing to participate from low-risk positions because the monopoly dominant individuals maintain over access to resources is incomplete. Addressing this possibility, however, requires analysis of detailed records of participation in naturally-occurring encounters.

RHP, subjective resource value and patterns of engagement

In a number of species, intergroup aggression is reduced because subordinate groups alter their direction of travel to avoid interactions with competitively stronger neighbors (McComb et al. 1994; Wilson et al. 2001; Kitchen 2004; Furrer et al. 2011). Capuchin monkeys exhibit long-term home range fidelity (Di Bitetti 2001b), and neighboring groups engage in repeated interactions; therefore, individuals should be able to use prior experience to assess the probable outcome of the encounter prior to initiating aggression. Both the willingness of individuals to approach the neighboring group and the speed at which they approach suggest that capuchin monkeys are sensitive to the relative competitive ability of groups. As the probability of eventually winning the encounter decreased, females were more hesitant to participate in defense of a food resource. Yet, even when confronting a group to which encounters were always lost, the probability of female defection only increased to 28%. Furthermore, males did not modify their response in accordance with the potential for winning the intergroup encounter, nor did decreasing the probability of winning the encounter promote defection. In the presence of a high-quality food resource, males were equally likely to approach neighboring groups with decidedly higher competitive ability (both an unfavourable numerical asymmetry and a history of consistent supplants at shared resources) as they were to approach more closely matched competitors. Anecdotal evidence from naturally-occurring intergroup encounters supports these findings; upon hearing long-distance whistle series in their vicinity, individuals sometimes approach larger groups only to flee the area once contact is initiated (C.J. Scarry, unpublished data). In the absence of frequent defection, free-riding is unlikely to cause sufficient intercontest variation in realized RHP to explain this behavior.

One possibility is that variation in party sizes could lead to a disconnect between the numerical assymetry of a given contest relative to the total group size of neighboring groups (McComb et al. 1994; Wilson et al. 2001). A growing body of evidence suggests that tufted capuchin monkeys may facultatively adjust foraging party size to resource abundance (Lynch Alfaro 2007). At Iguazú, individuals in large groups form temporary subgroups that range semi-independently for several hours at a time, especially during periods of low resource availability (Janson et al. 2012). As a result of this reduced group cohesiveness, a call from a single individual in a larger group may not provide an accurate measure of the numerical asymmetry for the current contest. Yet capuchin monkeys do not exhibit “chorusing” behavior, in which multiple individuals overlap in the timing of long-distance vocalizations providing an honest signal of relative group size (McComb et al. 1994; Wilson et al. 2001; Kitchen 2004). Therefore, individuals may frequently be required to assess the relative threat presented by a neighboring group using incomplete information. The nature of the playback experiments, wherein a call was presented from a single individual with no subsequent vocal support from group mates, may have suggested the possibility of subgroup formation.

This possibility, however, is not well supported by the data from the naturally-occurring intergroup encounters. Although occasional reversals occurred when only a subgroup of the dominant group was present (N = 2), most dyadic dominance relations were highly consistent. The relatively low frequency of reversals suggests that prior experience could be used to reliably assess the outcome of an escalated contest prior to initiating aggression. Thus, individuals in subordinate groups appear to be initiating encounters that will almost invariably be lost if aggression escalates. While non-renewable resources that are critical to an individual’s reproductive success (e.g., nest sites) may promote “desperado” tactics (e.g., female jumping spiders, Elias et al. 2010), whereby individuals escalate aggression even when only a small probability of winning exists (Grafen 1987), the provisioning platforms – although a high-quality resource – do not appear to meet this criterion.

The willingness to participate may not result from an error in assessment of the opponent's RHP, but rather an inability to assess the neighboring group's subjective valuation of the resource, the result of state-dependent fitness returns (Janson and Vogel 2006). Resources were contested only when they provided immediate benefits. I chose platform locations from among provisioning sites that were already familiar to the groups due to on-going research on foraging cognition (Janson 1996; Janson 1998b; Di Bitetti and Janson 2001b; Janson 2007). In some cases the focal group had been feeding at these locations almost every winter for over a decade. Yet only during provisioning periods did group members demonstrate an interest in the presence of neighboring groups, increasing their travel speed and approaching the speaker. Losing long-term access to the provisioning site equates with losing a perennially renewable high-quality resource, but during periods of natural resource availability, individuals did not defend the site. It is not the risk of territorial incursion (Heinsohn 1997; Crofoot 2007), but rather the immediate loss of energy gain that promoted defense in this study.

In the current study, I attempted to maintain a consistent subjective resource value for the focal animal, holding *per capita* availability constant across groups and limiting the timing of experiments relative to daily foraging activities. I could not, however, control for the "opponent's" subjective resource valuation. Among capuchin monkeys, in within-group competition, an individual's willingness to contest access to food resources is associated with its hunger level (Janson and Vogel 2006). Similarly, sated individuals may be unwilling to defend resources against neighboring groups because the marginal value of continued access to the food resource is low. Indeed, all but one of the cases of defection during active provisioning occurred when the focal animal had already fed at a provisioning site and may have been sated. The solitary playback call with no response may, instead, be interpreted as an unwillingness to defend the resource by individuals that have already moved away from the site. This vocalization generally serves as a "rallying" call (Di Bitetti 2001a) to elicit support from dispersed group members. Rather than initiating an intergroup encounter with the goal of reversing normal dominance relations, subordinate groups may be testing to see whether their presence will be tolerated, in which case, their approach may serve to evict lagging individuals prior to resource depletion. Accordingly, approaches towards competitively stronger groups appear more tentative. Individuals accelerate more slowly when confronting a group against which they have little chance of winning.

Furthermore, the temporal pattern of challenges by subordinate groups is in keeping with this interpretation. Subgrouping behavior is less common during the summer (Janson et al. 2012) when ripe fruit is found in larger, semi-isolated patches (Di Bitetti 2001b). Yet it is during this period that individuals appear most willing to challenge a competitively stronger neighbor for access to food resources (C.J. Scarry, personal observation). In contrast, during the winter, resources are more dispersed, and subordinate groups frequently avoid encounters, changing their direction of movement and becoming quieter after hearing an extragroup vocalization. Given the rapid gut passage time of capuchin monkeys (~2 hours, Milton 1984), a high degree of intercontest variation in the level of satiation within the dominant group probably occurs. Consequently, subordinate groups may benefit from a 'Prober-Retaliator' strategy (Maynard Smith and Price 1973) – initiating contact but retreating if met with aggression – provided that the state-dependent fitness returns to individuals are high.

Recent work has emphasized the importance of an individual-based approach to studies of intergroup aggression in social animals (Kitchen and Beehner 2007). The current study, however underscores the potential for state-dependent fitness returns to introduce significant intercontest variation in individual assessment of the costs and benefits of aggression (Janson and Vogel 2006). While some measures of time-varying measures of individual state have been included in previous studies (e.g., reproductive state: McComb et al. 1993; McComb et al. 1994; Steenbeek 1999), few studies have considered the potential effects of satiation on individual response. Among primates, a strong phylogenetic signal exists in gut-passage time (Lambert 1998), suggesting a similar pattern might exist in apparent sensitivity to the asymmetry in competitive ability of groups in contests over food resources. Similar to tufted capuchin monkeys, intergroup aggression among white-faced capuchin monkeys (*Cebus capucinus*: Crofoot 2007) and black-and-white colobus monkeys (*Colobus guereza*: Harris 2006) functions to defend access to high-quality food resources. Subordinate groups of white-faced capuchin monkeys occasionally displace competitively stronger neighboring groups (Crofoot et al. 2008), which may reflect rapid variation in satiation-levels associated with rapid gut passage times (Lambert 1998). In contrast, black-and-white colobus monkeys, which have relatively longer gut passage times (Lambert 1998), appear more sensitive to the relative competitive ability of competing groups (Harris 2010). Further analyses of patterns of intergroup aggression – taking into account interspecific variation in physiology – may elucidate the role of subjective resource value on individual assessment of the costs and benefits of aggression.

References

Altmann J (1974) Observational study of behavior - sampling methods. Behaviour 49:227-267

Bates D, Maechler M, Bolker B (2011) lme4 - Linear mixed-effects models using S4 classes. R package version 0.999375-42, URL http://lme4.r-forge.r-project.org/

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

Broom M, Borries C, Koenig A (2004) Infanticide and infant defence by males - modelling the conditions in primate multi-male groups. Journal of Theoretical Biology 231:261-270

Broom M, Koenig A, Borries C (2009) Variation in dominance hierarchies among group-living animals: modeling stability and the likelihood of coalitions. Behavioral Ecology 20:844-855

Brown AD, Zunino GE (1990) Dietary variability in *Cebus apella* in extreme habitats: evidence for adaptability. Folia Primatologica 54:187-195

Cant MA, Otali E, Mwanguhya F (2002) Fighting and mating between groups in a cooperatively breeding mammal, the banded mongoose. Ethology 108:541-555

Carosi M, Heistermann M, Visalberghi E (1999) Display of proceptive behaviors in relation to urinary and fecal progestin levels over the ovarian cycle in female tufted capuchin mokeys. Hormones and Behavior 36:252-265

Cheney DL (1987) Interactions and relationships between groups. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate Societies. University of Chicago Press, Chicago, pp 267-281

Cheney DL, Seyfarth RM (1982) Recognition of individuals within and between groups of free-ranging vervet monkeys. American Zoologist 22:519-529

Cheney DL, Seyfarth RM (1987) The influence of intergroup competition on the survival and reproduction of female vervet monkeys. Behavioral Ecology and Sociobiology 21:375-386

Crofoot MC (2007) Mating and feeding competition in white-faced capuchins (*Cebus capucinus*): the importance of short- and long-term strategies. Behaviour 144:1473-1495

Crofoot MC, Gilby IC, Wikelski MC, Kays RW (2008) Interaction location outweighs the competitive advantage of numerical superiority in *Cebus capucinus* intergroup contests. Proceedings of the National Academy of Sciences of the United States of America 105:577-581

Davies NB, Houston AI (1981) Owners and satellites - the economics of territory defense in the Pied Wagtail, *Motacilla alba*. Journal of Animal Ecology 50:157-180

De Vries H (1995) An improved test of linearity in dominance hierarchies containing unknown or tied relationships. Animal Behaviour 50:1375-1389

De Vries H, Stevens JMG, Vervaecke H (2006) Measuring and testing the steepness of dominance hierarchies. Animal Behaviour 71:585-592

Di Bitetti MS (1997) Evidence for an important social role of allogrooming in a platyrrhine primate. Animal Behaviour 54:199-211

Di Bitetti MS (2001a) Food Associated Calls in the Tufted Capuchin Monkey (*Cebus apella*). In: Ecology and Evolution. Stony Brook University, Stony Brook

Di Bitetti MS (2001b) Home-range use by the tufted capuchin monkey (*Cebus apella nigritus*) in a subtropical rainforest of Argentina. Journal of Zoology 253:33-45

Di Bitetti MS, Janson CH (2001a) Reproductive socioecology of tufted capuchins (*Cebus apella nigritus*) in northeastern Argentina. International Journal of Primatology 22:127-142

Di Bitetti MS, Janson CH (2001b) Social foraging and the finder's share in capuchin monkeys, *Cebus apella*. Animal Behaviour 62:47-56

Di Bitetti MS, Paviolo A, De Angelo CD, Di Blanco YE (2008) Local and continental correlates of the abundance of a neotropical cat, the ocelot (*Leopardus pardalis*). Journal of Tropical Ecology 24:189-200

Elias DO, Botero CA, Andrade MCB, Mason AC, Kasumovic MM (2010) High resource valuation fuels "desperado" fighting tactics in female jumping spiders. Behavioral Ecology 21:868-875

Emlen ST, Oring LW (1977) Ecology, sexual selection, and evolution of mating systems. Science 197:215-223

Enquist M, Leimar O (1987) Evolution of fighting behavior: the effect of variation in resource value. Journal of Theoretical Biology 127:187-205

Furrer RD, Kyabulima S, Willems EP, Cant MA, Manser MB (2011) Location and group size influence decisions in simulated intergroup encounters in banded mongooses. Behavioral Ecology 22:493-500

Garber PA (1988) Diet, foraging patterns, and resource defense in a mixed species troop of *Saguinus mystax* and *Saguinus fuscicollis* in Amazonian Peru. Behaviour 105:18-34

Getty T (1989) Are dear enemies in a war of attrition? Animal Behaviour 37:337-339

Grafen A (1987) The logic of divisively asymmetric contests: respect for ownership and the desperado effect. Animal Behaviour 35:462-467

Grinnell J, Packer C, Pusey AE (1995) Cooperation in male lions - kinship, reciprocity or mutualism. Animal Behaviour 49:95-105

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

Harris TR (2006) Between-group contest competition for food in a highly folivorous population of black and white colobus monkeys (*Colobus guereza*). Behavioral Ecology and Sociobiology 61:317-329

Harris TR (2010) Multiple resource values and fighting ability measures influence intergroup conflict in guerezas (*Colobus guereza*). Animal Behaviour 79:89-98

Hauck WW, Donner A (1977) Wald's test as applied to hypotheses in logit analysis. Journal of the American Statistical Association 72:851-853

Heinsohn R (1997) Group territoriality in two populations of African lions. Animal Behaviour 53:1143-1147

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

Janson CH (1984) Female choice and mating system of the brown capuchin monkey *Cebus apella* (Primates: Cebidae). Zeitschrift Fuer Tierpsychologie 65:177-200

Janson CH (1985) Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). Behavioral Ecology and Sociobiology 18:125-138

Janson CH (1988) Food competition in brown capuchin monkeys (*Cebus apella*): Quantitative effects of group size and tree productivity. Behaviour 105:53-76

Janson CH (1990) Ecological consequences of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. Animal Behaviour 40:922-934

Janson CH (1996) Toward an experimental socioecology of primates: Examples from Argentine brown capuchin monkeys (*Cebus apella nigritus*). In: Norconk MA, Rosenberger AL, Garber PA (eds) Adaptive Radiations of Neotropical Primates. Plenum Press, New York, pp 309-325

Janson CH (1998a) Capuchin counterpoint. In: Ciochon RL, Nisbett RA (eds) The Primate Anthology: Essays on Primate Behavior, Ecology and Conservation from Natural History. Prentice Hall, Upper Saddle River, NJ

Janson CH (1998b) Experimental evidence for spatial memory in foraging wild capuchin monkeys, *Cebus apella*. Animal Behaviour 55:1229-1243

Janson CH (2007) Experimental evidence for route integration and strategic planning in wild capuchin monkeys. Animal Cognition 10:341-356

Janson CH, Baldovino MC, Di Bitetti MS (2012) The group life cycle and demography of brown capuchin monkeys (*Cebus [apella] nigritus*) in Iguazú National Park, Argentina. In: Kappeler PM, Watts DP (eds) Long-Term Field Studies of Primates. Springer, Heidelberg, pp 185-212

Janson CH, Di Bitetti MS (1997) Experimental analysis of food detection in capuchin monkeys: Effects of distance, travel speed, and resource size. Behavioral Ecology and Sociobiology 41:17-24

Janson CH, Vogel ER (2006) Hunger and aggression in capuchin monkeys. In: Hohmann G, Robbins MM, Boesch C (eds) Feeding Ecology in Apes and Other Primates: Ecological, Physical and Behavioral Aspects. Cambridge University Press, Cambridge, pp 285-311

Kitchen DM (2004) Alpha male black howler monkey responses to loud calls: effect of numeric odds, male companion behaviour and reproductive investment. Animal Behaviour 67:125-139

Kitchen DM (2006) Experimental test of female black howler monkey (*Alouatta pigra*) responses to loud calls from potentially infanticidal males: Effects of numeric odds, vulnerable offspring, and companion behavior. American Journal of Physical Anthropology 131:73-83

Kitchen DM, Beehner JC (2007) Factors affecting individual participation in group-level aggression among non-human primates. Behaviour 144:1551-1581

Kitchen DM, Horwich RH, James RA (2004) Subordinate male black howler monkey (*Alouatta pigra*) responses to loud calls: Experimental evidence for the effects of intra-group male relationships and age. Behaviour 141:703-723

Korstjens AH, Nijssen EC, Noe R (2005) Intergroup relationships in western black-and-white colobus, *Colobus polykomos polykomos*. International Journal of Primatology 26:1267-1289

Lambert JE (1998) Primate digestion: Interactions among anatomy, physiology, and feeding ecology. Evolutionary Anthropology 7:8-20

Lynch Alfaro J (2007) Subgrouping patterns in a group of wild *Cebus apella nigritus*. International Journal of Primatology 28:271-289

Manson JH, Wrangham RW (1991) Intergroup aggression in chimpanzees and humans. Current Anthropology 32:369-390

Mares R, Young AJ, Levesque DL, Harrison N, Clutton-Brock TH (2011) Responses to intruder scents in the cooperatively breeding meerkat: sex and social status differences and temporal variation. Behavioral Ecology 22:594-600

Maynard Smith J (1974) The theory of games and the evolution of animal contests. Journal of Theoretical Biology 47:209-221

Maynard Smith J, Parker GA (1976) Logic of asymmetric contests. Animal Behaviour 24:159-175

McComb K, Packer C, Pusey A (1994) Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. Animal Behaviour 47:379-387

McComb K, Pusey A, Packer C, Grinnell J (1993) Female lions can identify potentially infanticidal males from their roars. Proceedings of the Royal Society of London Series B-Biological Sciences 252:59-64

Milton K (1984) The role of food processing factors in primate food choice. In: Rodman P, Cant J (eds) Adaptations for Foraging in Nonhuman Primates: Contributions to an Organismal Biology of Prosimians, Monkeys and Apes. Columbia University Press, New York, pp 249-279

Mosser A, Packer C (2009) Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. Animal Behaviour 78:359-370

Nunn CL (2000) Collective benefits, free-riders, and male extra-group conflict. In: Kappeler PM (ed) Primate Males: Causes and Consequences of Variation in Group Composition. Cambridge Univ Press, Cambridge, pp 192-204

Nunn CL, Deaner RO (2004) Patterns of participation and free riding in territorial conflicts among ringtailed lemurs (*Lemur catta*). Behavioral Ecology and Sociobiology 57:50-61

Nunn CL, Lewis RJ (2001) Cooperation and collective action in animal behaviour. In: Noe R, Van Hooff JA, Hammerstein P (eds) Economics in Nature: Social Dilemmas, Mate Choice and Biological Markets. Cambridge Univ Press, Cambridge, pp 42-66

Packer C, Scheel D, Pusey AE (1990) Why lions form groups: food is not enough. American Naturalist 136:1-19

Palombit RA (1993) Lethal territorial aggression in a white-handed gibbon. American Journal of Physical Anthropology 31:311-318

Parker GA (1974) Assessment strategy and evolution of fighting behavior. Journal of Theoretical Biology 47:223-243

Parker GA, Rubenstein DI (1981) Role assessment, reserve strategy, and acquisition of information in asymmetric animal conflicts. Animal Behaviour 29:221-240

Paviolo A, Di Blanco YE, De Angelo CD, Di Bitetti MS (2009) Protection affects the abundance and activity patterns of pumas in the Atlantic Forest. Journal of Mammalogy 90:926-934

Peres CA (1989) Costs and benefits of territorial defense in wild golden lion tamarins, *Leontopithecus rosalia*. Behavioral Ecology and Sociobiology 25:227-233

Peres CA (1992) Consequences of joint-territoriality in a mixed-species group of tamarin monkeys. Behaviour 123:220-246

Perry S (1996) Intergroup encounters in wild white-faced capuchins (*Cebus capucinus*). International Journal of Primatology 17:309-330

Plavcan JM, van Schaik CP (1992) Intrasexual competition and canine dimorphism in anthropoid primates. American Journal of Physical Anthropology 87:461-477

Pope T (1990) The reproductive consequences of male cooperation in the red howler monkey: Paternity exclusion in multi-male and single-male troops using genetic markers. Behavioral Ecology and Sociobiology 27:439-446

R Development Core Team (2010) R: A language and environment for statistical computing. In: R Foundation for Statistical Computing, Vienna, Austria, URL http://www.R-project.org/.

Ramírez-Llorens P, Di Bitetti MS, Baldovino MC, Janson CH (2008) Infanticide in black capuchins (*Cebus apella nigritus*) in Iguazú National Park, Argentina. American Journal of Primatology 70:473-484

Robinson J (1986) Seasonal variation in use of time and space by the wedge-capped capuchin monkey, *Cebus olivaceus*: Implications for foraging theory. Smithsonian Contributions to Zoology 431:1-60

Rosell F, Gundersen G, Le Galliard JF (2008) Territory ownership and familiarity status affect how much male root voles (*Microtus oeconomus*) invest in territory defence. Behavioral Ecology and Sociobiology 62:1559-1568

Rubenstein DI (1986) Ecology and sociality in horses and zebras. In: Rubenstein D, Wrangham R (eds) Ecological Aspects of Social Evolution: Birds and Mammals. Princeton University Press, Princeton, NJ, pp 282-302

Smith RJ, Jungers WL (1997) Body mass in comparative primatology. Journal of Human Evolution 32:523-559

Steenbeek R (1999) Tenure related changes in wild Thomas's langurs. I: Between-group interactions. Behaviour 136:595-625

Sterck EHM, Watts DP, van Schaik CP (1997) The evolution of female social relationships in nonhuman primates. Behavioral Ecology and Sociobiology 41:291-309

Temeles EJ (1994) The role of neighbours in territorial systems: when are they 'dear enemies'? Animal Behaviour 47:339-350

Terborgh J (1983) Five New World Primates: A Study in Comparative Ecology. Princeton University Press, Princeton, New Jersey

Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual Selection and the Descent of Man. Aldine, Chicago, pp 136-179

van Schaik C, P (1996) Social evolution in primates: The role of ecological factors and male behaviour. Proceedings of the British Academy:9-3

Vargas JdJ, Whitacre D, Mosquera R, Albuquerque J, Piana R, Thiollay J-M, Márquez C, Sánchez JE, Lezama-López M, Midence S, Matola S, Aguilar S, Rettig N, Sanaiotti T (2006)

Estado y distribución actual del águila arpía (*Harpia harpyja*) en Centro y Sur América. Ornitologia Neotropical 17:39-55

Venables W, Ripley B (2002) Modern Applied Statistics with S, 4 edn. Springer, New York

Vogel E, Janson C (2007) Predicting the frequency of food-related agonism in white-faced capuchin monkeys (*Cebus capucinus*), using a novel focal-tree method. American Journal of Primatology 69:533-550

Watts DP, Mitani JC (2001) Boundary patrols and intergroup encounters in wild chimpanzees. Behaviour 138:299-327

Watts DP, Muller M, Amsler SJ, Mbabazi G, Mitani JC (2006) Lethal intergroup aggression by chimpanzees in Kibale National Park, Uganda. American Journal of Primatology 68:161-180

Wheeler BC (2009) Monkeys crying wolf? Tufted capuchin monkeys use anti-predator calls to usurp resources from conspecifics. Proceedings of the Royal Society B-Biological Sciences 276:3013-3018

Wich SA, Assink PR, Becher F, Sterck EHM (2002) Playbacks of loud calls to wild thomas langurs (Primates; *Presbytis thomasi*): The effect of familiarity. Behaviour 139:79-87

Wich SA, Sterck EHM (2007) Familiarity and threat of opponents determine variation in Thomas langur (*Presbytis thomasi*) male behaviour during between-group encounters. Behaviour 144:1583-1598

Williams JM, Oehlert GW, Carlis JV, Pusey AE (2004) Why do male chimpanzees defend a group range? Animal Behaviour 68:523-532

Wilson ML, Hauser MD, Wrangham RW (2001) Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? Animal Behaviour 61:1203-1216

Wilson ML, Wrangham RW (2003) Intergroup relations in chimpanzees. Annual Review of Anthropology 32:363-392

Ydenberg RC, Giraldeau LA, Falls JB (1988) Neighbours, strangers, and the asymmetric war of attrition. Animal Behaviour 36:343-347

Figure 4.1 The location of provisioning sites from which playback experiments were conducted within the home ranges for the three groups (95% kernel density estimate) for the three groups.

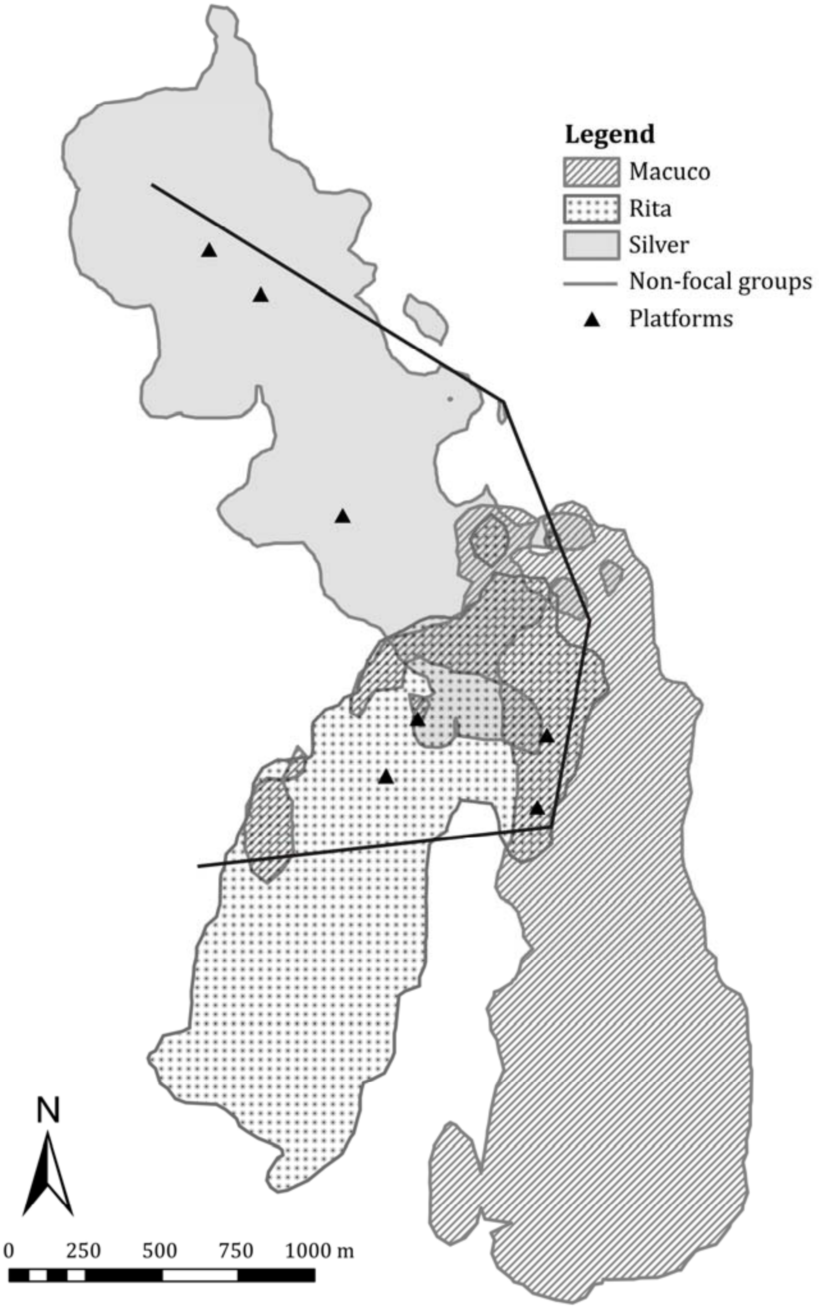


Figure 4.2 The effect of the presence of a high-quality food resource on the probability of individual approach. Response values are not sex specific, rather they represent an average individual.

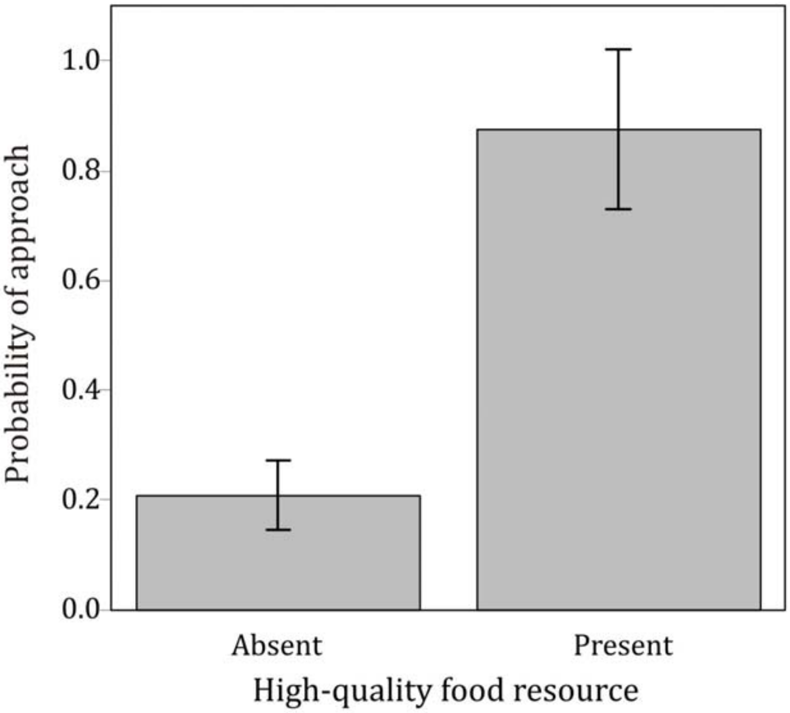


Figure 4.3 The effect of the presence of a high-quality food resource on individual rate of acceleration. Response values are not sex specific, rather they represent an average individual.

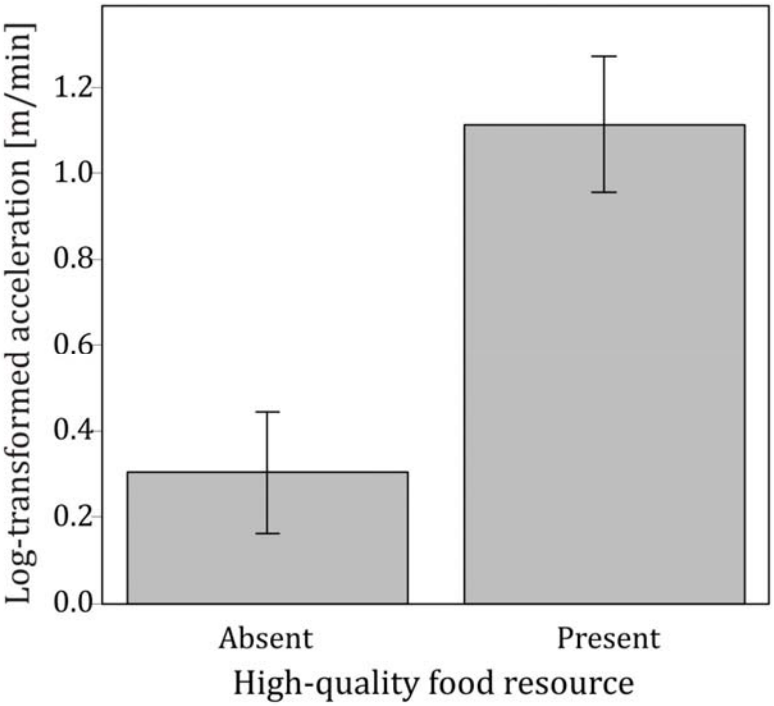


Figure 4.4 Sex-specific responses to the playback stimulus in the presence or absence of a high-quality food resource.

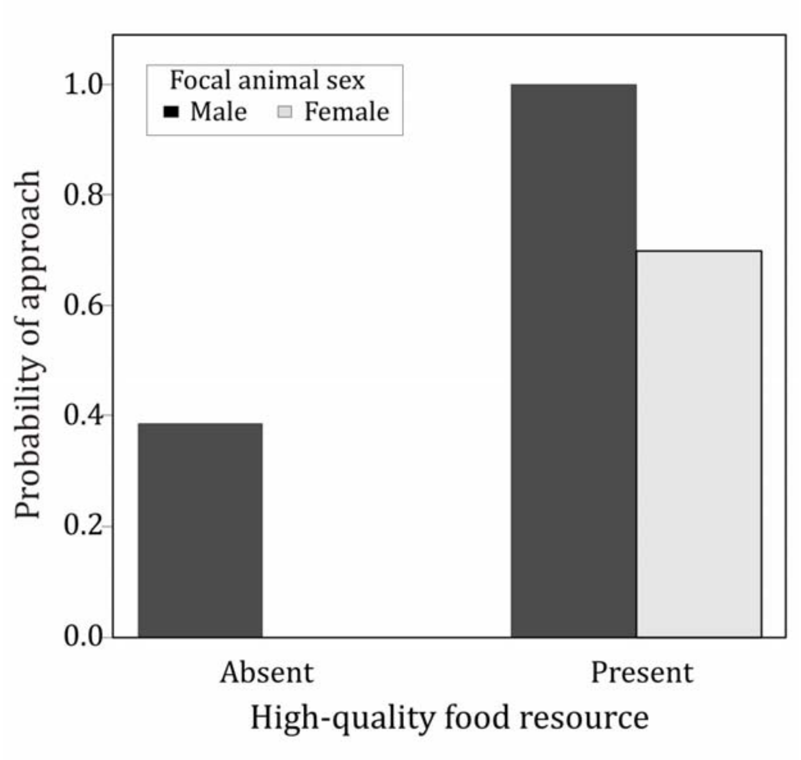


Figure 4.5 Approaches or defections in relation to the relative competitive a`bility of the neighboring groups by females (a) and males (b). The presence (solid line) or absence (dashed line) of a high-quality food resource also affected individual participation.

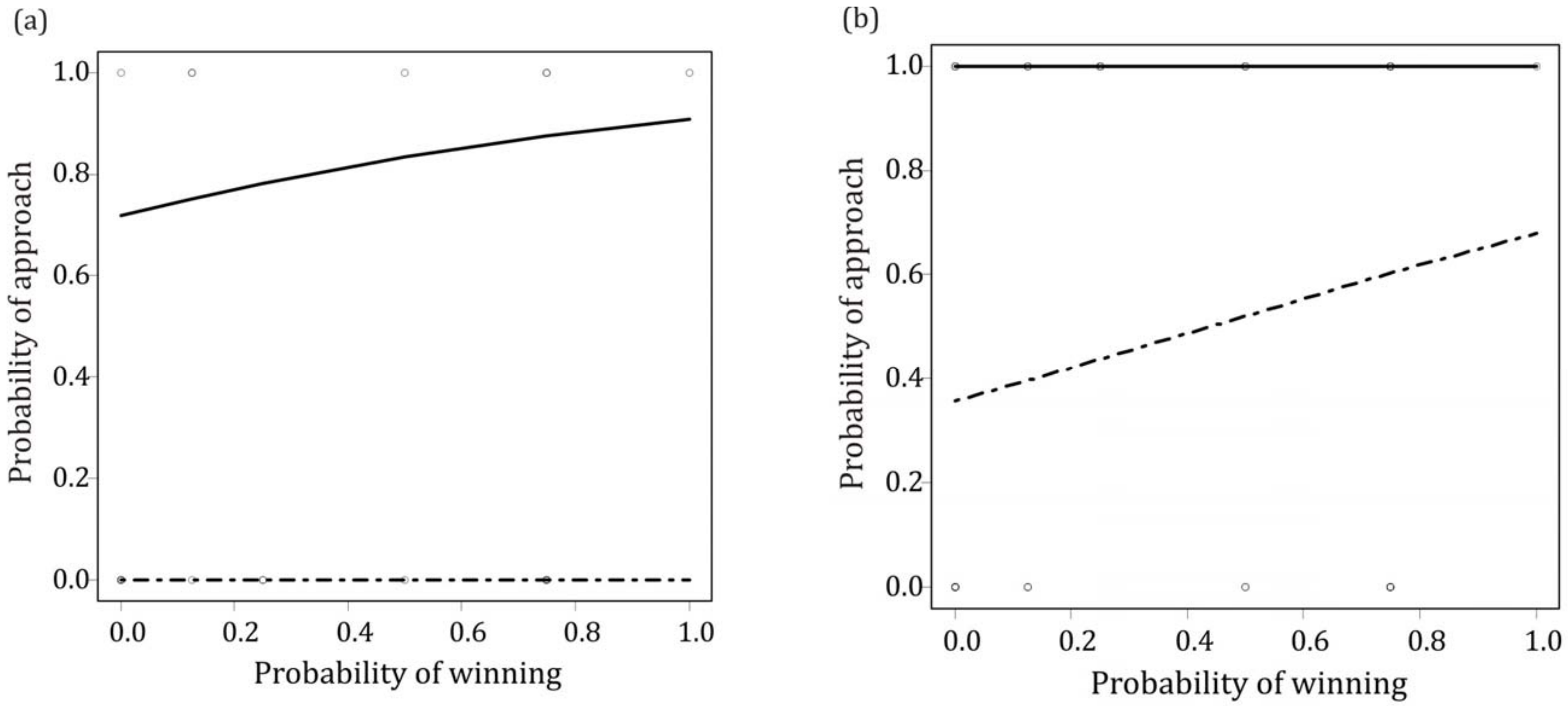


Figure 4.6 The effects of the probability of winning an encounter on individual rate of acceleration following the presentation of the playback stimulus. Rate of acceleration was also affected by the presence (solid line) or absence (dashed line) of a high-quality food resource. Data points represent individual acceleration in response to the playback stimulus in the presence (open circle) or absence (plus) of the food resource.

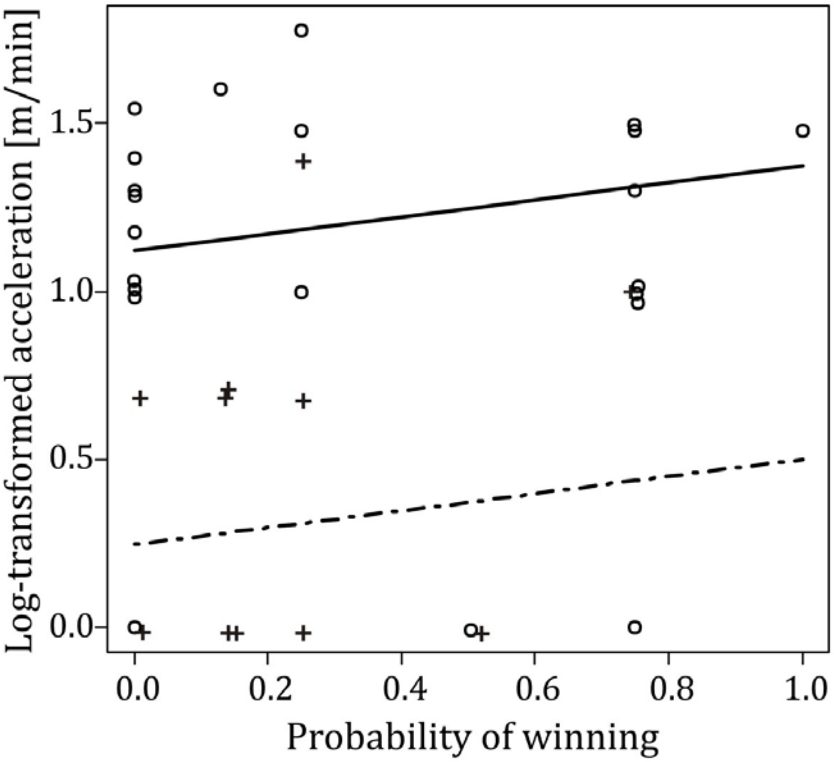


Table 4.1 Outcomes of natural intergroup encounters among groups utilizing the provisioning areas used for playback experiments.

		Loser			
		Yacaratía	Macuco*	Silver*	Rita*
Winner	Yacaratía	–	3	1	23
	Macuco*	1	–	3	23
	Silver*	1		–	
	Rita*		5§		–

* Focal group
§ Losses by Macuco group occurred following the male takeover

Table 4.2 Factors affecting the probability of approaching the playback speaker (N = 48).

Model term	Estimate§	df	$X^{2§}$		
Contest factors					
High-quality food resource		1	32.81	<0.001	***
Absent	0.00				
Present	26.63				
Sexually-receptive female		1	0.352	0.55	
Absent	0.00				
Present	-0.80				
Probability of winning	11.68	1	0.880	0.35	
Individual factors					
Sex		1	13.45	<0.001	***
Female	0.00				
Male	22.61				
Rank		1	2.97	0.23	
Subordinate	0.00				
Intermediate	-4.96				
Dominant	-1.58				
Focal identity (random term)	-23.03				
Interaction terms					
Sex:Probability of winning		1	3.85	0.05	*
Female:Probability of winning	0.00				
Male:Probability of winning	-12.46				

§Reliable standard error estimates could not be obtained because of the dominating effect of the presence of defendable food resource on the probability of approach.

Table 4.3 Factors affecting individual acceleration (m/min; log-transformed) following the playback stimulus (N = 35).

Model term	Estimate	(SE)	df	X^2	p	
Contest factors						
High-quality food resource			1	20.20	<0.001	***
Absent	0.000					
Present	0.875	(0.166)				
Sexually-receptive female			1	0.015	0.90	
Absent	0.000					
Present	-0.010	(0.218)				
Probability of winning	0.251	(0.274)	1	13.59	<0.001	***
Individual factors						
Sex			1	3.11	0.078	
Female	0.000					
Male	0.274	(0.159)				
Rank			2	<0.001	1	
Subordinate	0.000					
Intermediate	-0.057	(0.358)				
Dominant	0.042	(0.207)				
Focal identity (random term)	0.248	(0.173)				

Chapter 5:
Individual patterns of participation during naturally-occurring intergroup encounters among tufted capuchin monkeys (*Cebus apella* [*Sapajus*] *nigritus*)

Abstract

In group-living species, conflicts between groups frequently involve multiple individuals participating in aggression towards the opposing group. Although defense is a cooperative action, the relative costs and benefits to the individual can vary widely among group members, promoting disparate patterns of participation among group mates. Among Argentine tufted capuchin (*Cebus apella* [*Sapajus*] *nigritus*), male group size is critical in determining the outcome of aggressive intergroup encounters over contestable food resources, yet the relative contribution by dominant versus subordinate males is unclear. Moreover, adult females regularly participate in intergroup aggression, although it appears their support may add little to the competitive ability of the group. Here, I examined the properties of individuals and encounters that influence willingness to participate in and escalate intergroup aggression by tufted capuchin monkeys at Iguazú National Park, Argentina. All group members varied their responses in accordance with the relative male group size of the encountered group, being less likely to participate when the encountered group had a numerical advantage. Male rank had no effect on the probability of participation or leadership; however, subordinate males had higher opportunity costs, pursuing neighboring groups farther and remaining longer at the site of the interaction. In accordance with their smaller body size, females were less likely to behave aggressively during intergroup encounters than males, but when their group was at a competitive disadvantage female leadership increased even when a vulnerable infant was present. Low reproductive skew among females appears to drive strategies reflecting the immediate benefits of increased access, while limited mating opportunities promote cooperation by subordinate males that are queueing for reproductive positions.

Introduction

In many social-living species, encounters between neighboring groups are aggressive (see Cheney 1987), involving chases, threat displays and occasionally lethal attacks. If group members cooperate in defense of shared resources, large group size may provide a competitive advantage during intergroup aggression (McComb et al. 1994; Wilson et al. 2001; Kitchen et al. 2004; Kitchen 2006; Bonanni et al. 2011; Furrer et al. 2011; Crofoot and Gilby 2012). In spite of the potential for mutual benefits, however, group members frequently pursue disparate strategies during aggressive intergroup encounters based on varying individual assessments of the costs and benefits of participation (Lazaro-Perea 2001; Young et al. 2005). Moreover, contests between groups frequently occur over public goods such as territories (Peres 1989; Williams et al. 2004; Mosser and Packer 2009; Port et al. 2011) or large food patches that can support multiple individuals (Terborgh 1983) – non-excludable resources that cannot be partitioned in accordance to the costs of escalated aggression borne by the individual. As a result, collective intergroup aggression is vulnerable to ‘free-riders’ – individuals that share the benefits of ownership while contributing only minimally. Widespread free-riding could swamp the competitive advantage of large group size (Nunn 2000; Nunn and Lewis 2001), creating a collective action problem (Olson 1965). Nevertheless, many of the mechanisms proposed to explain dyadic cooperation can be extended to cooperative territorial defense involving larger groups, including mutualism (Maynard Smith 1982; Brown 1983), kin selection (Hamilton 1964), and reciprocal altruism (Trivers 1971). Identifying the factors influencing individual participation in escalated conflicts is a critical first step in understanding how groups are able to maintain cooperation when costs and benefits of participation are distributed unevenly across group members.

These patterns are frequently complicated, however, because individuals are neither unconditional defectors nor cooperators, demonstrating instead conditional strategies of participation (cf. Heinsohn and Packer 1995). For a given contest, individual assessments of the costs and benefits of participation may vary due to a range of factors, including: sex (Cords 2007), reproductive status, and the presence of dependent offspring (McComb et al. 1993; Wich et al. 2002a). In addition, the probability of winning and marginal value of each additional cooperator may affect individual participation (Heinsohn and Packer 1995); some individuals cooperate only when their participation has the greatest effect on the outcome (Kitchen 2006), whereas others defect when their group has a competitive disadvantage but cooperate nominally in other situations. These individual strategies may vary with age (Heinsohn et al. 2002; Cords 2007), reproductive status (McComb et al. 1993; Lazaro-Perea 2001), rank (Lazaro-Perea 2001; Kitchen 2004; Kitchen et al. 2004) or personality (Heinsohn & Packer 1995).

In the current study, I investigate the factors influencing patterns of individual participation and defection during intergroup encounters among free-ranging tufted capuchin monkeys (*Cebus apella [Sapajus] nigritus*) at Iguazú National Park, Argentina. Interactions between neighboring groups of this population are generally aggressive (Di Bitetti 2001), but only rarely involve direct contact between individuals in opposing groups (Scarry and Tujague 2012). Instead, intergroup encounters are characterized by long distance chases and threat displays, with members of the losing group generally retreating farther into their own home range (Di Bitetti 2001). Although both males and females participate in intergroup aggression (Di Bitetti 2001) over contested food resources (Janson 1986; Chapter 2), the relative competitive ability of the group depends primarily on male group size (Chapter 3). Due to their smaller body size (Smith and Jungers 1997) and less developed weaponry (Plavcan and van Schaik 1992), the costs of escalated conflicts may be significantly higher for females than males, which could promote a sex-based difference in participation. Females with dependent infants must further balance the potential for infanticidal attacks by extragroup individuals versus the benefits of gaining access to additional resources to offset the increased energy costs of lactation and infant handling. Therefore, before testing the mechanisms promoting stable cooperation, I examine whether variation in the potential costs and benefits influences individual willingness to escalate aggression (Maynard Smith and Parker 1976).

If individual participation in collective defense is promoted through kin selection (Hamilton 1964), participation should be most common among individuals with many close relatives so that the benefits of inclusive fitness offset the direct costs involved (e.g., *Lemur catta*: Nunn and Deaner 2004). Because high-ranking individuals can monopolize access to key resources through intragroup competition (Janson 1984; Janson 1985; Janson 1988; Di Bitetti and Janson 2001b), theoretical considerations suggest within-group dominance relationships may also affect patterns of participation in intergroup encounters. Dominant individuals belong to a privileged group; thus, they may be willing to contribute proportionally more to the defensive effort (Cheney 1981; Janson 1986; Perry 1996; Nunn 2000; Nunn and Lewis 2001) whereas subordinate individuals refrain. On the other hand, intergroup dominance provides increased *per capita* availability of food resources (Chapter 3); therefore, both mutualism and reciprocity predict that no rank differences should be apparent during intergroup aggression because both dominants and subordinates perceive the value of maintaining access. If reciprocal altruism is maintaining cooperation, however, participation should be infrequent among subordinate individuals that are not tolerated at contested food resources (i.e., subordinate adult males).

Methods

Study site and subjects

Iguazú National Park in Misiones, Argentina, is a 60 000 ha preserve in the southern Atlantic Forest. The site is characterized by a humid subtropical climate with marked seasonal variation in the production of fruits and insects (Di Bitetti 2001), which corresponds to temperature and daylight seasonality (Brown and Zunino 1990). Average availability of capuchin food resources reaches its lowest point during the austral winter (June – August), during which point, the production of fleshy fruits is limited primarily to exotic species found around abandoned human settlements (see Janson et al. 2012 for a complete description of the site), and groups may expand their ranging behavior while foraging for patchily distributed insect resources (Di Bitetti 2001). The site boasts a nearly complete predator community (see Janson et al. 2012 for a complete list of predator species); however, local densities of mid- to large-bodied felids are low (Di Bitetti et al. 2008; Paviolo et al. 2009) and harpy eagles (*Harpia harpyja*) – which prey heavily upon capuchin monkeys at other sites (Rettig 1978) – are currently absent (Vargas et al. 2006) and have not been observed with the Area Cataratas since the site was logged over 70 years ago.

Tufted capuchin monkeys (*Cebus apella* [*Sapajus*] *nigritus*) are small-bodied, frugivorous primates that reside in multi-male, multi-female groups. At Iguazú, capuchin group size ranges from 5-44 independently locomoting individuals (Janson et al. 2012), characterized by male dispersal and female philopatry (Di Bitetti 1997). Both male and female intragroup dominance relationship form linear hierarchies; groups have a single dominant male that occupies a central spatial position (Janson 1990; Janson and Di Bitetti 1997), surrounded by high-ranking females and tolerated juveniles and infants. In addition to the dominant male, social groups may contain up to five subordinate adult males (Ramírez-Llorens et al. 2008) that forage around the periphery of the group with subordinate females and untolerated juveniles (i.e., older juvenile males).

To identify the factors promoting individual participation in intergroup aggression, I followed four fully-habituated groups with overlapping home ranges (Table 5.1). Maternal relationships are known for all natal individuals (i.e., not adult males) in the Gundolf, Macuco, and Rita groups due to long-term demographic monitoring and behavioral studies of these groups (see Janson et al. 2012). Because the dominant male has priority-of-access in mating (Janson 1984; Lynch Alfaro 2005), there is a high probability that infants of a single birth cohort share a common sire, but comprehensive paternity analyses have not yet been conducted (but see Escobar-Parao 1999).

Behavioral data collection

During all-day follows of focal groups, I recorded ranging behavior at 15-minute intervals, noting the location of the group's center (Janson 1990) using a handheld Garmin GPS60Cx (<10 m error). When UTM coordinates could not be obtained from the center of the group directly, I projected the location of the group center using the direction and distance from the observer's location or the geo-referenced trail system.

I also recorded all demographic changes occurring within the four groups during this period, including: infant births, male immigrations and emigrations, and disappearances or deaths of other group members. Date of birth for all infants can be pinpointed to within a two week period.

I recorded the outcome of dyadic intragroup aggression *ad libitum* (Altmann 1974); however, I did not have sufficient records to construct complete intragroup dominance hierarchies in order to assign cardinal ranks to individuals (De Vries 1998; Klass and Cords 2011). Instead, I classified individuals as high-, mid- and low-ranking depending on whether or not aggression was received from and/or directed to same-sex individuals. These categories correspond to distinct socio-spatial subgroups which differ in their access to both food resources (Di Bitetti & Janson 2001b) and mates (Janson 1984).

I defined an intergroup encounter as occurring whenever members of the focal group interacted with extragroup individuals – either through visual or vocal contact – regardless of whether all group members were present or not. At the onset of an encounter, I discontinued all other data collection protocols to note the time and location of initial contact, before beginning to conduct *ad libitum* sampling (Altmann 1974) of individual behavioral responses. Due to the rapid chases involved with encounters between neighboring groups, I was frequently only able to register reactions by a fraction of the group. Only for the smaller groups (Rita, Gundolf) was I able to collect complete records of the behavioral responses of all individuals during a single encounter. In other circumstances, all records from a given encounter may be of either participating or defecting individuals. Because the identity of the individuals that I could observe depended on my position relative to the group prior to the encounter – and not on the behavioral response of the individual, I have no reason to expect an intra-individual bias towards participation or defection.

During encounters, I used the following criteria to categorize behavioral responses:

1. Whether or not the individual participated in intergroup aggression. Participants included all individuals that moved towards the other group, maintaining proximity during at least a portion of the chase. Although this definition permits a degree of lagging during participation, individuals that arrived at the location only after all members of the opposing group had fled were not considered to have participated.

2. Whether or not the individual was a leader during the aggressive portion of an encounter. By participating at the front edge of the group, other group members could not serve as a buffer against extragroup individuals, such that these individuals accepted a greater risk of incurring injury.

3. Whether or not the individual exhibited brief or persistent participation. Persistence is defined as continuing to remain in proximity to the neighboring group, directing aggressive behavior towards extragroup individuals, after other individuals have returned to normal pre-contact behavior. Similar to leaders, persistent individuals accepted additional costs because time invested in continuing to pursue the neighboring group was cut from other activities.

4. Whether or not the individual fled from the neighboring group. This category includes all individuals that retreated following initial contact, whether or not they participated briefly; however, individuals that simply failed to participate (i.e., remained in a constant location) were not considered to have fled.

Statistical analyses

I analyzed the factors affecting individual participation by performing generalized linear mixed-effects modeling (GLMM) using the ‘lmer’ function in lme4 package (Bates et al. 2011) for the R statistical environment (R Development Core Team 2010). I ran separate analyses using a logit-link function for the following independent variables: individual participation, leadership, persistence and flight. To control for repeated measures on an individual, I included individual identity as a random factor in all models. I also included the group dyad because individual response may be affected by identity of the encountered group and variation in intergroup social relationships unrelated to between-group contest competition (e.g., male relatedness, prior history of interaction). Finally, nested within the interacting dyad, I included a unique identifier for each encounter as a random factor to control for bias due to the spatial position of the observer relative to the group when the encounter occurred. This approach ensures that data for each recorded individual during each encounter is measured relative to both the individual’s own general propensity to participate and the behaviors of other group members in the context of that particular encounter.

I first ran combined analyses of male and female behaviors, including sex, rank, and age class as fixed effects and distance from the home range center and the asymmetry in male group size between the competing groups as continuous variables. To examine variables that either could not be determined for males or were relevant only to females, I created a second dataset that included number of maternal kin, infant age in weeks, and reproductive status (i.e., gestating or otherwise). I included the number of group members that were related to each adult female through the maternal line by a relatedness coefficient (r) greater than 0.25 (i.e., mother-offspring, siblings, grandmother-grandoffspring) to address the potential for indirect fitness benefits to promote individual participation. I identified pregnant females by back-calculating 155 days (gestation length: Nagle and Denari 1983) from known or suspected (N = 3) parturition. Saturated models contained all fixed effects, continuous variables, and several biologically relevant interaction terms (i.e., asymmetry by distance by sex three-way interaction, infant age by asymmetry or sex by dominance two-way interactions). Using the ‘anova’ function, which analyzes the log-likelihood that the difference in the Akaike Information Criterion (AIC) value of two candidate models is significant after controlling for the number of explanatory variables in each model, I tested whether the saturated model improved the AIC relative to a null model including only random factors. I then removed all terms that did not significantly reduce the AIC to select the best model predicting patterns of individual participation.

Results

Individual participation and flight

Individuals of both sexes are less likely to participate when the opposing group has more adult males with a slight increase in participation near the periphery by males (Figure 5.1; Table 5.2). While females appear more sensitive to the asymmetry in male group size (Table 5.2), neither the number of maternal relatives, infant age, or pregnancy affected the probability that a female participated in intergroup aggression (Table 5.3). Juveniles of both sexes are less likely to participate in intergroup encounters than adults and subadults (Table 5.2).

Although males are more likely than females to behave aggressively briefly prior to fleeing (GLMM, individual sex: $X_1 = 14.30$; $p < 0.001$), the probability that an individual eventually flees from the opposing group is unaffected by sex (Table 5.4). Rather, as the relative asymmetry in male group size increases, both males and females in the outnumbered group are more likely to flee (Table 5.4). Mid-ranked individuals are generally less likely to flee relative to other group members (Figure 5.2; Table 5.4), but the probability that these individuals will flee remains high (~45%) if the difference in relative male group size exceeds one individual. Examining only flight responses by females, however, individual rank had no effect after controlling for infant age and gestation (Table 5.5).

Male leadership and persistence

In general, males are more likely to lead encounters than are females (GLMM, individual sex: $t = 3.110$; $p = 0.002$), with the probability that a male will participate as leader increasing when the opposing group is at a numerical disadvantage (Table 5.6). No differences are apparent between dominant and subordinate adult males in their predisposition to lead encounters; however, juvenile males are less likely to lead encounters (Table 5.6).

Relative to the dominant male, however, subordinate males are significantly more likely to persist at the site of an encounter (Figure 5.3; Table 5.7), continuing to direct aggressive behaviors towards extragroup individuals after other group members have returned to pre-contact behavior (e.g., feeding, foraging, social interactions). Both dominant and subordinate males are more likely to persist if their group has a numerical advantage (Table 5.7).

Female leadership

Although less common than encounters with male leadership ($X^2_1 = 12.97$, $p < 0.001$), female leaders were observed during 63.5% of encounters (N = 33 of 52 encounters for which information regarding the identity of leaders was available). Females are less likely than males to be the only sex leading an encounter ($X^2_1 = 4.31$, $p = 0.038$), so the majority of these encounters (94.2%) also involved male leaders; however, female leadership occurred during three encounters in which the resident males fled without participating.

While the average adult male led during 38.9% of encounters for which participation records were available, individual adult females led only 15.3% of the encounters (range: 0% – 50%). Although significant interindividual variation occurs (GLMM, individual random effect: $X^2_1 = 5.61$, $p = 0.018$), dominance has no effect on the probability that a female leads an encounter (GLMM, dominance: $X^2_2 = 1.38$, $p = 0.50$), and neither the number of maternal relatives nor the gestational state of the individual are significant predictors in the best fit model (Table 5.8). Instead, females are more likely to lead encounters when their group has markedly fewer males (Table 8), especially when their infant is young. In contrast, among groups more closely matched in male numbers, the probability of female leadership increases with infant age (Figure 5.4).

Discussion

Numerical assessment

The results suggest that, similar to other species (McComb et al. 1994; Wilson et al. 2001; Kitchen 2004; Bonanni et al. 2011), tufted capuchin monkeys assess the numeric odds prior to participating in intergroup aggression. Tufted capuchin monkeys do not exhibit chorusing behavior that would allow individuals to assess the relative number of opponents before visual or physical contact. Yet both dominant and subordinate males participate as leaders, whereas other group members frequently lag slightly behind, which allows individuals to rapidly assess the relative number of males in competing groups. When facing an opposing group that has more adult males and, thus, the probability of winning is low, both males and females are unlikely to participate. Instead, individuals will retreat without engaging in escalated aggression if the opposing group has a surplus of two or more males. As a result of this general pattern, direct physical contact during intergroup encounters is infrequent (Scarry and Tujague 2012).

In spite of the relatively low costs of intergroup aggression, the general tendency of males to participate more than females is not unexpected considering the sexual dimorphism exhibited by capuchin monkeys (Plavcan and van Schaik 1992; Smith and Jungers 1997). Adult males are approximately 45% heavier than adult females (Smith and Jungers 1997); thus, the potential costs of escalated contests are significantly higher for smaller-bodied females. When possible, females would benefit from free-riding on the defensive efforts of resident males, gaining the benefits of access without risking the potential costs. Yet female capuchin monkeys do not appear to follow the most cost-effective strategy – participating primarily when the odds are even and their support will have the greatest impact on the outcome of the encounter (Kitchen 2006). Instead, females are most likely to participate when the probability of winning an encounter is already high because their group has relatively more males. By investing energy in chasing the other group when their group already has a competitive edge, females may increase the apparent numerical advantage. Rather than providing critical support in winning escalated encounters (Chapter 3), female participation may serve as a low-cost mechanism to reinforce existing dominance relationships through psychological intimidation (cf. savannah baboon intragroup dominance relationships: Silk 2002).

Although less likely overall to participate, females in groups with relatively fewer adult males are more likely to lead intergroup aggression. No sex difference is apparent among fleeing individuals within outnumbered groups, so the pattern does not simply reflect an absence of participating males. In general, females are providing additional support to resident male during these encounters, which may increase the opportunity costs of exclusive access. Thus females in subordinate groups may be able to ensure continued access to shared resources through participation (cf. Stamps and Krishnan 2001).

The influence of location

In many species, individuals value the center of their home range more than the periphery (Giraldeau and Ydenberg 1987; Wich et al. 2002b; Crofoot and Gilby 2012), either because the risk of complete territory loss is higher following a lost encounter at the center (cf. strategic-center hypothesis: Giraldeau and Ydenberg 1987) or because increased familiarity with the area facilitates optimal resource utilization (e.g., Davies and Houston 1981). As a result, in many species, individuals react most strongly to intrusions that occur close to the center of their home range (Giraldeau and Ydenberg 1987; Wich et al. 2002b; Crofoot and Gilby 2012). Yet tufted capuchin monkeys appear more likely to participate during intergroup encounters that occur near the periphery. If intergroup chases continue until the opposing group has been expelled from the home range (Di Bitetti 2001), the energetic costs for participating individuals may be low during these encounters due to the short distance to be covered, promoting participation during encounters along the periphery. In contrast, for encounters occuring near the center of the home range, the energy and opportunity costs involved are higher, which may promote defection. Further analyses are needed, however, to assess how location affects the relative costs and benefits of participation.

The influence of infant age

In many species, behavioral responses by females are mediated by the presence of vulnerable offspring due to the risk of infanticidal attacks by extragroup males (McComb et al. 1993; Steenbeek 1999; Korstjens et al. 2005). Among tufted capuchin monkeys, however, extragroup males have not been observed to attempt infanticidal attacks. While infanticide appears to be the greatest cause of mortality during the infant dependency period (Ramírez-Llorens et al. 2008), all known or suspected attacks have been by perpetrated by group members. Mothers of vulnerable infants may still perceive greater costs of participation due to the risk of redirected aggression (Cords 2007) or the greater energetic burdens due of transporting young infants.

Nevertheless, among tufted capuchin monkeys, the presence of a young infant does not uniformly inhibit female participation during intergroup encounters, suggesting the increased importance of home range maintenance among females with the additional energetic burden of lactation (McComb et al. 1994). Moreover, because capuchin monkeys are income breeders with seasonal reproduction, access to food resources during the early period of infant dependency is critical in determining female interbirth intervals (Di Bitetti and Janson 2001a). Consequently, in numerically disadvantaged groups, females with young infants are more likely to lead intergroup aggression. In contrast in larger groups, females with dependent offspring are able to free-ride on the behavior of other group members.

During the rapid chase following an encounter, older infants occasionally become separated from the main body of the group (C.J. Scarry, unpublished data). Although these lost individuals have been reunited with their group on all known occasions, the apparent decline in female leadership with infant age within outnumber groups may also be associated with the need to collect offspring that travel independently during normal group activities.

The maintenance of collective defense

Although striking, the absence of a significant dominance effect in either sex is consistent with the results of previous playback experiments (Chapters 2, 4), wherein rank did not significantly affect the initial response of individuals to simulated intergroup encounters occurring near provisioning platforms. Given that willingness to participate in the collective effort is expected to be influenced by the relative benefits to the individual, this pattern suggests that mutual benefits of exclusive access to group-controlled resources promote individual participation in collective defense.

Among tufted capuchin monkeys, intragroup dominance hierarchies affect individual feeding access in contestable patches (Janson 1988), which suggests that subordinate females may not benefit immediately from defending individual high-quality food resources. In spite of this advantage of high rank, however, no dominance effect on female lifetime reproductive success is apparent within the population (Janson et al. 2012), potentially because the relatively low predation risk permits relaxed group cohesion. Subordinate females forage farther from the center of the group (Di Bitetti and Janson 2001b) – positions normally associated with increased predation risk (Janson 1990), which may allow them to take advantage of smaller alternative resources to reduce the costs of within-group contest competition. Consequently, all resident females may benefit through the increased *per capita* availability of food resource accorded by intergroup dominance (Chapter 3). Rather than the benefits of intragroup dominance or inclusive fitness, patterns of participation by females may reflect differences in individual personality (cf. Heinsohn and Packer 1995).

The absence of a dominance effect among adult males in either willingness to participate in or lead intergroup aggression is less readily explained by the benefits of exclusive access to the home range; increased access to food resources does not directly increase male lifetime reproductive success (Trivers 1972). Because dominant males maintain priority-of-access in mating (Janson 1984, 1998; B. Tiddi, personal communication) and presumably sire the majority of infants, they are predicted to accept higher costs of participation. As expected, the few cases of direct contact aggression observed involved dominant males exclusively; however, subordinate males frequently persist after other group members resume foraging or social behavior, incurring higher opportunity costs than dominant males. No extragroup copulations were observed (C.J. Scarry, unpublished data), suggesting that subordinate males cannot increase their reproductive success by sneaking copulations following intergroup encounters (e.g., Cant et al. 2002; Young et al. 2007). Nevertheless, the prolonged chases and threats towards extragroup males may allow subordinate males to garner valuable information about the relative competitive ability of future rivals. Yet juvenile natal males – the individuals most likely to transfer groups (Janson et al. 2012) and, therefore, benefit from assessing reproductive opportunities offerred by neighboring groups (Cheney and Seyfarth 1983; Lazaro-Perea 2000) – are less active participants. Due to their smaller body size, they may be employing an alternate strategy (i.e., prospecting), remaining with the neighboring group for several hours and engaging in affiliative behaviors (e.g., allogrooming, play: C.J. Scarry, unpublished data).

Alternatively, the long dominant male tenures (Janson et al. 2012) and high apparent reproductive skew (Janson 1998) create the potential for cooperation to be maintained due to reproductive queueing and delayed reciprocity (Wiley and Rabenold 1984; Kokko and Johnstone 1999). If subordinate males are queueing to breed (cf. meerkats, *Suricata suricatta*: Clutton-Brock et al. 2001; spotted hyena, *Crocuta crocuta*: East and Hofer 2001), the costs to future reproductive success incurred through participation in intergroup aggression may be low relative to the costs of potentially inheriting a home range with increased overlap with neighboring groups. The absence of subordinate male participation in direct physical aggression during intergroup encounters is consistent with the higher potential costs to future reproductive opportunities (Field et al. 2006). Because juvenile males will not remain to breed in their natal group (Janson et al. 2012), the inclusive fitness benefits of defending the range may be insufficient to promote high-cost participation, especially as they near the age of dispersal (Clutton-Brock et al. 2002).

The long wait to potentially attain an alpha male position (Janson et al. 2012) provides the opportunity for additional direct benefits to subordinate males, if participation in intergroup encounters is included within an existing market economy, trading altruistic behaviors for tolerance (Tiddi et al. 2011). Within this framework, coalitionary partners trade in different currencies, but the reciprocal benefits of this transaction may be enough to maintain cooperation (Trivers 1971); social tolerance by group mates may be critical for subordinate males to avoid the deleterious physiological effects of long-term stress (Abbott et al. 2003; Sapolsky 2005), that could impact future rank attainment. Further analyses are necessary to disentangle the relative importance of short-term and long-term benefits of cooperation by subordinate males.

References

Altmann J (1974) Observational study of behavior - sampling methods. Behaviour 49:227-267

Bates D, Maechler M, Bolker B (2011) lme4 - Linear mixed-effects models using S4 classes. R package version 0.999375-42, URL http://lme4.r-forge.r-project.org/

Bonanni R, Natoli E, Cafazzo S, Valsecchi P (2011) Free-ranging dogs assess the quantity of opponents in intergroup conflicts. Animal Cognition 14:103-115

Brown AD, Zunino GE (1990) Dietary variability in *Cebus apella* in extreme habitats: evidence for adaptability. Folia Primatologica 54:187-195

Brown JL (1983) Cooperation—a biologist's dilemma. Advances in the Study of Behavior 13:1-37

Cant MA, Otali E, Mwanguhya F (2002) Fighting and mating between groups in a cooperatively breeding mammal, the banded mongoose. Ethology 108:541-555

Cheney DL (1981) Intergroup encounters among free-ranging vervet monkeys. Folia Primatologica 35:124-146

Cheney DL (1987) Interactions and relationships between groups. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate Societies. University of Chicago Press, Chicago, pp 267-281

Cheney DL, Seyfarth R (1983) Nonrandom dispersal in free-ranging vervet monkeys: Social and genetic consequences. American Naturalist 122:392-412

Clutton-Brock TH, Brotherton PNM, Russell AF, O'Rain MJ, Gaynor D, Kansky R, Griffin A, Manser M, Sharpe L, McIlrath GM, Small T, Moss A, Monfort S (2001) Cooperation, control and concession in meerkat groups. Science 291:478

Clutton-Brock TH, Russell AF, Sharpe LL, Young AJ, Balmforth Z, McIlrath GM (2002) Evolution and development of sex differences in cooperative behavior in meerkats. Science 297:253-256

Cords M (2007) Variable participation in the defense of communal feeding territories by blue monkeys in the Kakamega Forest, Kenya. Behaviour 144:1537-1550

Crofoot MC, Gilby IC (2012) Cheating monkeys undermine group strength in enemy territory. Proceedings of the National Academy of Sciences of the United States of America 109:501-505

East ML, Hofer H (2001) Male spotted hyenas (*Crocuta crocuta*) queue for status in social groups dominated by females. Behavioral Ecology 12:558-568

Davies NB, Houston AI (1981) Owners and satellites - the economics of territory defense in the Pied Wagtail, *Motacilla alba*. Journal of Animal Ecology 50:157-180

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

Di Bitetti MS (1997) Evidence for an important social role of allogrooming in a platyrrhine primate. Animal Behaviour 54:199-211

Di Bitetti MS (2001) Home-range use by the tufted capuchin monkey (*Cebus apella nigritus*) in a subtropical rainforest of Argentina. Journal of Zoology 253:33-45

Di Bitetti MS, Janson CH (2001a) Reproductive socioecology of tufted capuchins (*Cebus apella nigritus*) in northeastern Argentina. International Journal of Primatology 22:127-142

Di Bitetti MS, Janson CH (2001b) Social foraging and the finder's share in capuchin monkeys, *Cebus apella*. Animal Behaviour 62:47-56

Di Bitetti MS, Paviolo A, De Angelo CD, Di Blanco YE (2008) Local and continental correlates of the abundance of a neotropical cat, the ocelot (*Leopardus pardalis*). Journal of Tropical Ecology 24:189-200

Field J, Cronin A, Bridge C (2006) Future fitness and helping in social queues. Nature 441:214-217

Giraldeau LA, Ydenberg R (1987) The center-edge effect: the result of a war of attrition between territorial contestants? Auk 104:535-538

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

Heinsohn R, Packer C, Pusey AE (2002) Development of cooperative territoriality in juvenile lions. Proceedings of the Royal Society of London Series B-Biological Sciences 263:475-479

Janson CH (1984) Female choice and mating system of the brown capuchin monkey *Cebus apella* (Primates: Cebidae). Zeitschrift Fuer Tierpsychologie 65:177-200

Janson CH (1985) Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). Behavioral Ecology and Sociobiology 18:125-138

Janson CH (1986) The mating system as a determinant of social evolution in capuchin monkeys (*Cebus*). In: Else JG, Lee PC (eds) Primate Ecology and Conservation. Cambridge University Press, New York, pp 169-179

Janson CH (1988) Food competition in brown capuchin monkeys (*Cebus apella*): Quantitative effects of group size and tree productivity. Behaviour 105:53-76

Janson CH (1990) Social correlates of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. Animal Behaviour 40:910-921

Janson CH (1998) Capuchin counterpoint. In: Ciochon RL, Nisbett RA (eds) The Primate Anthology: Essays on Primate Behavior, Ecology and Conservation from Natural History. Prentice Hall, Upper Saddle River, NJ

Janson CH, Baldovino MC, Di Bitetti MS (2012) The group life cycle and demography of brown capuchin monkeys (*Cebus [apella] nigritus*) in Iguazú National Park, Argentina. In: Kappeler PM, Watts DP (eds) Long-Term Field Studies of Primates. Springer, Heidelberg, pp 185-212

Janson CH, Di Bitetti MS (1997) Experimental analysis of food detection in capuchin monkeys: Effects of distance, travel speed, and resource size. Behavioral Ecology and Sociobiology 41:17-24

Kitchen DM (2004) Alpha male black howler monkey responses to loud calls: effect of numeric odds, male companion behaviour and reproductive investment. Animal Behaviour 67:125-139

Kitchen DM (2006) Experimental test of female black howler monkey (*Alouatta pigra*) responses to loud calls from potentially infanticidal males: Effects of numeric odds, vulnerable offspring, and companion behavior. American Journal of Physical Anthropology 131:73-83

Kitchen DM, Horwich RH, James RA (2004) Subordinate male black howler monkey (*Alouatta pigra*) responses to loud calls: Experimental evidence for the effects of intra-group male relationships and age. Behaviour 141:703-723

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

Kokko H, Johnstone RA (1999) Social queuing in animal societies: a dynamic model of reproductive skew. Proceedings of the Royal Society of London Series B-Biological Sciences 266:571-578

Korstjens AH, Nijssen EC, Noe R (2005) Intergroup relationships in western black-and-white colobus, *Colobus polykomos polykomos*. International Journal of Primatology 26:1267-1289

Lazaro-Perea C (2000) Social interactions within and between groups in wild common marmosets (*Callithrix jacchus*) In. Univ Wisconsin, Madison, pp ix, 154

Lazaro-Perea C (2001) Intergroup interactions in wild common marmosets, *Callithrix jacchus*: Territorial defence and assessment of neighbours. Animal Behaviour 62:11-21

Lynch Alfaro J (2005) Male mating strategies and reproductive constraints in a group of wild tufted capuchin monkeys (*Cebus apella nigritus*). American Journal of Primatology 67:313-328

Maynard Smith J (1982) Evolution and the Theory of Games. Cambridge University Press, Cambridge

Maynard Smith J, Parker GA (1976) Logic of asymmetric contests. Animal Behaviour 24:159-175

McComb K, Packer C, Pusey A (1994) Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. Animal Behaviour 47:379-387

McComb K, Pusey A, Packer C, Grinnell J (1993) Female lions can identify potentially infanticidal males from their roars. Proceedings of the Royal Society of London Series B-Biological Sciences 252:59-64

Mosser A, Packer C (2009) Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. Animal Behaviour 78:359-370

Nunn CL (2000) Collective benefits, free-riders, and male extra-group conflict. In: Kappeler PM (ed) Primate Males: Causes and Consequences of Variation in Group Composition. Cambridge Univ Press, Cambridge, pp 192-204

Nunn CL, Deaner RO (2004) Patterns of participation and free riding in territorial conflicts among ringtailed lemurs (*Lemur catta*). Behavioral Ecology and Sociobiology 57:50-61

Nunn CL, Lewis RJ (2001) Cooperation and collective action in animal behaviour. In: Noe R, Van Hooff JA, Hammerstein P (eds) Economics in Nature: Social Dilemmas, Mate Choice and Biological Markets. Cambridge Univ Press, Cambridge, pp 42-66

Olson M (1965) The Logic of Collective Action. Harvard University Press, Cambidge, MA

Paviolo A, Di Blanco YE, De Angelo CD, Di Bitetti MS (2009) Protection affects the abundance and activity patterns of pumas in the Atlantic Forest. Journal of Mammalogy 90:926-934

Peres CA (1989) Costs and benefits of territorial defense in wild golden lion tamarins, *Leontopithecus rosalia*. Behavioral Ecology and Sociobiology 25:227-233

Perry S (1996) Intergroup encounters in wild white-faced capuchins (*Cebus capucinus*). International Journal of Primatology 17:309-330

Plavcan JM, van Schaik CP (1992) Intrasexual competition and canine dimorphism in anthropoid primates. American Journal of Physical Anthropology 87:461-477

R Development Core Team (2010) R: A language and environment for statistical computing. In: R Foundation for Statistical Computing, Vienna, Austria, URL http://www.R-project.org/.

Ramírez-Llorens P, Di Bitetti MS, Baldovino MC, Janson CH (2008) Infanticide in black capuchins (*Cebus apella nigritus*) in Iguazú National Park, Argentina. American Journal of Primatology 70:473-484

Rettig NL (1978) Breeding behavior of the harpy eagle (*Harpia harpyja*). Auk 95:629-643

Scarry CJ, Tujague MP (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 74:804-810

Silk JB (2002) Practice random acts of aggression and senseless acts of intimidation: The logic of status contests in social groups. Evolutionary Anthropology 11:221-225

Smith RJ, Jungers WL (1997) Body mass in comparative primatology. Journal of Human Evolution 32:523-559

Stamps JA, Krishnan VV (2001) How territorial animals compete for divisible space: a learning-based model with unequal competitors. American Naturalist 157:154-169

Steenbeek R (1999) Tenure related changes in wild Thomas's langurs. I: Between-group interactions. Behaviour 136:595-625

Terborgh J (1983) Five New World Primates: A Study in Comparative Ecology. Princeton University Press, Princeton, New Jersey

Tiddi B, Aureli F, di Sorrentino EP, Janson CH, Schino G (2011) Grooming for tolerance? Two mechanisms of exchange in wild tufted capuchin monkeys. Behavioral Ecology 22:663-669

Trivers RL (1971) Evolution of reciprocal altruism. Quarterly Review of Biology 46:35-57

Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual Selection and the Descent of Man. Aldine, Chicago, pp 136-179

Vargas JdJ, Whitacre D, Mosquera R, Albuquerque J, Piana R, Thiollay J-M, Márquez C, Sánchez JE, Lezama-López M, Midence S, Matola S, Aguilar S, Rettig N, Sanaiotti T (2006) Estado y distribución actual del águila arpía (*Harpia harpyja*) en Centro y Sur América. Ornitologia Neotropical 17:39-55

Wich SA, Assink PR, Becher F, Sterck EHM (2002a) Playbacks of loud calls to wild thomas langurs (Primates; *Presbytis thomasi*): The effect of familiarity. Behaviour 139:79-87

Wich SA, Assink PR, Becher F, Sterck EHM (2002b) Playbacks of loud calls to wild Thomas langurs (Primates; *Presbytis thomasi*): The effect of location. Behaviour 139:65-78

Wiley RH, Rabenold KN (1984) The evolution of cooperative breeding by delayed reciprocity and queuing for favorable social positions. Evolution 38:609-621

Williams JM, Oehlert GW, Carlis JV, Pusey AE (2004) Why do male chimpanzees defend a group range? Animal Behaviour 68:523-532

Wilson ML, Hauser MD, Wrangham RW (2001) Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? Animal Behaviour 61:1203-1216

Young AJ, Carlson AA, Clutton-Brock T (2005) Trade-offs between extraterritorial prospecting and helping in a cooperative mammal. Animal Behaviour 70:829-837

Young AJ, Spong G, Clutton-Brock T (2007) Subordinate male meerkats prospect for extra-group paternity: alternative reproductive tactics in a cooperative mammal. Proceedings of the Royal Society B-Biological Sciences 274:1603-1609

Table 5.1 Compositions of study groups.

Group	Adult Males	Adult Females	Total
Gundolf	1	4-5	15-18
Macuco	4-5	8-9	26-32
Rita	2	4	11-13
Silver	4	6	22

Table 5.2 Best fit model of individual participation (N = 358) after controlling for individual identity, encounter ID, and group dyad.

	Estimate	**SE**	**t-value**	***P***
(Intercept)	-0.59	0.80	-0.74	0.457
Distance [m]	0.00	0.00	1.73	0.084
Male asymmetry	1.42	0.44	3.23	0.001
Sex (male)	0.94	0.97	0.97	0.332
Age (juvenile)	-1.85	0.57	-3.24	0.001
Distance*Male asymmetry	-0.001	0.001	-1.75	0.079
Distance*Sex (male)	0.002	0.001	1.04	0.299
Male asymmetry*Sex (male)	-1.53	0.53	-2.91	0.004
Distance*Male asymmetry*Sex (male)	0.002	0.001	2.49	0.013

Table 5.3 Best fit model of adult female participation (N = 124) after controlling for individual identity, encounter ID, and group dyad.

	Estimate	**SE**	**t-value**	***p***
(Intercept)	-1.87	1.26	-1.48	0.138
Gestating	-0.42	0.68	-0.62	0.536
Infant age [weeks]	0.004	0.003	1.43	0.154
Distance [m]	0.002	0.001	1.90	0.058
Male asymmetry	0.55	0.21	2.61	0.009
Number of maternal relatives	0.04	0.10	0.34	0.733

Table 5.4 Best fit model of individual flight (N = 344) after controlling for individual identity, encounter ID, and group dyad.

		Estimate	**SE**	**t-value**	***p***
(Intercept)		0.59	1.06	0.55	0.580
Distance [m]		0.00	0.00	-1.78	0.075
Male asymmetry		-1.95	0.53	-3.70	<0.001
Sex (male)		-0.04	0.73	-0.05	0.960
Dominance	**Mid-ranked**	-1.80	0.76	-2.37	0.018
	Low-ranked	-1.32	0.84	-1.57	0.117
Distance*Male asymmetry		0.00	0.00	0.78	0.438

Table 5.5 Best fit model of adult female flight (N = 127) after controlling for individual identity, encounter ID, and group dyad.

		Estimate	**SE**	**t-value**	***p***
(Intercept)		11.26	5.24	2.15	0.032
Number of maternal relatives		-0.25	0.41	-0.62	0.536
Dominance	Mid-ranked	-3.22	3.70	-0.87	0.383
	Low-ranked	-3.49	3.16	-1.11	0.269
Infant age [weeks]		0.01	0.02	0.77	0.440
Distance [m]		-0.02	0.01	-2.71	0.007
Male asymmetry		-3.35	1.09	-3.09	0.002

Table 5.6 Best fit model of adult male leadership (N = 142) after controlling for individual identity, encounter ID, and group dyad.

	Estimate	**SE**	**t-value**	***p***
(Intercept)	-0.19	0.74	-0.26	0.794
Distance [m]	0.001	0.001	1.28	0.201
Male asymmetry	0.46	0.17	2.66	0.008
Juvenile	-2.34	0.72	-3.25	0.001

Table 5.7 Best fit model of adult male persistence (N = 102) after other individuals have returned to normal activities (e.g., foraging, social, etc.) after controlling for individual identity, encounter ID, and group dyad.

	Estimate	**SE**	**t-value**	***p***
(Intercept)	0.13	0.96	0.14	0.892
Distance [m]	0.000	0.001	-0.30	0.767
Male asymmetry	0.48	0.21	2.31	0.021
Rank (subordinate)	1.42	0.57	2.49	0.013

Table 5.8 Best fit model of adult female leadership (N = 74) after controlling for individual identity, encounter ID, and group dyad.

	Estimate	**SE**	**t-value**	***p***
(Intercept)	-16.08	5.78	-2.78	0.005
Distance [m]	0.01	0.00	2.81	0.005
Gestating	1.01	0.50	2.00	0.045
Number of maternal relatives	0.39	0.58	0.69	0.494
Infant age [weeks]	0.02	0.01	1.56	0.118
Male asymmetry	-1.49	0.61	-2.42	0.015
Infant age*Male asymmetry	0.01	0.00	2.29	0.022

Figure 5.1 Predicted probability of individual participation in intergroup encounters as a function of distance from the center of the home range. Encounters in which the focal group is relatively larger are shown in blue, while the reverse is shown in red. The dashed line indicates encounters between evenly matched groups. Line weights and values shown in the left margin indicate the degree of asymmetry.

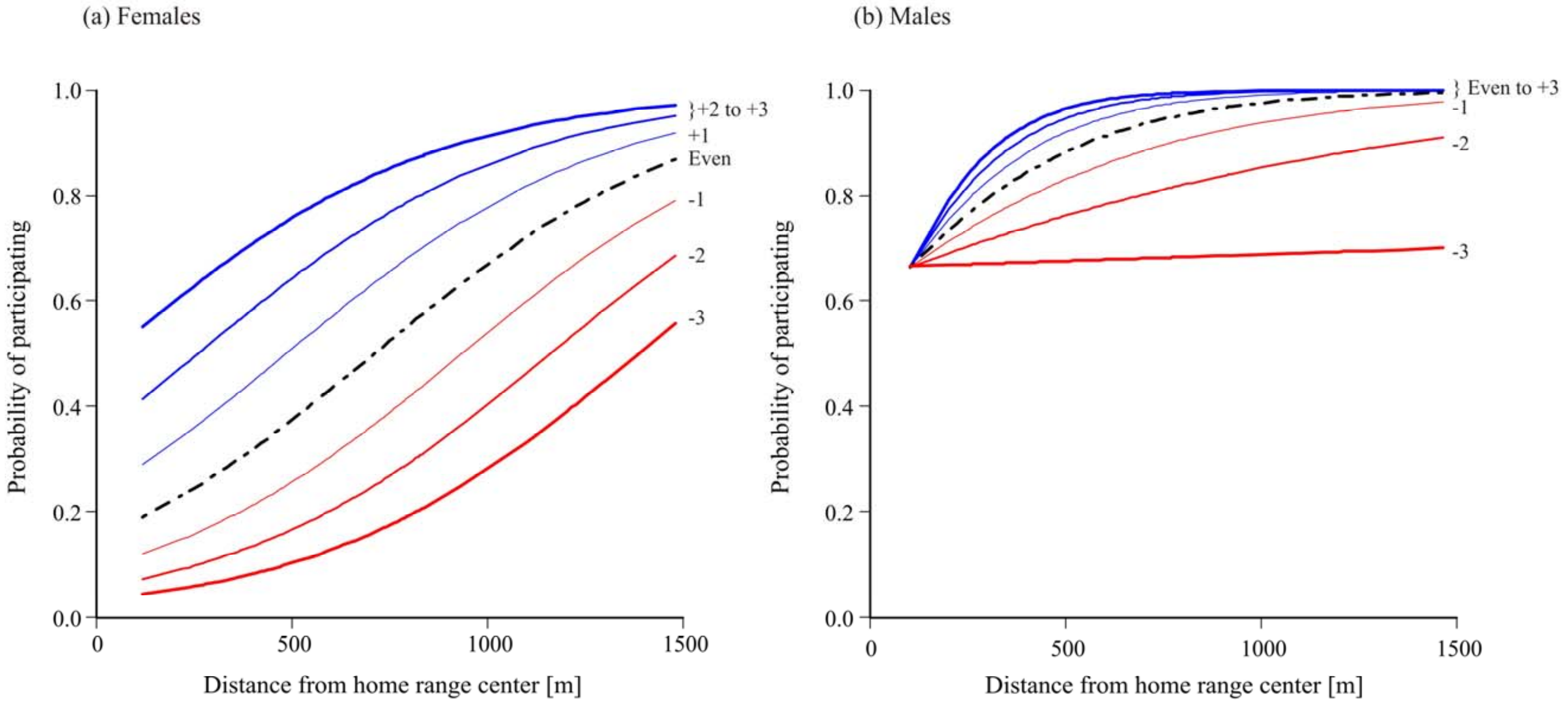


Figure 5.2 Predicted probability that an individual flees from an intergroup encounters as a function of the asymmetry in male group size and individual dominance rank.

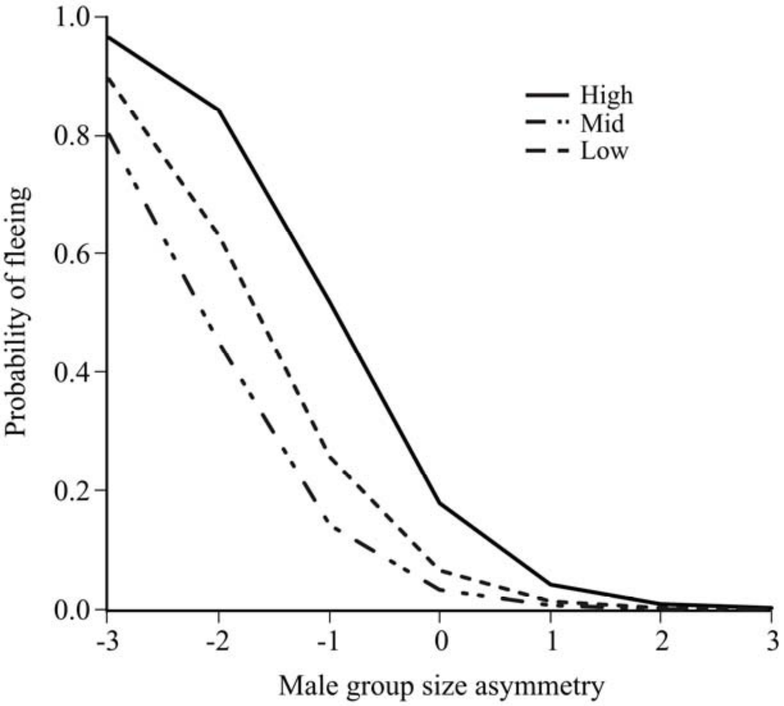
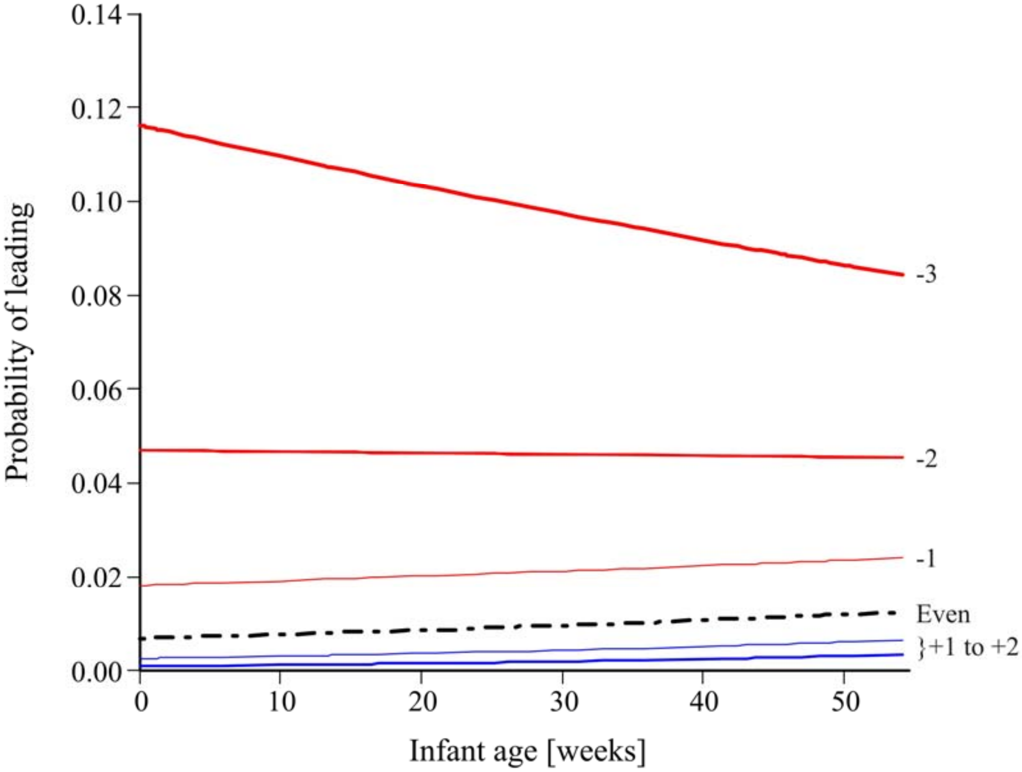


Figure 5.3 Predicted probability that an adult male persists in aggressive behavior following an intergroup encounter after other individuals have resumed pre-contact behavior as a function of the asymmetry in male group size and individual dominance rank.

Figure 5.4 Predicted probability that an adult female will lead an intergroup encounter as a function of infant age. Encounters in which the focal group is relatively larger are shown in blue, while the reverse is shown in red. The dashed line indicates encounters between evenly matched groups. Line weights and values shown in the left margin indicate the degree of asymmetry.



Chapter 6:
Intergroup aggression in Argentine tufted capuchin monkeys: Discussion and future directions

Summary of the dissertation

The goals of this dissertation were to: 1) identify the function of aggressive behavior during intergroup encounters among tufted capuchin monkeys (*Cebus apella* [*Sapajus*] *nigritus*), 2) examine the factors that influence the outcome of intergroup encounters, 3) assess the potential strength of between-group contest competition in terms of resource use and gain, and 4) examine individual strategies of participation and defection during aggressive encounters to identify the factors influencing individual assessment of the costs and benefits of collective action. Because between-group competition over mates and resources is a pivotal factor in theoretical models of the evolution of social behavior (Emlen & Oring 1977; Wrangham 1980; Rubenstein 1986; van Schaik 1989, 1996; Isbell 1991; Sterck et al. 1997), studies of interactions between groups have focused on identifying the function of intergroup aggression. Yet in the absence of direct measures of reproductive success, most studies have relied on proxy measures with limited relevance to the factors of interest (reviewed in Harris 2007). In recent years, studies examining the correlates of escalated aggression during intergroup encounters have suggested that due to a focus on sex differences in participation and the context of encounters the importance of between-group contest competition has been underestimated among non-human primates (Fashing 2001; Harris 2006; Crofoot 2007). This study uses a unique experimental design to disentangle the role of resource defense and mate defense in promoting aggression between neighboring groups.

Similarly, although well-known from studies of lions (McComb et al. 1993; McComb et al. 1994; Heinsohn and Packer 1995), individual variation in participation and the occurrence of contingent cooperation (e.g., Alouatta pigra: Kitchen 2004; Kitchen et al. 2004b; Kitchen 2006) are virtually undocumented among primates, especially how patterns of free-riding affect cooperative defense and the long-term benefits to individuals.

Functions of intergroup aggression

The current study provides strong evidence that resource defense is the main function of intergroup aggression among Argentine tufted capuchins (Chapter 2), adding support to the growing body of evidence suggesting that the relative importance of between-group contest competition among non-human primates has been underestimated by focusing on sex-based differences in patterns of participation (Fashing 2001; Harris 2006; Crofoot 2007). When in proximity to high-quality food resources, all group members, regardless of sex or dominance, demonstrated an interest in the presence of neighboring groups, increasing their travel speed and approaching the speaker. In the absence of the provisioning platforms, only males were observed to approach the speaker and these approaches lacked the urgency observed when food was present. Females occasionally responded to the playback with whistle vocalizations or by becoming vigilant, but they never approached the speaker during periods of natural resource availability.

Although male aggression during intergroup encounters is frequently assumed to reflect direct mate defense (Emlen and Oring 1977; Cheney 1987), male responses to simulated intergroup encounters showed no effect attributable to the presence of a receptive female in the focal group (Chapters 2 and 4). In other species, male tactics to increase reproductive success through intergroup encounters may include engaging in extragroup copulations (Kinnaird 1992; Palombit 1994; Cowlishaw 1995; Reichard 1995; Reichard and Sommer 1997; Agoramoorthy and Hsu 2000; Kitchen et al. 2004a; Young et al. 2007), taking over reproductive positions in neighboring social groups (Grinnell et al. 1995; Steenbeek 1999; Wich et al. 2002a; Kitchen 2004), or influencing female transfer decisions (for species with female dispersal: e.g., Watts 1989; Sicotte 1993; Steenbeek 1999). None of these behaviors were observed during intergroup encounters within the capuchin monkey population at Iguazú (C.J. Scarry, unpublished data). Although male transfers in the context of intergroup encounters have been observed, takeovers by extragroup males are extremely rare. Instead, immigrants are generally smaller individuals that enter low in the male hierarchy, waiting several years before being able to successfully challenge the alpha male (Janson 2012). Additionally, no extragroup copulations have been observed. Thus, the absence of an effect of female sexual behavior on male aggressive response is consistent with the absence of extragroup copulations and takeovers during naturally-occurring intergroup encounters within the population.

In contrast to previous studies of primate intergroup aggression, I did not specifically address the possibility that infant defense or infanticidal attacks drive aggression towards neighboring groups (Wich et al. 2002a; Korstjens et al. 2005; Harris 2006; Wich and Sterck 2007; Harris 2010). The co-occurrence of female philopatry and limited mating access for newly immigrated males is inconsistent with direct benefits to between-group infanticidal attacks by males (Broom et al. 2004). In keeping with this assumption, while multiple infanticides by resident individuals have been documented following changes in the male dominance hierarchy (Ramírez-Llorens et al. 2008; B. Tiddi and C.J. Scarry, unpublished data), no evidence for infanticide by extragroup males has been observed in this population. Moreover, females will assist males in directing coalitionary threats at adult males in neighboring groups within days of giving birth (Chapter 5), suggesting that the perceived risk of infanticide and redirected aggression during intergroup aggression is low. The greatest risk appears to be of the infant becoming separated from the group during the rapid chase that characterizes intergroup encounters. Occasionally, infants have been observed in neighboring groups immediately following an intergroup encounter (B. Tiddi, personal communication); however, all known instances were resolved with the infant being successfully reunited with its own group, without visible injuries (C. Scarry, personal observation). If infanticide were an important function of aggression between groups, the safe return of vulnerable infants from a neighboring group to its natal group should instead be rare to nonexistent.

The effects of male hired guns on between-group contest competition

Among species in which both sexes participate in intergroup aggression, males and females may differ in their relative contribution to the collective effort. Because male and female group sizes are frequently correlated (e.g., primates: Mitani et al. 1996), these two measures of fighting ability can be difficult to disentangle (e.g., Crofoot et al. 2008). In the current study, however, I was able to determine that while both sexes participate during aggressive intergroup encounters (Chapter 5), the competitive strength of groups is determined by relative male group size (Chapter 3; Scarry and Tujague 2012). In many species, groups may value the center of their home range more than the periphery, creating location-dependent differences in the motivation of competitors that allow small groups to win near the center of their home range (cf. Giraldeau and Ydenberg 1987; Crofoot et al. 2008). Among tufted capuchin monkeys, however, similar asymmetries in competitors' assessments of the value of resource ownership are insufficient to allow small groups to win escalated conflicts against their larger neighbors. Instead, the benefits of large male group size appear to swamp the effects of a home-field advantage.

That male group size determines the outcome of intergroup aggression over food resources in the absence of female dispersal suggests that male tufted capuchins serve as "hired guns" (Rubenstein 1986), contributing to the defense of the resources critical for reducing female interbirth intervals and promoting infant survivorship (*Colobus guereza*: Fashing 2001; Harris 2006). Immediate energetic returns drive aggressive responses by group members (Chapter 4), rather than the mere presence of a neighboring group within the home range or core area. Yet intergroup dominance also effects long-term resource availability for group members (Chapter 3). While most groups maintain exclusive access to a portion of their home range, large male group size facilitates the maintenance of a larger area of exclusive access, whereas smaller groups exhibit a higher degree of home range overlap with neighboring groups. By excluding other groups from the core area, aggressively dominant groups share fewer of the food resources available. Thus, although no differences exist between groups in the quality of core areas – as assessed by the density of food species (viz. Cheney and Seyfarth 1987; Harris 2006), the costs of between-group scramble competition may be reduced within the core areas of dominant groups. The presence and participation of additional males increases the absolute quantity of food resources available per individual. As a result, resident females appear to be able to compensate for the increased costs of within-group scramble competition in larger groups, and no group size effect is apparent in *per capita* reproductive rates (Janson et al. 2012).

Male cooperation

Increasing group size is frequently assumed to enhance the resource holding potential of a group (Wrangham 1980; Isbell 1991). Yet in many primates large male group size does not enhance competitive ability, either because the dominant male is the sole participant in intergroup aggression (e.g., *Cebus apella*: Janson 1986) or because intragroup mate guarding generates a collective action problem (e.g., *Colobus guereza*: Harris 2010). That each additional male enhances the competitive ability of the group (cf. lions, *Panthera leo*: Grinnell et al. 1995) indicates that tufted capuchin monkeys are able to overcome the potential collective action problem while engaging in intergroup aggression (Nunn 2000; Nunn and Lewis 2001). In contrast to several previously studied species (Harris 2010; Crofoot and Gilby 2012), although free-riding may occur, the collective strength of groups with more males is not disproportionately reduced by defectors (Chapter 3).

Subordinate males assist dominant males and females in aggressively defending access to food resources (Chapters 2, 4 and 5). Rather than lagging behind during intergroup encounters, participating only from low risk positions (Heinsohn and Packer 1995; Kitchen et al. 2004b), subordinate males occupy positions at the leading edge of the group and are typically the last individuals to resume pre-contact behavior (Chapter 5). Although fights during intergroup encounters are extremely rare (Scarry and Tujague 2012), the risk of physical injury is augmented by the opportunity costs due to lost energy and feeding time (Peres 1989).

Similar collective action by males during intergroup aggression is well documented among non-human primates in the context of mate defense (see Cheney 1987; Nunn 2000). Extragroup males may increase the costs of scramble competition for fertilizations (Nunn 2000; Berghanel et al. 2010) or expel current male residents (Pope 1990; Fedigan and Jack 2004; Port et al. 2010), thereby reducing mating access for male residents. The presence of a mutual enemy may promote aggression by both dominant and subordinate males even when reproduction is highly skewed.

Theory suggests that males should cooperate similarly in defense of group-controlled food resources (Wrangham 1980) when access to such resources can increase offspring survival or the frequency of mating opportunities (Rubenstein 1986). Empirical work, however, suggests that cooperation in this context is more difficult to maintain (but see Williams et al. 2004; Harris 2010; Crofoot and Gilby 2012), possibly due to the more indirect nature of benefits to male reproductive success accrued through access to food relative to additional mating opportunities (Trivers 1972). Future studies should examine mechanism(s) allowing tufted capuchin males at Iguazú to overcome the potential collective action problem, focusing specifically on the payoffs of participation for subordinate males.

Individual assessment

In a number of species, individuals assess the relative probability of winning an intergroup encounter prior to direct interactions, and refrain from engaging in escalated encounters when the probability of winning is low (Parker 1974; Maynard Smith and Parker 1976; Parker and Rubenstein 1981). Although tufted capuchin groups do not appear to universally avoid confrontations with stronger neighbors when the benefits of winning are high (Chapter 4), individual assessments of the profitability of participation demonstrate clear sensitivity to the asymmetry in competitive ability (Chapter 5). Further analyses are needed to determine whether individuals are using previous experience (Ydenberg et al. 1988; Getty 1989; Temeles 1994; Wich et al. 2002a; Wich and Sterck 2007; Rosell et al. 2008) or an assessment of the current competitive asymmetry (McComb et al. 1994; Grinnell et al. 1995; Wilson et al. 2001; Kitchen et al. 2004b; Furrer et al. 2011).

Although sex-based differences in participation are well known, in the current study female participation in intergroup encounters was common (Chapter 5). Yet in an earlier analysis, which included some of the same focal groups, Di Bitetti (2001) noted only limited participation by females. One potential explanation for this difference is that females among non-study groups were not fully-habituated at the time of the previous study, and would flee from the presence of researchers (M.S. Di Bitetti, personal communication). Increases in human presence at the site over the last decade, in conjunction with on-going research efforts over the last 15 years have increased tolerance of human presence, which may influence female willingness to participate in the already stressful encounters. This difference, however, raises the possibility that similar absences of female participation in other primate studies (see Cheney 1987) may reflect habituation effort.

In contrast to the center-edge effects known from previous studies of behavioral responses to intruders among birds (reviewed in Giraldeau and Ydenberg 1987) and primates (Wich et al. 2002b; Crofoot et al. 2008), wherein the probability of defection is increased among members of intruding groups relative to owners, among capuchins at Iguazú the probability of individual participation increases with distance from the home range center (Chapter 5). This difference may reflect the reduced individual investment needed to expel intruders (Di Bitetti 2001) or indicate that the mechanism underlying territory maintenance differs from previously studied species. Increased individaul participation among subordinate groups during encounters near the periphery may increase the opportunity costs of maintaining exclusive access to an area, permitting coexistent by unevenly matched competitors (cf. Stamps and Krishnan 2001; see below).

Capuchins at Iguazú in comparison with other capuchin species

In other populations, tufted capuchin monkeys are noted for both their strong within-group contest competition for food resources (Janson 1985; Janson 1988) and uni-male breeding system (Janson 1984; Janson 1998; Lynch Alfaro 2005). Similarly, at Iguazú, high reproductive success for alpha males has been inferred from their higher frequency of mating during the peri-ovulatory period, as indicated by female sexual behavior (Lynch Alfaro 2005). The high degree of participation by subordinate males and male-male cooperation during intergroup encounters, therefore, stands in stark contrast to Peruvian tufted capuchins (*Cebus apella* [*Sapajus*] *macrocephalus*), where the dominant male is solely responsible for intergroup aggression (Janson 1985, 1986). In this pattern, tufted capuchins at Iguazú are more similar to the non-tufted capuchins, *Cebus capucinus* (Perry 1996; Perry 1998) and *C. albifrons* (Janson 1986), with multiple males working together to defend access to food resources.

Among *C. albifrons*, in which a single male does not monopolize access to food resources, matings are equitably distributed among males, and all males participate in intergroup aggression (Defler 1982; Janson 1986). Although female preference for the dominant male is similarly reduced in *C. capucinus* (Izar et al. 2009; Muniz et al. 2010), the alpha male appears to monopolize mating opportunities and have relatively higher reproductive success (Jack and Fedigan 2006; Izar et al. 2009; Muniz et al. 2010). Yet despite occasional defections, dispersed collaboration appears common among males, including coalitionary threats directed towards extragroup males (Perry 1996). Given the high frequency of parallel dispersal among male white-faced capuchins of all ages (Jack and Fedigan 2004b; Jack and Fedigan 2004a), researchers initially suggested that non-breeding subordinate males engaged in intergroup aggression to support male kin and increase their inclusive fitness (Fedigan and Jack 2004), similar to the pattern observed in red howlers (Pope 1990). However, Muniz and colleagues (2010) found that at Lomas Barbudal most alpha males are not closely related to their coalitionary partners. Rather, the risk of aggressive takeovers by numerically stronger groups of outside males (Rose and Fedigan 1995; Fedigan and Jack 2004) and the low probability of successful entry into another group in the absence of support (Gros-Louis et al. 2003; Fedigan and Jack 2004; Jack and Fedigan 2004b), may result in mutual benefits of cooperation by adult males. When reproductive opportunities are absent for males not residing in bisexual groups, the limited mating access accorded to subordinate males to benefit, even in the face of high mating skew (Grinnell et al. 1995).

Unresolved questions for future investigation

Energetic consequences of intergroup dominance

While suggestive of a competitive regime with strong between-group contest competition (Chapter 3), further analyses are needed to determine whether energetic benefits accrued by subordinate individuals offset the costs of within-group competition, given the ability of dominant individuals to monopolize individual resources (Janson 1985; Janson 1988; Janson 1990; Di Bitetti and Janson 2001). Recent analysis of long-term demographic records from the Iguazú population found no evidence of a rank effect on female reproductive success (Janson et al. 2012), but the underlying mechanism is unclear. The willingness of subordinate individuals to contribute to group defense of resources – in the absence of either obvious coercion or punishment for defection – strongly suggests that they derive some form of benefits to reproductive success.

Maintenance of male cooperation

Although existing theoretical and empirical work suggests that cooperation by males in defense of food resources is difficult to maintain (van Schaik 1996; Nunn 2000; but see Williams et al. 2004; Harris 2010; Crofoot and Gilby 2012), many of the mechanisms proposed to explain dyadic cooperation can be extended to cooperative territorial defense involving larger groups of males, including reciprocal altruism (Trivers 1971) or private incentives (Nunn 2000), kin selection (Hamilton 1964), and punishment or coercion (Clutton-Brock and Parker 1995). At present, the role of these various mechanisms in allowing male tufted capuchin monkeys to overcome the potential collective action problem is not clear.

In contrast to the pattern observed at Iguazú, among Peruvian tufted capuchin monkeys (*Cebus apella* [*Sapajus*] *macrocephalus*) subordinate males do not commonly participate in aggressive intergroup encounters (Janson 1986). Instead, because the dominant male receives the majority of the benefits (e.g., increased mating access: Janson 1984; increased access to contestable food resources: Janson 1985; Janson 1988), he contributes proportionally more to the defensive effort (Nunn 2000; Nunn and Lewis 2001). Within this population, however, competition over resources within groups is stronger than between groups (Janson 1985; Janson 1988). Given the increased pressure from neighboring groups at Iguazú, however, dominant males may benefit from conceding a fraction of their reproductive opportunities in exchange for subordinates' cooperation (Frank 1996; Ruxton and van der Meer 1997), rather than ceding access to the core area and increasing within-group competition for resources. If both dominants and subordinates perceive themselves to have a reproductive investment in offspring that may be born in their group, they may cooperate during intergroup aggression over food resources. Although coalitionary partners trade in different currencies – participation in intergroup aggression by subordinate males is provided in exchange for reproductive access granted by the dominant male (cf. concessions model of reproductive skew: Vehrencamp 1983a, 1983b; Keller and Reeve 1994; Clutton-Brock 1998; but see Port and Kappeler, 2010 for a critique of the applicability of class skew models to non-human primates) – the reciprocal benefits of this transaction could be enough to maintain cooperation (Trivers 1971).

While classic models of reproductive skew do not consider the potential for female mate selection (but see Cant and Reeve 2002; Williams 2004), female tufted capuchin monkeys actively solicit copulations from subordinate males (Janson 1984). The existence of intersexual conflict raises the possibility that resident females – and not the dominant male – offer individual males private incentives to promote their participation in group resource defense (Cant and Reeve 2002). Moreover, if females control the distribution of paternity within the group, males may use aggressive behavior during encounters to advertise quality and influence female mate choice (cf. costly signaling theory: Zahavi 1975). Disentangling the role of private incentives offered by resident females versus the dominant male will require both behavioral indicators of mating conflict and genetic measures of reproductive skew. To date comprehensive genetic analyses of paternity are unavailable (but see Escobar-Paramo 1999); nevertheless paternity assignments determined through behavioral records of copulations during the conceptive ovulation suggest that the dominant male monopolizes the majority of matings (Janson 1998; B. Tiddi, pers. comm.).

Furthermore, because tufted capuchin monkeys at Iguazú are seasonal breeders (Di Bitetti and Janson 2000), copulations received in exchange for participation will not have the potential for conception during approximately seven months of the year; rather, the probability of future mating opportunities may be increased by absorbing the immediate costs of intergroup aggression. Due to the delayed nature of reciprocity, however, temporal discounting may cause males to undervalue the eventual repayment (Kagel et al. 1986). Instead, short-term reciprocal benefits such as increased tolerance at contested food resources and affiliative contact (e.g., grooming) may be more important in promoting male participation in intergroup aggression. These affiliative interactions may provide more direct benefits through improved physical condition and reduced physiological consequences of stress (see Sapolsky 2005), which may facilitate eventual rank acquisition and increased lifetime reproductive success among males.

Resident females support the dominant male in male intragroup agonistic interactions, which helps to stabilize the male dominance hierarchy and prolongs male tenures (Janson et al. 2012). These long dominant male tenures (Janson et al. 2012) coupled with high mating skew (Janson 1998) create the potential for cooperation to be promoted due to reproductive queueing and delayed reciprocity (Wiley and Rabenold 1984; Kokko and Johnstone 1999). Because extragroup mating opportunities are virtually absent (C.J. Scarry, unpublished data), subordinate males experience delays in their prime reproductive period, until they are able to attain alpha status (cf. meerkats, *Suricata suricatta*: Clutton-Brock et al. 2001; spotted hyena, *Crocuta crocuta*: East and Hofer 2001). The costs to future reproductive success incurred through participation in intergroup aggression may be low relative to the costs of potentially inheriting a home range with increased overlap with neighboring groups.

Alternatively, by cooperating primarily with close kin, males might accrue sufficient benefits through inclusive fitness to offset the direct costs involved (Hamilton 1964) even if reproductive access among males is uneven (Pope 1990; Packer et al. 1991). While inclusive fitness benefits of cooperation are discussed primarily for members of the philopatric sex because interactions with kin are believed to be more feasible (but see Lukas et al. 2005), co-residence with kin can also occur through cohort dispersal (e.g., *Cebus capucinus*: Jack and Fedigan 2004a) or preferential dispersal into groups with kin (e.g., *Chlorocebus aethiops*: Cheney and Seyfarth 1983). At Iguazú, there is no evidence of cohort dispersal (Janson et al. 2012), but recent anecdotal evidence of preferential dispersal to groups with kin (C.J. Scarry, unpublished data) raises the possibility that immigrant males may be closely related. The low samples size available to demonstrate biased dispersal by males, however, means that the relative impact of this behavior for the genetic structuring of the population is currently unclear but could be assess given a genetic sampling of the broader population.

Finally, it is possible that subordinate males receive only minimal benefits from cooperative participation in group defense. Instead, cooperation might be maintained through punishment or coercion of defectors (Boyd and Richerson 1992; Clutton-Brock and Parker 1995). In captivity, tufted capuchin monkeys exhibit sensitivity to inequity when performing cooperative tasks (e.g., Brosnan and de Waal 2003). Given a history of unequal division of rewards, individuals may refrain from cooperating even when doing so would constitute a net gain to the actor (i.e., spiteful behavior: Brosnan et al. 2006; Takimoto and Fujita 2011), especially as individual investment in the cooperative effort increases (van Wolkenten et al. 2007). If individuals perceive that a failure to contribute to the collective benefit will result in either physical attack (Mulder and Langmore 1993; Monnin et al. 2002) or expulsion from a social group (Wong et al. 2007; Bruintjes and Taborsky 2008; Cant et al. 2010), the risk of punishment may outweigh the relative costs of cooperation. Although direct punishment of selfish individuals has not been observed in other contexts (e.g., failure to give food calls: Di Bitetti 2005), there may be more incentive to punish individuals that defect during intergroup aggression because the costs to individuals are higher.

Maintenance of home ranges

Among capuchin monkeys at Iguazú, small groups are not outcompeted due to home range expansion by larger coalitions. Instead, long-term range stability occurs across a range of group sizes (Di Bitetti 2001). Yet the absence of a significant center-edge effect in either individual participation (Chapter 5) or the outcome of intergroup aggression (Chapter 3) belies the suggestion that stable coexistence is promoted through location-dependent resource valuation (Crofoot and Gilby 2012).

Critically, unlike mates or nesting sites, space is a divisible resource (Maynard Smith 1982), so a winner-take-all payoff structure is inappropriate (Maynard Smith and Parker 1976; Stamps and Krishnan 2001); wide areas of home range overlap can occur between neighboring groups (Di Bitetti 2001; Chapter 3). Instead, the dual nature of the negative stimulus provided by intergroup encounters – both winning and losing groups incur costs due to the long distance chase involved (Di Bitetti 2001) – may reduce the attractiveness of a location for both parties. Previous attempts to explain underutilization of areas where home ranges overlap by incorporating symmetry between groups in participant costs have met with limited success (risk aversion model: Wrangham et al. 2007). These analyses, however, focused primarily on high-cost aggression that leads to injury and/or death of participants, rather than less aggressive interactions, and paid little attention to the energetic costs involved in interactions.

Despite the absence of preferential control of areas of high resource density, dominant groups are able to maintain exclusive access to a larger area (Chapter 3), potentially decreasing the costs of between-group scramble competition (Janson and van Schaik 1988). Due to the more intermediate costs of engagement (i.e., long distance chases *vs.* lethal attacks), large groups may tolerate subordinate intruders rather than exerting the effort necessary to totally exclude them, and significant overlap should arise between neighbors. By repeatedly "nagging" at larger neighbors (e.g., initiating encounters and fleeing), subordinate groups increase the opportunity costs of maintaining exclusive access to an area. Rather than by winning encounters, through persistence in the face of repeated defeat, newly formed groups may be able to establish and maintain home ranges even when facing competitively stronger neighbors with concordant center-edge perception or a home-field advantage (Stamps and Krishnan 2001). In the absence of deliberate boundary patrols (Di Bitetti 2001), smaller subordinate groups can establish and maintain home ranges in the underutilized interstitial areas (Wrangham et al. 2007) between larger dominant groups.

References

Agoramoorthy G, Hsu MJ (2000) Extragroup copulation among wild red howler monkeys in Venezuela. Folia Primatologica 71:147-151

Berghanel A, Schulke O, Ostner J (2010) Coalition formation among Barbary macaque males: the influence of scramble competition. Animal Behaviour 80:675-682

Boyd R, Richerson PJ (1992) Punishment allows the evolution of cooperation (or anything else) in sizable groups. Ethology and Sociobiology 13:171-195

Broom M, Borries C, Koenig A (2004) Infanticide and infant defence by males - modelling the conditions in primate multi-male groups. Journal of Theoretical Biology 231:261-270

Brosnan SF, de Waal FBM (2003) Monkeys reject unequal pay. Nature 425:297-299

Brosnan SF, Freeman C, De Waal FBM (2006) Partner's behavior, not reward distribution, determines success in an unequal cooperative task in capuchin monkeys. American Journal of Primatology 68:713-724

Bruintjes R, Taborsky M (2008) Helpers in a cooperative breeder pay a high price to stay: effects of demand, helper size and sex. Animal Behaviour 75:1843-1850

Cant MA, Hodge SJ, Bell MBV, Gilchrist JS, Nichols HJ (2010) Reproductive control via eviction (but not the threat of eviction) in banded mongooses. Proceedings of the Royal Society B-Biological Sciences 277:2219-2226

Cant MA, Reeve HK (2002) Female control of the distribution of paternity in cooperative breeders. American Naturalist 160:602-611

Cheney D, Seyfarth R (1983) Nonrandom dispersal in free-ranging vervet monkeys: Social and genetic consequences. American Naturalist 122:392-412

Cheney DL (1987) Interactions and relationships between groups. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate Societies. University of Chicago Press, Chicago, pp 267-281

Cheney DL, Seyfarth RM (1987) The influence of intergroup competition on the survival and reproduction of female vervet monkeys. Behavioral Ecology and Sociobiology 21:375-386

Clutton-Brock TH (1998) Reproductive skew, concessions and limited control. Trends in Ecology & Evolution 13:288-292

Clutton-Brock TH, Parker GA (1995) Punishment in animal societies. Nature 373:209-216

Cowlishaw G (1995) Behavioural patterns in baboon group encounters: the role of resource competition and male reproductive strategies. Behaviour 132:75-86

Crofoot MC (2007) Mating and feeding competition in white-faced capuchins (*Cebus capucinus*): the importance of short- and long-term strategies. Behaviour 144:1473-1495

Crofoot MC, Gilby IC (2012) Cheating monkeys undermine group strength in enemy territory. Proceedings of the National Academy of Sciences of the United States of America 109:501-505

Crofoot MC, Gilby IC, Wikelski MC, Kays RW (2008) Interaction location outweighs the competitive advantage of numerical superiority in *Cebus capucinus* intergroup contests. Proceedings of the National Academy of Sciences of the United States of America 105:577-581

Defler T (1982) A comparison of intergroup behavior in *Cebus albifrons* and *C. apella*. Primates 23:385-392

Di Bitetti MS (2001) Home-range use by the tufted capuchin monkey (*Cebus apella nigritus*) in a subtropical rainforest of Argentina. Journal of Zoology 253:33-45

Di Bitetti MS (2005) Food-associated calls and audience effects in tufted capuchin monkeys, Cebus apella nigritus. Animal Behaviour 69:911-919

Di Bitetti MS, Janson CH (2000) When will the stork arrive? patterns of birth seasonality in Neotropical primates. American Journal of Primatology 50:109-130

Di Bitetti MS, Janson CH (2001) Social foraging and the finder's share in capuchin monkeys, *Cebus apella*. Animal Behaviour 62:47-56

Emlen ST, Oring LW (1977) Ecology, sexual selection, and evolution of mating systems. Science 197:215-223

Escobar-Paramo P (1999) Inbreeding avoidance and the evolution of male mating strategies. Ph.D. thesis: State University of New York at Stony Brook.

Fashing PJ (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 50:219-230

Fedigan LM, Jack KM (2004) The demographic and reproductive context of male replacements in *Cebus capucinus*. Behaviour 141:755-775

Frank SA (1996) Policing and group cohesion when resources vary. Animal Behaviour 52:1163-1169

Furrer RD, Kyabulima S, Willems EP, Cant MA, Manser MB (2011) Location and group size influence decisions in simulated intergroup encounters in banded mongooses. Behavioral Ecology 22:493-500

Getty T (1989) Are dear enemies in a war of attrition? Animal Behaviour 37:337-339

Giraldeau LA, Ydenberg R (1987) The center-edge effect: the result of a war of attrition between territorial contestants? Auk 104:535-538

Grinnell J, Packer C, Pusey AE (1995) Cooperation in male lions - kinship, reciprocity or mutualism. Animal Behaviour 49:95-105

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

Hamilton WD (1964) Genetical evolution of social behaviour I. Journal of Theoretical Biology 7:1-16

Harris TR (2005) Roaring, intergroup aggression, and feeding competition in black and white colobus monkeys (*Colobus guereza*) at Kanyawara, Kibale National Park, Uganda. In: Anthropology. Yale University, New Have, CT, pp 253

Harris TR (2006) Between-group contest competition for food in a highly folivorous population of black and white colobus monkeys (*Colobus guereza*). Behavioral Ecology and Sociobiology 61:317-329

Harris TR (2007) Testing mate, resource and infant defence functions of intergroup aggression in non-human primates: issues and methodology. Behaviour 144:1521-1535

Harris TR (2010) Multiple resource values and fighting ability measures influence intergroup conflict in guerezas (*Colobus guereza*). Animal Behaviour 79:89-98

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

Isbell LA (1991) Contest and scramble competition: patterns of female aggression and ranging behavior among primates. Behavioral Ecology 2:143-155

Izar P, Stone A, Carnegie S, Nakai E (2009) Sexual selection, female choice and mating systems. In: Garber P, Estrada A, Bicca-Marques J, Heymann E, Strier K (eds) South American Primates: Comparative Perspectives in the Study of Behavior, Ecology and Conservation. Springer, New York, pp 157-189

Jack K, Fedigan L (2004a) Male dispersal patterns in white-faced capuchins, *Cebus capucinus*. Part 1: patterns and causes of natal emigration. Animal Behaviour 67:761-769

Jack K, Fedigan L (2004b) Male dispersal patterns in white-faced capuchins, *Cebus capucinus*. Part 2: patterns and causes of secondary dispersal. Animal Behaviour 67:771-782

Jack K, Fedigan L (2006) Why be alpha male? Dominance and reproductive success in wild white-faced capuchins (*Cebus capucinus*). In: Estrada A, Garber P, Pavelka M, Luecke L (eds) New Perspectives in the Study of Mesoamerican Primates: Distribution, Ecology, Behavior and Conservation. Springer, New York, pp 367-386

Janson CH (1984) Female choice and mating system of the brown capuchin monkey *Cebus apella* (Primates: Cebidae). Zeitschrift Fuer Tierpsychologie 65:177-200

Janson CH (1985) Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). Behavioral Ecology and Sociobiology 18:125-138

Janson CH (1986) The mating system as a determinant of social evolution in capuchin monkeys (*Cebus*). In: Else JG, Lee PC (eds) Primate Ecology and Conservation. Cambridge University Press, New York, pp 169-179

Janson CH (1988) Food competition in brown capuchin monkeys (*Cebus apella*): Quantitative effects of group size and tree productivity. Behaviour 105:53-76

Janson CH (1990) Ecological consequences of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. Animal Behaviour 40:922-934

Janson CH (1998) Capuchin counterpoint. In: Ciochon RL, Nisbett RA (eds) The Primate Anthology: Essays on Primate Behavior, Ecology and Conservation from Natural History. Prentice Hall, Upper Saddle River, NJ

Janson CH (2012) Reconciling rigor and range: observations, experiments, and quasi-experiments in field primatology. International Journal of Primatology:1-22

Janson CH, Baldovino MC, Di Bitetti MS (2012) The group life cycle and demography of brown capuchin monkeys (*Cebus [apella] nigritus*) in Iguazú National Park, Argentina. In: Kappeler PM, Watts DP (eds) Long-Term Field Studies of Primates. Springer, Heidelberg, pp 185-212

Janson CH, van Schaik CP (1988) Recognizing the many faces of primate food competition: Methods. Behaviour 105:165-186

Kagel JH, Green L, Caraco T (1986) When foragers discount the future: constraint or adaptation? Animal Behaviour 34:271-283

Keller L, Reeve HK (1994) Partitioning of reproduction in animal societies. Trends in Ecology & Evolution 9:98-102

Kinnaird MF (1992) Variable resource defense by the Tana River crested mangabey. Behavioral Ecology and Sociobiology 31:115-122

Kitchen DM (2004) Alpha male black howler monkey responses to loud calls: effect of numeric odds, male companion behaviour and reproductive investment. Animal Behaviour 67:125-139

Kitchen DM (2006) Experimental test of female black howler monkey (*Alouatta pigra*) responses to loud calls from potentially infanticidal males: Effects of numeric odds, vulnerable offspring, and companion behavior. American Journal of Physical Anthropology 131:73-83

Kitchen DM, Cheney DL, Seyfarth RM (2004a) Factors mediating inter-group encounters in savannah baboons (*Papio cynocephalus ursinus*). Behaviour 141:197-218

Kitchen DM, Horwich RH, James RA (2004b) Subordinate male black howler monkey (*Alouatta pigra*) responses to loud calls: Experimental evidence for the effects of intra-group male relationships and age. Behaviour 141:703-723

Korstjens AH, Nijssen EC, Noe R (2005) Intergroup relationships in western black-and-white colobus, *Colobus polykomos polykomos*. International Journal of Primatology 26:1267-1289

Lukas D, Reynolds V, Boesch C, Vigilant L (2005) To what extent does living in a group mean living with kin? Molecular Ecology 14:2181-2196

Lynch Alfaro J (2005) Male mating strategies and reproductive constraints in a group of wild tufted capuchin monkeys (*Cebus apella nigritus*). American Journal of Primatology 67:313-328

Maynard Smith J (1982) Evolution and the Theory of Games. Cambridge University Press, Cambridge

Maynard Smith J, Parker GA (1976) Logic of asymmetric contests. Animal Behaviour 24:159-175

McComb K, Packer C, Pusey A (1994) Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. Animal Behaviour 47:379-387

McComb K, Pusey A, Packer C, Grinnell J (1993) Female lions can identify potentially infanticidal males from their roars. Proceedings of the Royal Society of London Series B-Biological Sciences 252:59-64

Mitani JC, Gros-Louis J, Manson JH (1996) Number of males in primate groups: comparative tests of competing hypotheses. American Journal of Primatology 38:315-332

Monnin T, Ratnieks FLW, Jones GR, Beard R (2002) Pretender punishment induced by chemical signalling in a queenless ant. Nature 419:61-65

Mulder RA, Langmore NE (1993) Dominant males punish helpers for temporary defection in superb fairy-wrens. Animal Behaviour 45:830-833

Muniz L, Perry S, Manson JH, Gilkenson H, Gros-Louis J, Vigilant L (2010) Male dominance and reproductive success in wild white-faced capuchins (*Cebus capucinus*) at Lomas Barbudal, Costa Rica. American Journal of Primatology 72:1118-1130

Nunn CL (2000) Collective benefits, free-riders, and male extra-group conflict. In: Kappeler PM (ed) Primate Males: Causes and Consequences of Variation in Group Composition. Cambridge Univ Press, Cambridge, pp 192-204

Nunn CL, Lewis RJ (2001) Cooperation and collective action in animal behaviour. In: Noe R, Van Hooff JA, Hammerstein P (eds) Economics in Nature: Social Dilemmas, Mate Choice and Biological Markets. Cambridge Univ Press, Cambridge, pp 42-66

Packer C, Gilbert DA, Pusey AE, Obrien SJ (1991) A molecular genetic analysis of kinship and cooperation in African lions. Nature 351:562-565

Palombit R (1994) Extra-pair copulations in a monogamous ape. Animal Behaviour 47:721-723

Parker GA (1974) Assessment strategy and evolution of fighting behavior. Journal of Theoretical Biology 47:223-243

Parker GA, Rubenstein DI (1981) Role assessment, reserve strategy, and acquisition of information in asymmetric animal conflicts. Animal Behaviour 29:221-240

Peres CA (1989) Costs and benefits of territorial defense in wild golden lion tamarins, *Leontopithecus rosalia*. Behavioral Ecology and Sociobiology 25:227-233

Perry S (1996) Intergroup encounters in wild white-faced capuchins (*Cebus capucinus*). International Journal of Primatology 17:309-330

Perry S (1998) Male-male social relationships in wild white-faced capuchins, *Cebus capucinus*. Behaviour 135:139-172

Pope T (1990) The reproductive consequences of male cooperation in the red howler monkey: Paternity exclusion in multi-male and single-male troops using genetic markers. Behavioral Ecology and Sociobiology 27:439-446

Port M, Johnstone RA, Kappeler PM (2010) Costs and benefits of multi-male associations in redfronted lemurs (*Eulemur fulvus rufus*). Biology Letters 6:620-622

Port, M, Kappeler PM (2010) The utility of reproductive skew models in the study of male primates, a critical evaluation. Evolutionary Anthropology 19:46-56.

Ramírez-Llorens P, Di Bitetti MS, Baldovino MC, Janson CH (2008) Infanticide in black capuchins (*Cebus apella nigritus*) in Iguazú National Park, Argentina. American Journal of Primatology 70:473-484

Reichard U (1995) Extra-pair copulation in a monogamous gibbons (*Hylobates lar*). Ethology 100:99-112

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

Rose LM, Fedigan LM (1995) Vigilance in white-faced capuchins, *Cebus capucinus,* in Costa Rica. Animal Behaviour 49:63-70

Rosell F, Gundersen G, Le Galliard JF (2008) Territory ownership and familiarity status affect how much male root voles (*Microtus oeconomus*) invest in territory defence. Behavioral Ecology and Sociobiology 62:1559-1568

Rubenstein DI (1986) Ecology and sociality in horses and zebras. In: Rubenstein D, Wrangham R (eds) Ecological Aspects of Social Evolution: Birds and Mammals. Princeton University Press, Princeton, NJ, pp 282-302

Ruxton GD, van der Meer J (1997) Policing: It pays the strong to protect the weak. Trends in Ecology & Evolution 12:250-251

Sapolsky RM (2005) The influence of social hierarchy on primate health. Science 308:648-652

Scarry CJ, Tujague MP (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 74:804-810

Sicotte P (1993) Inter-group encounters and female transfer in mountain gorillas: influence of group composition on male behavior. American Journal of Primatology 30:21-36

Stamps JA, Krishnan VV (2001) How territorial animals compete for divisible space: a learning-based model with unequal competitors. American Naturalist 157:154-169

Steenbeek R (1999) Tenure related changes in wild Thomas's langurs. I: Between-group interactions. Behaviour 136:595-625

Sterck EHM, Watts DP, van Schaik CP (1997) The evolution of female social relationships in nonhuman primates. Behavioral Ecology and Sociobiology 41:291-309

Takimoto A, Fujita K (2011) I acknowledge your help: capuchin monkeys' sensitivity to others' labor. Animal Cognition 14:715-725

Temeles EJ (1994) The role of neighbours in territorial systems: when are they 'dear enemies'? Animal Behaviour 47:339-350

Trivers RL (1971) Evolution of reciprocal altruism. Quarterly Review of Biology 46:35-57

Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual Selection and the Descent of Man. Aldine, Chicago, pp 136-179

van Schaik CP (1989) The ecology of social relationships amongst female primates. In: Standen V, Foley RA (eds) Comparative Socioecology: The Behavioral Ecology of Humans and Other Mammals. Blackwell Scientific Publications, Oxford, pp 195-218

van Schaik CP (1996) Social evolution in primates: The role of ecological factors and male behaviour. Proceedings of the British Academy 88:9-3

van Wolkenten M, Brosnan SF, De Waal FBM (2007) Inequity responses of monkeys modified by effort. Proceedings of the National Academy of Sciences of the United States of America 104:18854-18859

Vehrencamp SL (1983a) A model for the evolution of despotic versus egalitarian societies. Animal Behaviour 31:667-682.

Vehrencamp SL (1983b) Optimal degree of skew in cooperative societies. American Zoologist 23:327-335.

Watts DP (1989) Infanticide in mountain gorillas: New cases and a reconsideration of the evidence. Ethology 81:1-18

Wich SA, Assink PR, Becher F, Sterck EHM (2002a) Playbacks of loud calls to wild thomas langurs (Primates; *Presbytis thomasi*): The effect of familiarity. Behaviour 139:79-87

Wich SA, Assink PR, Becher F, Sterck EHM (2002b) Playbacks of loud calls to wild Thomas langurs (Primates; *Presbytis thomasi*): The effect of location. Behaviour 139:65-78

Wich SA, Sterck EHM (2007) Familiarity and threat of opponents determine variation in Thomas langur (*Presbytis thomasi*) male behaviour during between-group encounters. Behaviour 144:1583-1598

Wiley RH, Rabenold KN (1984) The evolution of cooperative breeding by delayed reciprocity and queuing for favorable social positions. Evolution 38:609-621

Williams DA (2004) Female control of reproductive skew in cooperatively breeding brown jays (*Cyanocorax morio*). Behavioral Ecology and Sociobiology 55:370-380

Williams JM, Oehlert GW, Carlis JV, Pusey AE (2004) Why do male chimpanzees defend a group range? Animal Behaviour 68:523-532

Wilson ML, Hauser MD, Wrangham RW (2001) Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? Animal Behaviour 61:1203-1216

Wong MYL, Buston PM, Munday PL, Jones GP (2007) The threat of punishment enforces peaceful cooperation and stabilizes queues in a coral-reef fish. Proceedings of the Royal Society B-Biological Sciences 274:1093-1099

Wrangham R, Crofoot M, Lundy R, Gilby I (2007) Use of overlap zones among group-living primates: a test of the risk hypothesis. Behaviour 144:1599-1619

Wrangham RW (1980) An ecological model of female-bonded primate groups. Behaviour 75:262-300

Ydenberg RC, Giraldeau LA, Falls JB (1988) Neighbours, strangers, and the asymmetric war of attrition. Animal Behaviour 36:343-347

Young AJ, Spong G, Clutton-Brock T (2007) Subordinate male meerkats prospect for extra-group paternity: alternative reproductive tactics in a cooperative mammal. Proceedings of the Royal Society B-Biological Sciences 274:1603-1609

Zahavi A (1975) Mate selection—a selection for a handicap. Journal of Theoretical Biology 53:205-214

References

Abbott DH, Keverne EB, Bercovitch FB, Shively CA, Mendoza SP, Saltzman W, Snowdon CT, Ziegler TE, Banjevic M, Garland Jr T, Sapolsky RM (2003) Are subordinates always stressed? a comparative analysis of rank differences in cortisol levels among primates. Hormones and Behavior 43:67-82

Agoramoorthy G, Hsu MJ (2000) Extragroup copulation among wild red howler monkeys in Venezuela. Folia Primatologica 71:147-151

Albers PCH, de Vries H (2001) Elo-rating as a tool in the sequential estimation of dominance strengths. Animal Behaviour 61:489-495

Altmann J (1974) Observational study of behavior - sampling methods. Behaviour 49:227-267

Altmann J, Altmann SA, Hausfater G (1978) Primate infant's effects on mother's future reproduction. Science 201:1028-1030

Areta JI, Bodrati A, Cockle K (2009) Specialization on *Guadua* bamboo seeds by three bird species in the Atlantic Forest of Argentina. Biotropica 41:66-73

Axelrod R (1984) The Evolution of Cooperation. Basic Books, New York

Bartlett T (2003) Intragroup and intergroup social interactions in white-handed gibbons. International Journal of Primatology 24:239-259

Bates D, Maechler M, Bolker B (2011) lme4 - Linear mixed-effects models using S4 classes. R package version 0.999375-42, URL http://lme4.r-forge.r-project.org/

Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society Series B (Methodological) 57:289-300

Berghanel A, Schulke O, Ostner J (2010) Coalition formation among Barbary macaque males: the influence of scramble competition. Animal Behaviour 80:675-682

Beyer HL (2004) Hawth's Analysis Tools for ArcGIS. URL http://www.spatialecology.com/htools

Boggess J (1984) Infant killing and male reproductive strategies in langurs (*Presbytis entellus*). In: Hausfater G, Hrdy SB (eds) Infanticide: Comparative and Evolutionary Perspectives, Aldine Publishing Company, New York, pp 283-310

Bonanni R, Natoli E, Cafazzo S, Valsecchi P (2011) Free-ranging dogs assess the quantity of opponents in intergroup conflicts. Animal Cognition 14:103-115

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

Borgerhoff Mulder M (1990) Kipsigis womens preferences for wealthy men - evidence for female choice in mammals. Behavioral Ecology and Sociobiology 27:255-264

Borries C (1993) Ecology of female social relationships: Hanuman langurs (*Presbytis entellus*) and the van Schaik model. Folia Primatologica 61:21-30

Borries C (1997) Infanticide in seasonally breeding multimale groups of Hanuman langurs (*Presbytis entellus*) in Ramnagar (South Nepal). Behavioral Ecology and Sociobiology 41:139-150

Boyd R, Richerson PJ (1992) Punishment allows the evolution of cooperation (or anything else) in sizable groups. Ethology and Sociobiology 13:171-195

Bradbury JW, Vehrencamp SL (1977) Social-organization and foraging in emballonurid bats, III: mating systems. Behavioral Ecology and Sociobiology 2:1-17

Bradley BJ, Doran-Sheehy DM, Lukas D, Boesch C, Vigilant L (2004) Dispersed male networks in western gorillas. Current Biology 14:510-513

Broom M, Borries C, Koenig A (2004) Infanticide and infant defence by males - modelling the conditions in primate multi-male groups. Journal of Theoretical Biology 231:261-270

Broom M, Koenig A, Borries C (2009) Variation in dominance hierarchies among group-living animals: modeling stability and the likelihood of coalitions. Behavioral Ecology 20:844-855

Brosnan SF, de Waal FBM (2003) Monkeys reject unequal pay. Nature 425:297-299

Brosnan SF, Freeman C, De Waal FBM (2006) Partner's behavior, not reward distribution, determines success in an unequal cooperative task in capuchin monkeys. American Journal of Primatology 68:713-724

Brown AD, Zunino GE (1990) Dietary variability in *Cebus apella* in extreme habitats: evidence for adaptability. Folia Primatologica 54:187-195

Brown JL (1964) Social regulatory mechanisms in bird populations - territoriality. American Zoologist 4:270-270

Brown JL (1983) Cooperation—a biologist's dilemma. Advances in the Study of Behavior 13:1-37

Bruintjes R, Taborsky M (2008) Helpers in a cooperative breeder pay a high price to stay: effects of demand, helper size and sex. Animal Behaviour 75:1843-1850

Bygott JD, Bertram BCR, Hanby JP (1979) Male lions in large coalitions gain reproductive advantages. Nature 282:839-841

Cant MA, Hodge SJ, Bell MBV, Gilchrist JS, Nichols HJ (2010) Reproductive control via eviction (but not the threat of eviction) in banded mongooses. Proceedings of the Royal Society B-Biological Sciences 277:2219-2226

Cant MA, Otali E, Mwanguhya F (2002) Fighting and mating between groups in a cooperatively breeding mammal, the banded mongoose. Ethology 108:541-555

Cant MA, Reeve HK (2002) Female control of the distribution of paternity in cooperative breeders. The American Naturalist 160:602-611

Carosi M, Heistermann M, Visalberghi E (1999) Display of proceptive behaviors in relation to urinary and fecal progestin levels over the ovarian cycle in female tufted capuchin mokeys. Hormones and Behavior 36:252-265

Chase ID, Bartolomeo C, Dugatkin LA (1994) Aggressive interactions and inter-contest interval: how long do winners keep winning? Animal Behaviour 48:393-400

Cheney DL (1981) Intergroup encounters among free-ranging vervet monkeys. Folia Primatologica 35:124-146

Cheney DL (1987) Interactions and relationships between groups. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate Societies. University of Chicago Press, Chicago, pp 267-281

Cheney DL, Seyfarth RM (1977) Behaviour of adult and immature male baboons during inter-group encounters. Nature 269:404-406

Cheney DL, Seyfarth RM (1982) Recognition of individuals within and between groups of free-ranging vervet monkeys. American Zoologist 22:519-529

Cheney DL, Seyfarth RM (1983) Nonrandom dispersal in free-ranging vervet monkeys: Social and genetic consequences. American Naturalist 122:392-412

Cheney DL, Seyfarth RM (1987) The influence of intergroup competition on the survival and reproduction of female vervet monkeys. Behavioral Ecology and Sociobiology 21:375-386

Clutton-Brock TH (1998) Reproductive skew, concessions and limited control. Trends in Ecology & Evolution 13:288-292

Clutton-Brock TH, Brotherton PNM, Russell AF, O'Rain MJ, Gaynor D, Kansky R, Griffin A, Manser M, Sharpe L, McIlrath GM, Small T, Moss A, Monfort S (2001) Cooperation, control and concession in meerkat groups. Science 291:478

Clutton-Brock TH, Harvey PH (1977) Primate ecology and social organization. Journal of Zoology 183: 1-39

Clutton-Brock TH, Parker GA (1995) Punishment in animal societies. Nature 373:209-216

Clutton-Brock TH, Russell AF, Sharpe LL, Young AJ, Balmforth Z, McIlrath GM (2002) Evolution and development of sex differences in cooperative behavior in meerkats. Science 297:253-256

Cords M (1987) Forest guenons and patas monkeys: male-male competition in one-male groups. In: Smuts BB, Cheney D, Seyfarth R, Wrangham R, Struhsaker T (eds) Primate Societies. University of Chicago Press, Chicago, pp 98-111

Cords M (2007) Variable participation in the defense of communal feeding territories by blue monkeys in the Kakamega Forest, Kenya. Behaviour 144:1537-1550

Cowlishaw G (1995) Behavioural patterns in baboon group encounters: the role of resource competition and male reproductive strategies. Behaviour 132:75-86

Crockett CM, Janson CH (2000) Infanticide in red howlers: female group size, male membership, and a possible link to folivory. In: van Schaik CP, Janson CH (eds) Infanticide By Males and Its Implications. Cambridge Univ Press, Cambridge, pp 75-98

Crockett CM, Sekulic R (1984) Infanticide in red howler monkeys (*Alouatta seniculus*). In: Hausfater G, Hrdy SB (eds) Infanticide: Comparative and Evolutionary Perspectives. Aldine Publishing Company, New York, pp 173-191

Crofoot MC (2007) Mating and feeding competition in white-faced capuchins (*Cebus capucinus*): the importance of short- and long-term strategies. Behaviour 144:1473-1495

Crofoot MC, Gilby IC (2012) Cheating monkeys undermine group strength in enemy territory. Proceedings of the National Academy of Sciences of the United States of America 109:501-505

Crofoot MC, Gilby IC, Wikelski MC, Kays RW (2008) Interaction location outweighs the competitive advantage of numerical superiority in *Cebus capucinus* intergroup contests. Proceedings of the National Academy of Sciences of the United States of America 105:577-581

Davies NB, Houston AI (1981) Owners and satellites - the economics of territory defense in the Pied Wagtail, *Motacilla alba*. Journal of Animal Ecology 50:157-180

De Vries H (1995) An improved test of linearity in dominance hierarchies containing unknown or tied relationships. Animal Behaviour 50:1375-1389

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

De Vries H, Stevens JMG, Vervaecke H (2006) Measuring and testing the steepness of dominance hierarchies. Animal Behaviour 71:585-592

Defler T (1982) A comparison of intergroup behavior in *Cebus albifrons* and *C. apella*. Primates 23:385-392

Di Bitetti MS (1997) Evidence for an important social role of allogrooming in a platyrrhine primate. Animal Behaviour 54:199-211

Di Bitetti MS (2001a) Food Associated Calls in the Tufted Capuchin Monkey (*Cebus apella*). In: Ecology and Evolution. Stony Brook University, Stony Brook

Di Bitetti MS (2001b) Home-range use by the tufted capuchin monkey (*Cebus apella nigritus*) in a subtropical rainforest of Argentina. Journal of Zoology 253:33-45

Di Bitetti MS (2005) Food-associated calls and audience effects in tufted capuchin monkeys, *Cebus apella nigritus*. Animal Behaviour 69:911-919

Di Bitetti MS, Janson CH (2000) When will the stork arrive? patterns of birth seasonality in Neotropical primates. American Journal of Primatology 50:109-130

Di Bitetti MS, Janson CH (2001a) Reproductive socioecology of tufted capuchins (*Cebus apella nigritus*) in northeastern Argentina. International Journal of Primatology 22:127-142

Di Bitetti MS, Janson CH (2001b) Social foraging and the finder's share in capuchin monkeys, *Cebus apella*. Animal Behaviour 62:47-56

Di Bitetti MS, Paviolo A, De Angelo CD, Di Blanco YE (2008) Local and continental correlates of the abundance of a neotropical cat, the ocelot (*Leopardus pardalis*). Journal of Tropical Ecology 24:189-200

Di Bitetti MS, Vidal EML, Baldovino MC, Benesovsky V (2000) Sleeping site preferences in tufted capuchin monkeys (*Cebus apella nigritus*). American Journal of Primatology 50:257-274

Dittus WPJ (1987) Group fusion among wild toque macaques - an extreme case of intergroup resource competition. Behaviour 100:247-291

Drews C (1993) The concept and definition of dominance in animal behaviour. Behaviour 125:283-31.

Earley RL (2010) Social eavesdropping and the evolution of conditional cooperation and cheating strategies. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2675-2686

Elias DO, Botero CA, Andrade MCB, Mason AC, Kasumovic MM (2010) High resource valuation fuels "desperado" fighting tactics in female jumping spiders. Behavioral Ecology 21:868-875

Ellefson JO (1974) A natural history of white-handed gibbons in the Malayan peninsula. Gibbon and Siamang 3:1-136

Emlen ST, Oring LW (1977) Ecology, sexual selection, and evolution of mating systems. Science 197:215-223

Enquist M, Leimar O (1987) Evolution of fighting behavior: the effect of variation in resource value. Journal of Theoretical Biology 127:187-205

Escobar-Paramo P (1999) Inbreeding avoidance and the evolution of male mating strategies. Ph.D. Thesis: State University of New York at Stony Brook.

Furrer RD, Kyabulima S, Willems EP, Cant MA, Manser MB (2011) Location and group size influence decisions in simulated intergroup encounters in banded mongooses. Behavioral Ecology 22:493-500

Fashing PJ (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 50:219-230

Fedigan LM, Jack KM (2004) The demographic and reproductive context of male replacements in *Cebus capucinus*. Behaviour 141:755-775

Fragaszy DM, Visalberghi E, Fedigan LM (2004) The Complete Capuchin: Biology of the Genus *Cebus*. Cambridge University Press, Cambridge

Frank SA (1996) Policing and group cohesion when resources vary. Animal Behaviour 52:1163-1169

Furrer RD, Kyabulima S, Willems EP, Cant MA, Manser MB (2011) Location and group size influence decisions in simulated intergroup encounters in banded mongooses. Behavioral Ecology 22:493-500

Ganzhorn JU (1995) Low-level forest disturbance effects on primary production, leaf chemistry, and lemur populations. Ecology 76:2084-2096

Garber PA (1988) Diet, foraging patterns, and resource defense in a mixed species troop of *Saguinus mystax* and *Saguinus fuscicollis* in Amazonian Peru. Behaviour 105:18-34

Garber PA (1989) Role of spatial memory in primate foraging patterns: *Saguinus mystax* and *Saguinus fuscicollis*. American Journal of Primatology 19:203-216

Getty T (1989) Are dear enemies in a war of attrition? Animal Behaviour 37:337-339

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 66:633-643

Giraldeau LA, Ydenberg R (1987) The center-edge effect: the result of a war of attrition between territorial contestants? Auk 104:535-538

Glickman ME, Doan T (2010) The UCSF Rating System. URL http://www.glicko.net/ratings/rating.system.pdf

Goodall J (1986) The Chimpanzees of Gombe: Patterns of Behavior. Harvard University Press, Cambridge

Grafen A (1987) The logic of divisively asymmetric contests: respect for ownership and the desperado effect. Animal Behaviour 35:462-467

Grant JWA, Chapman CA, Richardson KS (1992) Defended versus undefended home range size of carnivores, ungulates and primates. Behavioral Ecology and Sociobiology 31: 149-161

Grinnell J, Packer C, Pusey AE (1995) Cooperation in male lions - kinship, reciprocity or mutualism. Animal Behaviour 49:95-105

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

Hamilton WD (1964) Genetical evolution of social behaviour I. Journal of Theoretical Biology 7:1-16

Harris TR (2006) Between-group contest competition for food in a highly folivorous population of black and white colobus monkeys (*Colobus guereza*). Behavioral Ecology and Sociobiology 61:317-329

Harris TR, Fitch WT, Goldstein LM, Fashing PJ (2006) Black and white colobus monkey (*Colobus guereza*) roars as a source of both honest and exaggerated information about body mass. Ethol 112:911-920

Harris TR (2010) Multiple resource values and fighting ability measures influence intergroup conflict in guerezas (*Colobus guereza*). Animal Behaviour 79:89-98

Harrison MJS (1983) Territorial behaviour in the green monkey, *Cercopithecus sabaeus*: seasonal defense of local food supplies. Behavioral Ecology and Sociobiology 12:85-94

Hauck WW, Donner A (1977) Wald's test as applied to hypotheses in logit analysis. Journal of the American Statistical Association 72:851-853

Hausfater G (1972) Intergroup behavior of free-ranging rhesus monkeys (*Macaca mulatta*). Folia Primatologica 18:78-107

Heinsohn R (1997) Group territoriality in two populations of African lions. Animal Behaviour 53:1143-1147

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

Hill C (1994) The role of the female diana monkeys, *Cercopithecus diana*, in territorial defence. Animal Behaviour 47:425-431

Hirsch BT (2002) Social monitoring and vigilance behavior in brown capuchin monkeys (*Cebus apella*). Behavioral Ecology and Sociobiology 52:458-464

Højsgaard S, Halekoh U, Yan J (2006) The R Package geepack for generalized estimating equations. Journal of Statistical Software 15:1-11

Hrdy SB (1977) Infanticide as a primate reproductive strategy. American Scientist 65:40-49

Isbell LA (1991) Contest and scramble competition: patterns of female aggression and ranging behavior among primates. Behav Ecol 2:143-155

Izar P, Stone A, Carnegie S, Nakai E (2009) Sexual selection, female choice and mating systems. In: Garber P, Estrada A, Bicca-Marques J, Heymann E, Strier K (eds) South American Primates: Comparative Perspectives in the Study of Behavior, Ecology and Conservation. Springer, New York, pp 157-189

Jack K, Fedigan L (2004a) Male dispersal patterns in white-faced capuchins, *Cebus capucinus*. Part 1: patterns and causes of natal emigration. Animal Behaviour 67:761-769

Jack K, Fedigan L (2004b) Male dispersal patterns in white-faced capuchins, *Cebus capucinus*. Part 2: patterns and causes of secondary dispersal. Animal Behaviour 67:771-782

Jack K, Fedigan L (2006) Why be alpha male? Dominance and reproductive success in wild white-faced capuchins (*Cebus capucinus*). In: Estrada A, Garber P, Pavelka M, Luecke L (eds) New Perspectives in the Study of Mesoamerican Primates: Distribution, Ecology, Behavior and Conservation. Springer, New York, pp 367-386

Janson CH (1984) Female choice and mating system of the brown capuchin monkey *Cebus apella* (Primates: Cebidae). Zeitschrift Fuer Tierpsychologie 65:177-200

Janson CH (1985) Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). Behavioral Ecology and Sociobiology 18:125-138

Janson CH (1986) The mating system as a determinant of social evolution in capuchin monkeys (*Cebus*). In: Else JG, Lee PC (eds) Primate Ecology and Conservation. Cambridge University Press, New York, pp 169-179

Janson CH (1988a) Food competition in brown capuchin monkeys (*Cebus apella*): Quantitative effects of group size and tree productivity. Behaviour 105:53-76

Janson, CH (1988b) Intra-specific food competition and primate social structure: A synthesis. Behaviour, 105, 1-17

Janson CH (1990) Ecological consequences of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. Animal Behaviour 40:922-934

Janson CH (1994) Comparison of mating system across two populations of brown capuchin monkeys. American Journal of Primatology 33:217

Janson CH (1996) Toward an experimental socioecology of primates: Examples from Argentine brown capuchin monkeys (*Cebus apella nigritus*). In: Norconk MA, Rosenberger AL, Garber PA (eds) Adaptive Radiations of Neotropical Primates. Plenum Press, New York, pp 309-325

Janson CH (1998a) Capuchin counterpoint. In: Ciochon RL, Nisbett RA (eds) The Primate Anthology: Essays on Primate Behavior, Ecology and Conservation from Natural History. Prentice Hall, Upper Saddle River, NJ

Janson CH (1998b) Experimental evidence for spatial memory in foraging wild capuchin monkeys, *Cebus apella*. Animal Behaviour 55:1229-1243

Janson CH (2007) Experimental evidence for route integration and strategic planning in wild capuchin monkeys. Animal Cognition 10:341-356

Janson CH (2012) Reconciling rigor and range: observations, experiments, and quasi-experiments in field primatology. International Journal of Primatology:1-22

Janson CH, Baldovino MC, Di Bitetti MS (2012) The group life cycle and demography of brown capuchin monkeys (*Cebus [apella] nigritus*) in Iguazú National Park, Argentina. In: Kappeler PM, Watts DP (eds) Long-Term Field Studies of Primates. Springer, Heidelberg, pp 185-212

Janson CH, Di Bitetti MS (1997) Experimental analysis of food detection in capuchin monkeys: Effects of distance, travel speed, and resource size. Behavioral Ecology and Sociobiology 41:17-24

Janson CH, van Schaik CP (1988) Recognizing the many faces of primate food competition: Methods. Behaviour 105:165-186

Janson CH, Vogel ER (2006) Hunger and aggression in capuchin monkeys. In: Hohmann G, Robbins MM, Boesch C (eds) Feeding Ecology in Apes and Other Primates: Ecological, Physical and Behavioral Aspects. Cambridge Univ Press, Cambridge, pp 285-311

Jolly A (1972) Troop continuity and troop spacing in *Propithecus verreauxi* and *Lemur catta* at Berenty (Madagascar). Folia Primatologica 17:335-362

Kagel JH, Green L, Caraco T (1986) When foragers discount the future: constraint or adaptation? Animal Behaviour 34:271-283

Kavanagh M (1981) Variable territoriality among tantalus monkeys in Cameroon. Folia Primatologica 36:76-98

Keller L, Reeve HK (1994) Partitioning of reproduction in animal societies. Trends in Ecology & Evolution 9:98-102

Kinnaird MF (1992) Variable resource defense by the Tana River crested mangabey. Behavioral Ecology and Sociobiology 31:115-122

Kitchen DM (2004) Alpha male black howler monkey responses to loud calls: effect of numeric odds, male companion behaviour and reproductive investment. Animal Behaviour 67:125-139

Kitchen DM (2006) Experimental test of female black howler monkey (*Alouatta pigra*) responses to loud calls from potentially infanticidal males: effects of numeric odds, vulnerable offspring, and companion behavior. Am J Phys Anthropol 131:73-83

Kitchen DM, Beehner JC (2007) Factors affecting individual participation in group-level aggression among non-human primates. Behaviour, 144, 1551-1581

Kitchen DM, Cheney DL, Seyfarth RM (2004a) Factors mediating inter-group encounters in savannah baboons (*Papio cynocephalus ursinus*). Behaviour 141:197-218

Kitchen DM, Horwich RH, James RA (2004b) Subordinate male black howler monkey (*Alouatta pigra*) responses to loud calls: experimental evidence for the effects of intra-group male relationships and age. Behaviour 141:703-723

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

Koenig A (2000) Competitive regimes in forest-dwelling Hanuman langur females (*Semnopithecus entellus*). Behavioral Ecology and Sociobiology 48:93-109

Koenig A (2002) Competition for resources and its behavioral consequences among female primates. International Journal of Primatology 23:759-783

Kokko H, Johnstone RA (1999) Social queuing in animal societies: a dynamic model of reproductive skew. Proceedings of the Royal Society of London Series B-Biological Sciences 266:571-578

Korstjens AH, Nijssen EC, Noe R (2005) Intergroup relationships in western black-and-white colobus, *Colobus polykomos polykomos*. International Journal of Primatology 26:1267-1289

Kruuk H (1972) The Spotted Hyena: A Study of Predation and Social Behavior. University of Chicago Press, Chicago

Kumar A, Kurup GU (1985) Inter-troop interactions in the lion-tailed macaque, *Macaca silenus*. In: Heltne PG (ed). The Lion-Tailed Macaque: Status and Conservation. Liss, New York, pp 91-107

Lambert JE (1998) Primate digestion: Interactions among anatomy, physiology, and feeding ecology. Evolutionary Anthropology 7:8-20

Lawes M, Henzi S (1995) Inter-group encounters in blue monkeys: How territorial must a territorial species be? Animal Behaviour 49:240-243

Lazaro-Perea C (2000) Social interactions within and between groups in wild common marmosets (*Callithrix jacchus*) In. Univ Wisconsin, Madison, pp ix, 154

Lazaro-Perea C (2001) Intergroup interactions in wild common marmosets, *Callithrix jacchus*: Territorial defence and assessment of neighbours. Animal Behaviour 62:11-21

Lloyd M (1967) `Mean Crowding'. Journal of Animal Ecology 36:1-30

Lukas D, Reynolds V, Boesch C, Vigilant L (2005) To what extent does living in a group mean living with kin? Molecular Ecology 14:2181-2196

Lynch Alfaro J (2005) Male mating strategies and reproductive constraints in a group of wild tufted capuchin monkeys (*Cebus apella nigritus*). American Journal of Primatology 67:313-328

Lynch Alfaro J (2007) Subgrouping patterns in a group of wild *Cebus apella nigritus*. International Journal of Primatology 28:271-289

Lynch Alfaro JW, Boubli JP, Olson LE, Di Fiore A, Wilson B, Gutiérrez-Espeleta GA, Chiou KL, Schulte M, Neitzel S, Ross V, Schwochow D, Nguyen MTT, Farias I, Janson CH, Alfaro ME (2012) Explosive Pleistocene range expansion leads to widespread Amazonian sympatry between robust and gracile capuchin monkeys. Journal of Biogeography 39:272-288

Manson JH, Wrangham RW (1991) Intergroup aggression in chimpanzees and humans. Current Anthropology 32:369-390

Mares R, Young AJ, Levesque DL, Harrison N, Clutton-Brock TH (2011) Responses to intruder scents in the cooperatively breeding meerkat: sex and social status differences and temporal variation. Behavioral Ecology 22:594-600

Maynard Smith J (1974) The theory of games and the evolution of animal contests. Journal of Theoretical Biology 47:209-221

Maynard Smith J (1982) Evolution and the Theory of Games. Cambridge University Press, Cambridge

Maynard Smith J, Parker GA (1976) Logic of asymmetric contests. Animal Behaviour 24:159-175

McComb K, Packer C, Pusey A (1994) Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. Animal Behaviour 47:379-387

McComb K, Pusey A, Packer C, Grinnell J (1993) Female lions can identify potentially infanticidal males from their roars. Proceedings of the Royal Society of London Series B-Biological Sciences 252:59-64

Meunier H, Molina-Vila P, Perry S (2012) Participation in group defence: proximate factors affecting male behaviour in wild white-faced capuchins. Animal Behaviour 83:621-628

Milton K (1981) Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental-development. Am Anthropol 83:534-548

Mitani JC, Gros-Louis J, Manson JH (1996) Number of males in primate groups: comparative tests of competing hypotheses. American Journal of Primatology 38:315-332

Mitani JC, Watts DP, Amsler S (2010) Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. Current Biology 20:R507-R508

Monnin T, Ratnieks FLW, Jones GR, Beard R (2002) Pretender punishment induced by chemical signalling in a queenless ant. Nature 419:61-65

Mosser A, Packer C (2009) Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. Animal Behaviour 78:359-370

Mulder RA, Langmore NE (1993) Dominant males punish helpers for temporary defection in superb fairy-wrens. Animal Behaviour 45:830-833

Muniz L, Perry S, Manson JH, Gilkenson H, Gros-Louis J, Vigilant L (2010) Male dominance and reproductive success in wild white-faced capuchins (*Cebus capucinus*) at Lomas Barbudal, Costa Rica. American Journal of Primatology 72:1118-1130

Mutschler T, Nievergelt CM, Feistner ATC (2000) Social organization of the Alaotran gentle lemur (*Hapalemur griseus alaotrensis*). American Journal of Primatology 50:9-24

Nagle CA, Denari JH (1983) The Cebus monkey (*Cebus apella*). In: Hearn J (ed) Reproduction in New World Primates: New Models in Medical Science. MTP Press, Lancaster, England, pp 39-67

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

Nicholson AJ (1954) An outline of the dynamics of animal populations. Australian Journal of Zoology 2:9-65

Nievergelt CM, Mutschler T, Feistner ATC (1998) Group encounters and territoriality in wild Alaotran gentle lemurs (*Hapalemur griseus alaotrensis*). American Journal of Primatology 46:251-258

Noë R, de Waal FBM, van Hooff JARAM (1980) Types of dominance in a chimpanzee colony. Folia Primatologica 34:90-110

Nunn CL (2000) Collective benefits, free-riders, and male extra-group conflict. In: Kappeler PM (ed) Primate Males: Causes and Consequences of Variation in Group Composition. Cambridge Univ Press, Cambridge, pp 192-204

Nunn CL, Deaner RO (2004) Patterns of participation and free riding in territorial conflicts among ringtailed lemurs (*Lemur catta*). Behavioral Ecology and Sociobiology 57:50-61

Nunn CL, Lewis RJ (2001) Cooperation and collective action in animal behaviour. In: Noe R, Van Hooff JA, Hammerstein P (eds) Economics in Nature: Social Dilemmas, Mate Choice and Biological Markets. Cambridge Univ Press, Cambridge, pp 42-66

Olson M (1965) The Logic of Collective Action. Harvard University Press, Cambidge, MA

Packer C (1979) Inter-troop transfer and inbreeding avoidance in *Papio anubis*. Animal Behaviour 27:1-36

Packer C (1986) The ecology of sociality in felids. In: Rubenstein D, Wrangham R (eds) Ecological Aspects of Social Evolution: Birds and Mammals. Princeton University Press, Princeton, pp 282-302

Packer C, Gilbert DA, Pusey AE, Obrien SJ (1991) A molecular genetic analysis of kinship and cooperation in African lions. Nature 351:562-565

Packer C, Pusey AE (1984) Infanticide in carnivores. In: Hausfater G, Hrdy SB (eds) Infanticide: Comparative and Evolutionary Perspectives, Aldine Publishing Company, New York, pp 31-42

Packer C, Scheel D, Pusey AE (1990) Why lions form groups: food is not enough. American Naturalist 136:1-19

Palombit R (1993) Lethal territorial aggression in a white-handed gibbon. American Journal of Physical Anthropology 31:311-318

Palombit R (1994) Extra-pair copulations in a monogamous ape. Animal Behaviour 47:721-723

Parker GA (1974) Assessment strategy and evolution of fighting behavior. Journal of Theoretical Biology 47:223-243

Parker GA, Rubenstein DI (1981) Role assessment, reserve strategy, and acquisition of information in asymmetric animal conflicts. Animal Behaviour 29:221-240

Paviolo A, Di Blanco YE, De Angelo CD, Di Bitetti MS (2009) Protection affects the abundance and activity patterns of pumas in the Atlantic Forest. Journal of Mammalogy 90:926-934

Peres CA (1989) Costs and benefits of territorial defense in wild golden lion tamarins, *Leontopithecus rosalia*. Behavioral Ecology and Sociobiology 25:227-233

Peres CA (1992) Consequences of joint-territoriality in a mixed-species group of tamarin monkeys. Behaviour 123:220-246

Perry S (1996) Intergroup encounters in wild white-faced capuchins (*Cebus capucinus*). International Journal of Primatology 17:309-330

Perry S (1998) Male-male social relationships in wild white-faced capuchins, *Cebus capucinus*. Behaviour 135:139-172

Pinheiro J, Bates D, DebRoy S, Sarkar D, Team RDC (2012) nlme: Linear and nonlinear mixed effects models. In, R package version 3.1-103 edn

Plavcan JM, van Schaik CP (1992) Intrasexual competition and canine dimorphism in anthropoid primates. American Journal of Physical Anthropology 87:461-477

Pope T (1990) The reproductive consequences of male cooperation in the red howler monkey: Paternity exclusion in multi-male and single-male troops using genetic markers. Behav Ecol and Sociobiol 27:439-446

Port M, Johnstone RA, Kappeler PM (2010) Costs and benefits of multi-male associations in redfronted lemurs (*Eulemur fulvus rufus*). Biology Letters 6:620-622

Port M, Kappeler PM, Johnstone RA (2011) Communal defense of territories and the evolution of sociality. American Naturalist 178:787-800

Pusey AE, Packer C (1987) Dispersal and philopatry. In: Smuts BB, Cheney DL, Seyfarth RM, Struhsaker TT, Wrangham RW (eds) Primate Societies. University of Chicago Press, Chicago, pp 250-266

Pusey AE, Packer C (1994) Infanticide in lions: consequences and counterstrategies. In: Parmigiani S, vom Saal FS (eds) Infanticide and Parental Care. Harwood Academic Publishers, Chur, Switzerland, pp 277-299

R Development Core Team (2010) R: A language and environment for statistical computing. In: R Foundation for Statistical Computing, Vienna, Austria, URL http://www.R-project.org/.

Ramírez-Llorens P, Di Bitetti MS, Baldovino MC, Janson CH (2008) Infanticide in black capuchins (*Cebus apella nigritus*) in Iguazú National Park, Argentina. American Journal of Primatology 70:473-484

Ramseyer A, Pele M, Dufour V, Chauvin C, Thierry B (2006) Accepting loss: the temporal limits of reciprocity in brown capuchin monkeys. Proceedings of the Royal Society B-Biological Sciences 273:179-184

Reichard U (1995) Extra-pair copulation in a monogamous gibbons (*Hylobates lar*). Ethology 100:99-112

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

Rettig NL (1978) Breeding behavior of the harpy eagle (*Harpia harpyja*). Auk 95:629-643

Robinson JG (1986) Seasonal variation in use of time and space by the wedge-capped capuchin monkey, *Cebus olivaceus*: Implications for foraging theory. Smithsonian Contributions to Zoology 431:1-60

Robinson JG (1988) Group size in wedge-capped capuchin monkeys *Cebus olivaceus* and the reproductive success of males and females. Behavioral Ecology and Sociobiology 23:187-197

Rosell F, Gundersen G, Le Galliard JF (2008) Territory ownership and familiarity status affect how much male root voles (*Microtus oeconomus*) invest in territory defence. Behavioral Ecology and Sociobiology 62:1559-1568

Rubenstein DI (1986) Ecology and sociality in horses and zebras. In: Rubenstein D, Wrangham R (eds) Ecological Aspects of Social Evolution: Birds and Mammals. Princeton University Press, Princeton, pp 282-302

Sapolsky RM (2005) The influence of social hierarchy on primate health. Science 308:648-652

Sauther ML, Sussman RW, Gould L (1999) The socioecology of the ringtailed lemur: Thirty-five years of research. Evol Anthropol 8:120-132

Scarry CJ, Tujague MP (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 74:804-810

Setchell JM, Smith T, Wickings EJ, Knapp LA (2010) Stress, social behaviour, and secondary sexual traits in a male primate. Hormones and Behavior 58:720-728

Sicotte P (1993) Inter-group encounters and female transfer in mountain gorillas: influence of group composition on male behavior. American Journal of Primatology 30:21-36

Sicotte P, Macintosh AJ (2004) Inter-group encounters and male incursions in *Colobus vellerosus* in central Ghana. Behaviour 141:533-553

Silk JB (2002) Practice random acts of aggression and senseless acts of intimidation: The logic of status contests in social groups. Evolutionary Anthropology 11:221-225

Smith RJ, Jungers WL (1997) Body mass in comparative primatology. Journal of Human Evolution 32:523-559

Smuts BB, Smuts RW (1993) Male aggression and sexual coercion of females in nonhuman primates and other animals: evidence and theoretical implications. Advances in the Study of Behavior 22

Stacey PB (1986) Group size and foraging efficiency in yellow baboons. Behavioral Ecology and Sociobiology 18:175-187

Stamps JA, Krishnan VV (2001) How territorial animals compete for divisible space: a learning-based model with unequal competitors. American Naturalist 157:154-169

Stanford CB (1991) The capped langur in Bangladesh: Behavioral ecology and reproductive tactics. Contributions to Primatology:1-179

Steenbeek R (1999) Tenure related changes in wild Thomas's langurs. I: Between-group interactions. Behaviour 136:595-625

Steenbeek R (2000) Infanticide by male and female choice in wild Thomas's langurs. In: Van Schaik CP, Janson CH (eds) Infanticide by Males and its Implications. Cambridge Univ Press, Cambridge, pp 153-177

Sterck EHM, Watts DP, van Schaik CP (1997) The evolution of female social relationships in nonhuman primates. Behavioral Ecology and Sociobiology 41:291-309

Stewart KJ, Harcourt AH (1987) Gorillas: Variation in female relationships. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate Societies. University of Chicago Press, Chicago, pp 155-164

Struhsaker T (1980) Comparison of the behavior and ecology of red colobus and redtail monkeys in the Kibale Forest, Uganda. African Journal of Ecology 18:33-51

Suzuki S, Noma N, Izawa K (1998) Inter-annual variation of reproductive parameters and fruit availability in two populations of Japanese macaques. Primates 39:313-324

Takimoto A, Fujita K (2011) I acknowledge your help: capuchin monkeys' sensitivity to others' labor. Animal Cognition 14:715-725

Temeles EJ (1994) The role of neighbours in territorial systems: when are they 'dear enemies'? Animal Behaviour 47:339-350

Terborgh J (1983) Five New World Primates: A Study in Comparative Ecology. Princeton University Press, Princeton

Tiddi B, Aureli F, di Sorrentino EP, Janson CH, Schino G (2011a) Grooming for tolerance? Two mechanisms of exchange in wild tufted capuchin monkeys. Behavioral Ecology 22:663-669

Tiddi B, Aureli F, Schino G, Voelkl B (2011b) Social relationships between adult females and the alpha male in wild tufted capuchin monkeys. American Journal of Primatology 73:812-820

Trivers RL (1971) Evolution of reciprocal altruism. Quarterly Review of Biology 46:35-57

Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual Selection and the Descent of Man. Aldine, Chicago, pp 136-179

VanderWaal KL, Mosser M, Packer C (2009) Optimal group size, dispersal decisions and postdispersal relationships in female African lions. Animal Behaviour 77:949-954.

van Noordwijk MA, van Schaik CP (1985) Male migration and rank acquisition in wild long-tailed macaques (*Macaca fascicularis*). Animal Behaviour 33:849-861

van Noordwijk MA, van Schaik CP (1987) Competition among female long-tailed macaques, *Macaca fascicularis*. Animal Behaviour 35:577-589

van Schaik CP (1983) Why are diurnal primates living in groups? Behaviour 87:120-144

van Schaik CP (1989) The ecology of social relationships amongst female primates. In: Standen V, Foley RA (eds) Comparative Socioecology: The Behavioral Ecology of Humans and Other Mammals. Blackwell Scientific Publications, Oxford, pp 195-218

van Schaik CP (1996) Social evolution in primates: The role of ecological factors and male behaviour. Proc Br Acad 88:9-3

van Schaik CP, Assink PR, Salafsky N (1992) Territorial behavior in southeast Asian langurs: Resource defense or mate defense? American Journal of Primatology 26:233-242 van Schaik CP, Kappeler PM (1997) Infanticide risk and the evolution of male-female associations in primates. Proceedings of the Royal Society of London Series B-Biological Sciences 264:1687-1694

van Wolkenten M, Brosnan SF, De Waal FBM (2007) Inequity responses of monkeys modified by effort. Proceedings of the National Academy of Sciences of the United States of America 104:18854-18859

Vargas JdJ, Whitacre D, Mosquera R, Albuquerque J, Piana R, Thiollay J-M, Márquez C, Sánchez JE, Lezama-López M, Midence S, Matola S, Aguilar S, Rettig N, Sanaiotti T (2006) Estado y distribución actual del águila arpía (*Harpia harpyja*) en Centro y Sur América. Ornitologia Neotropical 17:39-55

Vehrencamp SL (1983a) A model for the evolution of despotic versus egalitarian societies. Animal Behaviour 31:667-682.

Vehrencamp SL (1983b) Optimal degree of skew in cooperative societies. American Zoologist 23:327-335.

Venables W, Ripley B (2002) Modern Applied Statistics with S, 4 edn. Springer, New York

Vogel E, Janson C (2007) Predicting the frequency of food-related agonism in white-faced capuchin monkeys (*Cebus capucinus*), using a novel focal-tree method. American Journal of Primatology 69:533-550

Watts DP (1989) Infanticide in mountain gorillas: New cases and a reconsideration of the evidence. Ethology 81:1-18

Watts DP, Mitani JC (2001) Boundary patrols and intergroup encounters in wild chimpanzees. Behaviour 138:299-327

Watts DP, Muller M, Amsler SJ, Mbabazi G, Mitani JC (2006) Lethal intergroup aggression by chimpanzees in Kibale National Park, Uganda. American Journal of Primatology 68:161-180

Wheeler BC (2009) Monkeys crying wolf? Tufted capuchin monkeys use anti-predator calls to usurp resources from conspecifics. Proceedings of the Royal Society B-Biological Sciences 276:3013-3018

Wich SA, Assink PR, Becher F, Sterck EHM (2002a) Playbacks of loud calls to wild Thomas langurs (Primates; *Presbytis thomasi*): The effect of location. Behaviour 139:65-78

Wich SA, Assink PR, Becher F, Sterck EHM (2002b) Playbacks of loud calls to wild thomas langurs (Primates; *Presbytis thomasi*): The effect of familiarity. Behaviour 139:79-87

Wich SA, Sterck EHM (2007) Familiarity and threat of opponents determine variation in Thomas langur (*Presbytis thomasi*) male behaviour during between-group encounters. Behaviour 144:1583-1598

Williams DA (2004) Female control of reproductive skew in cooperatively breeding brown jays (*Cyanocorax morio*). Behavioral Ecology and Sociobiology 55:370-380

Williams J, Pusey A, Carlis J, Farm B, Goodall J (2002) Female competition and male territorial behaviour influence female chimpanzees' ranging patterns. Animal Behaviour 63:347-360

Williams JM, Oehlert GW, Carlis JV, Pusey AE (2004) Why do male chimpanzees defend a group range? Animal Behaviour 68:523-532

Wilson ML, Hauser MD, Wrangham RW (2001) Does participation in intergroup conflict depend on numerical assessment, range location, or rank for wild chimpanzees? Animal Behaviour 61:1203-1216

Wilson ML, Wrangham RW (2003) Intergroup relations in chimpanzees. Annual Review of Anthropology 32:363-392

Wong MYL, Buston PM, Munday PL, Jones GP (2007) The threat of punishment enforces peaceful cooperation and stabilizes queues in a coral-reef fish. Proceedings of the Royal Society B-Biological Sciences 274:1093-1099

Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164-168

Wrangham RW (1980) An ecological model of female-bonded primate groups. Behaviour 75:262-300

Wrangham RW, Crofoot MC, Lundy R, Gilby IC (2007) Use of overlap zones among group-living primates: a test of the risk hypothesis. Behaviour 144:1599-1619

Ydenberg RC, Giraldeau LA, Falls JB (1988) Neighbours, strangers, and the asymmetric war of attrition. Animal Behaviour 36:343-347

Young AJ, Carlson AA, Clutton-Brock T (2005) Trade-offs between extraterritorial prospecting and helping in a cooperative mammal. Animal Behaviour 70:829-837

Young AJ, Spong G, Clutton-Brock T (2007) Subordinate male meerkats prospect for extra-group paternity: alternative reproductive tactics in a cooperative mammal. Proceedings of the Royal Society B-Biological Sciences 274:1603-1609

Zahavi A (1975) Mate selection—a selection for a handicap. Journal of Theoretical Biology 53:205-214