Title
Collective decision-making and social foraging behavior in cohesive animal groups

Author
Davis, Grace Helen

Publication Date
2022

Collective decision-making and social foraging behavior in cohesive animal groups

By

GRACE H. DAVIS
DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Anthropology

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

Approved:

Margaret Crofoot, Co-Chair

Damien Caillaud, Co-Chair

Andrew Sih

Damien Farine

Committee in Charge

2023

TABLE OF CONTENTS

Acknowledgements……………………………………………………………………………..iv

Dedication…………………………………………………………………………………….xv

Abstract………………………………………………………………………………………xvi

Introduction………………………………………………………………………………....1

References……………………………………………………………………………..8

Chapter 1: Using optimal foraging theory to infer how groups make collective decisions……..13

Abstract………………………………………………………………………………13

Highlights…………………………………………………………………………….14

Glossary………………………………………………………………………………15

Optimal foraging theory and collective animal behavior………………………………..17

Applications of the marginal value theorem to cohesive social groups…………………19

Box 1. Basic social patch exploitation models…………………………………………..21

Predicting conflicts of interest over when to leave………………………………………24

Box 2. Heterogeneity in groups can generate conflicts in optimal patch departure times.26

Testing how groups resolve conflicts of interest to reach consensus………………...….28

Box 3. Using optimal foraging theory to reveal collective decision-making processes…30

Ecological drivers and evolutionary implications of collective departures………...……32

Using the marginal value theorem in empirical studies of collective decision-making…34

Concluding remarks……………………………………………………………...…….36

Outstanding questions…………………………………………………………………37

References……………………………………………………………………………..40

Chapter 2: Rank- and age-related differences in patch exploitation and foraging behavior in white-faced capuchin monkeys………………………………………………………………..50

Abstract……………………………………………………………………………….50

Introduction……………………………………………………………………………51

Methods……………………………………………………………………………….57

Results…………………………………………………………………………………69

Discussion……………………………………………………………………………..78

References……………………………………………………………………………..85

Chapter 3: When to go? Conflicts of interest and consensus costs over the timing of group movements in cohesive groups of white-faced capuchins……………………………………….96

Abstract……………………………………………………………………………..96

Introduction…………………………………………………………………………98

Methods……………………………………………………………………….....105

Results……………………………………………………………………………..123

Discussion……………………………………………………………...……137

References…………………………………………………………………………145

Supplementary materials…………………………………………………………..…153

ACKNOWLEDGEMENTS

Throughout my years in graduate school, I have had extraordinary support from so many people. Imagining all of the hundreds of humans who have helped me get where I am today is tremendous. I have had the immense privilege of being integrated into three academic communities in three different countries during my PhD: The University of California, Davis, The Smithsonian Tropical Research Institute in Panama, and The Max Planck Institute of Animal Behavior and University of Konstanz, Germany. At all three institutions, I have had outstanding mentors, brilliant colleagues, gifted students, and life-long friends. I am beyond grateful to each and every one of you.

To my advisor, Meg Crofoot. You are undoubtably a visionary scientist, constantly pushing the edge of the envelope for what is possible (and usually succeeding in astonishing ways). Watching you transition from a professor at UC Davis with just one student (me!) to a director at a Max Planck Institute with an entire department under your wing has been fascinating. We have been around the world together, from California to Panama to Kenya to Germany. The opportunities that you have provided me are exceptional, and I will be always grateful to you. You are the one who introduced me to the three major communities that I have been a part of during my PhD and you are the one who encouraged me to go to Panama for my dissertation. You set an incredibly high bar for me and my work, and I am so grateful that you always held me to it. I have loved those moments where you and I got to toss ideas and thought back and forth (and I hope there will be many more to come). You also allowed me to be an independent scientist and trusted me to conduct my own research and pursue my own ideas, preparing me in immeasurable ways for a future in research. Thank you for your generosity of countless resources throughout my PhD. I also thank you for supporting and standing up for me and my students when we encountered hardships in the field.

To Damien Farine. You've been there by my side since the beginning, and what a pleasure it is working with you. You are not only my mentor and closest collaborator, but you are my friend. You are an unbelievably brilliant and productive scientist. I am constantly in awe of not only how much you accomplish, but also how much care and support you thoughtfully give to those around you. Even when I doubted myself at times, you never failed to raise my spirits and encourage me. You never once doubted my abilities. This dissertation reflects many, many ideas that I learned directly from you. I credit you with spawning a great proportion of my ideas, but also allowing me to take them and run with them. I have fed off of your knowledge and your laser-focused work ethic. Thank you for always being patient with me, and always being there for me when I needed it most. And thank you for helping me with analyses, code, and writing for this dissertation. Working alongside you to develop new theories and ideas remains one of my favorite things. I look forward to a lifetime of working on research with you.

To my dissertation committee members, Meg Crofoot, Damien Farine, Andy Sih, and Damien Caillaud. I learned so much from all of you during my time in graduate school. Thank you for serving on my committees, reading my (sometimes far too long) proposals, encouraging me, teaching me, and guiding me every step of the way. Andy, I still to this day look back on my notes and PowerPoints from your ABGG core courses. Those classes were seminal to my learning. I have fond memories of belting Karaoke at ABGG parties with you. You are an endless source of positive feedback, helping me to realize my full potential. Damien C., thank you for serving as my committee chair for my qualifying exams, and as the graduate program advisor for my dissertation. You have given me excellent insights into how to improve my research, all the while cheering me on (and even bringing me chai while I was taking my written exams). Those weeks you came to field with us in Panama to dart monkeys were such fun, and I learned so much from your knowledge of veterinary science of how to best care for animals (and try not to break your nose in the process…).

To my counterpart, Lucia Tórrez-Herrera. Some of the very best memories of my life are with you beside me, whether it be waking up at 3:15 AM to track capuchin and spider monkeys all day in Panama, or safari-ing our way through the Great Migration in Kenya. Over the years, you have become one of the greatest friends of my life. I cannot thank you enough for all you did for me (and all you did to help collect this data contained within this dissertation—and so much more!). You are exceptionally talented, always coming to me with new thoughts, schemes, and ideas. You helped me to lead and mentor all the interns I hired for my fieldwork, endlessly supporting me and encouraging me. You also taught me Spanish and filled my field notebooks with new phrases (always making sure my grammer was in tact). As a journalist once wrote in Smithsonian Magazine: “Grace and Lucia communicate not only by walkie-talkie, but telepathically.” This statement is true; we are so in-sync with each other that we can read each other’s minds. It is an immense pleasure to learn from you in Panama and work side-by-side. Thank you for the thousands of hours (years…) you gave to helping my projects succeed. I cannot imagine a better person to help me accomplish this PhD and collect this data with than you.

To all of the Bachelor’s and Master’s students that I mentored, it has been far and away my greatest joy during my PhD to mentor you all: Allie Davis, Devin Lindsley, Gregg Cohen, Lynn Lewis-Bevan, Dan Herrera, Josue Ortega, My-Lan Le, Maria Creighton, Tatyana Herrera, Jean Concepcion, Jean-Paul Hirwa, Aulden Foltz, Ellen Dyer, Cassidy Martin, Alvaro Vega-

Hidalgo, and Maggie Mikula. All of you contributed to data collection and/or data processing and analysis for this dissertation, for which I am forever grateful. You put up with my rigorous field schedules and the harsh environment of the tropical rainforest. I am extremely proud of all that you accomplished, every one of you conducted your own independent projects with me, leading to theses, conference papers, presentations, and grant awards (amounting to over $52,000 no less!). Many of you are now in graduate school yourselves or pursuing your own ambitious careers. I am so impressed. I especially want to thank Lynn, Devin, and Tatyana who all somehow returned to BCI and braved multiple field seasons with me (Lynn for three times!). Your stamina and endless energy kept me on my toes and led to so many cherished memories.

To the administrative and scientific staff at the Smithsonian Tropical Research Institute in Panama, thank you for providing me with the infrastructure, logistical support, and mentorship to carry out my fieldwork on Barro Colorado Island. I especially want to thank my STRI scientific staff host, Rachel Page, who supported me throughout my many years in Panama (and continues to do so) and provided a productive environment, while also taking a firm stance to change the culture at STRI and support women and minorities in science. Thank you also to Bill Wcislo for supporting my research program and providing me feedback on my proposals. And to Oris Acevedo and Melissa Cano, thank you for the constant help you gave me and my field teams, from everything from obtaining permits for my research to office space to laboratory equipment. Thank you to the emergency response team at STRI and the guardabosques on BCI for quite literally saving our lives on one too many occasions.

Thank you also to the countless others who helped me with my research on BCI, especially Bob Lessnau, Nohely Fossatti, Roland Kays, and Ben Hirsch. I particularly want to thank Christina Campbell for giving me advice on studying the spider monkeys on the island,

and emboldening me work with these crazy animals. I still remember when we went out to find the spider monkeys and used our long calls, to immediate effect when the monkeys responded to us in seconds. It was meant to be. To those humans who I lived with for years in the field: our friendships, late night chats, and balcony beers (or Cuba libres in my case) are forever etched in my memory: Evan Gora, Jane Lucas, Max Adams, Claudio Manuel Monteza, Sharon Martinson, Maija Mallula, Kate Hunter, Amanda Savagian, Juan Carlos Penagos Zuluaga, Aidan Manubay, Ninon Meyer, Callum Kingwell, Meghan Strong, Aafke Oldenbeuving, Courtney Pellegrini, Gloria Glücksklee, Meagan Simons, Sammy Ari, Sara Fern, Michelle Spicer, and so many others.

To my many collaborators who have, and continue to, help me develop my research ideas: Damien Farine, Andy Sih, Damien Caillaud, Melissa Emery Thompson, Alie Ashbury, Mark Grote, Zack Kilpatrick, Ahmed Hady, Michael Noonan, Eric Payne, Tanya Berger-Wolf, as well as many others mentioned in these acknowledgements. I especially thank Mark for teaching me how to use the language R for my data analyses, guiding me through data processing, and providing invaluable advice on best practices to collect and record data. I also want to thank my professors at UC Davis who helped shape my research and my background knowledge, particularly: Robert Bettinger, Teresa Steele, Richard McElreath, Damien Caillaud, Andy Sih, Lynne Isbell, Jeffrey Schank, Tim Caro, and Tim Weaver.

To Melissa Emery Thompson and the members of the University of New Mexico, Albuquerque Comparative Human and Primate Physiology Center. Thank you for hosting me in your laboratories, where you taught me how to analyze my precious biological samples imported all the way from Panama. Melissa, are a steadfast and inspiring mentor and I am grateful for the opportunities I’ve had to work with you. You had intriguing ideas to further my research, and generously allowed me to run multiple physiological analyses on my samples (often at a very reduced cost). I have no doubt that my collaborations with you will continue to shape my research beyond my PhD.

To my mentors and professors before graduate school who helped me achieve my goals of getting a PhD and dedicated their time and resources to help me get my start in research: Dieter Steklis, Netzin Steklis, Larissa Swedell, Stacey Rucas, Elena Keeling, Francis Villablanca, Gita Kolluru, Emily Taylor, John Perrine, and Jaime George. I had such astonishing luck when I chose to go to Cal Poly, San Luis Obispo for my Bachelor's degree. My years at university allowed me to develop my skills, prepare for graduate school and beyond, and seek out abundant opportunities to get involved in research, all because of the support of these exceptional people. I must thank Dieter and Netzin especially for taking me out to my very first field research with primates in Rwanda. Tracking mountain gorillas, chimpanzees, baboons, and many other primates solidified by resolve for this career. You have helped inspire many ideas and supported me profusely when I was applying to graduate school (and even to this day). I also thank Larissa for all her guidance studying the chacma baboons in South Africa.

To my original lab members (the original "Crofeet" as we call ourselves), I have formed immense bonds with each and every one of you as we have traveled the world together and been by each other's sides through global pandemics, moving to new countries, and conducting intense fieldwork: Carter Loftus, Alexander Vining, Shauhin Alavi, Claudio Manuel Monteza, Rasmus Havmøller, Linnea Worsøe Havmøller, and Roi Harel. I especially must thank Carter and Shauhin for their help with data processing and coding. You all know how much you've meant to me, and I can't imagine a better group of (strong-willed) humans to work alongside.

To my communities at UC Davis, both in the Animal Behavior Graduate Group and the Evolutionary Anthropology program (and Ecology and Data Science): we have worked through the ups and downs of graduate school side-by-side, cheering each other on and learning from each other. Leaving Davis to move to Germany was not an easy decision, largely because of the strong bonds, friendships, and collaborations I cultivated at Davis. I loved how diverse and broad all of the research you conducted was. My own knowledge increased infinitely through my interactions with you. Thank you especially to my evolutionary anthropology cohort: Roshanne Bakhtiary, Jason Miszaniec, Mayowa Adegboyega, and Nick Hanten. We started our PhDs together, took our core courses together, triumphed over our preliminary exams and then our qualifying exams together, and now we are finishing our doctorates together. I want to especially thank my close friend Roshanne. You've been right there with me every moment and the memories we share of this journey together will last a lifetime. Special shout-outs go to my dear friends: Neetha Iyer, Susan Lagle, Tamar Marder, Kotrina Kajokaite, Amy Porter, Tez Stair, Matt Miller, Alec Scott, Meredith Lutz, Kelly Finn, Katrina Brock, Ryane Logsdon, Xinjun Zhang, Alexandra McInturf, Josie Hubbard, Allison Lau, Giulia Gallo, Blair Downey, Amelia Munson, and Lea Pollack.

To my communities at The Max Planck Institute of Animal Behavior and the University of Konstanz (and others in Konstanz): you made the move to Germany exciting and filled with adventures and new friendships, that have turned into deep connections. Enduring a pandemic together, in a foreign country for most of us, was survivable because of the support we gave each other. I also must thank the administrative and scientific support teams at the MPI and University who helped me navigate the bureaucracy of life in Germany (especially Jennifer Golbol and Katrin Dieter). I also want to thank Alie Ashbury for providing me with critical emotional and writing support during the last months of writing this dissertation. You've helped read almost this entire thesis, while reassuring me along the way. To my treasured friends here in Konstanz, thank you for all you have done to get me where I am today and providing a secure support system in which to finish my PhD: Kaz Uyehara, Ari Strandburg-Peshkin, Emily Grout, Kiran Dhanjal-Adams, Gerardo Perez, Arcan Kündük, Becca Myers, Pooja Gowda, Coco Monyemangene, Angela Albi, Ben Koger, Alison Govaerts, Jenna Kohles, Baptiste Ylreva, Kathrine Stewart, Zoë Goldsborough, Edward Hurme, Nina Hwang, Myles Menz, Jake Graving, Vivek Sridhar, Odd Jacobson, Jayme Weglarski, Tracy Montgomery, Alie Ashbury, Chase Nuñez, Eli Strauss, Camila Calderon, James Klarevas, Danai Papageorgiou, Gustavo Alarcón-Nieto, Adriana Maldonado, Martina Scacco, Jacob Davidson, Teja Curk, and so many others. Having such a diverse, supportive, intelligent, international community has been undoubtably the highlight of my time in Germany.

To the many friends that have supported me not just during graduate school, but throughout my life, cheering me on as I have moved around the world to chase my wild dreams: Kenalie Douglass, Missy Darnell, Jessy Darnell, Debby Darnell, Mark Darnell, Hannah Van Ark, Olivia O'Neil, Kasia Rasker, Melissa Rabin, Kaela Vetter, Alissa Mohr, Nina Jasper, Nancy Bartlett and so many others. All of you have always encouraged that spark in me to learn and adventure. You all also helped me navigate the challenges of living alone in another country during the pandemic. I especially want to thank the Darnell Family (who I claim as my own family, too) for pouring out your love and unwavering support for me every stage of my life. Mama Debby, you are the most generous, caring, loving human I know. Missy and Jessy, you are my sisters who I've grown up with, traveled with, and shared my whole life with. Thank you to Jessy for calling me practically daily, sending me thoughtful gifts, and helping me reach the finish line proud and excited for what is to come.

And last, but certainly, not least, to my family who have given their undying support of me and my passions my entire life. You encouraged the little biologist in me from an early age, when I was picking up earthworms and scribbling down behavioral observations of the ducks at the neighborhood park. You fostered my passion for the natural world and for learning, helping me overcome whatever obstacle came in my path. You also came to visit me every single one of my field seasons in Panama (five times), and hopped on a plane to see me in Germany two weeks after the EU re-opened its borders to Americans during the COVID pandemic. I could not be more grateful to have a family that is so intentional, so connected, and so full of energy. Such qualities stem from my grandparents, Marjorie Irvine Giles, Wallace Giles, Helen Davis, and Richard Davis. All four of my grandparents were committed to education (three of them professionally) and instilled in me a passion for knowledge and curiosity of the natural world. How exceedingly blessed I am to have such a family.

To my sister and twin, Allie Bean Davis. My very first field assistant. Somehow, I convinced you to come with me to Panama during my very first PhD field season, and you willingly got up before dawn and tracked monkeys all over the jungle with me. Being your sister is *the* greatest gift this world has given me. I have never met two sisters as bonded as we are. We have our own language and I can quite literally read your mind and vice versa. You are unshakeable and powerful, so much so that you are already using your talents to change this world for the better. I can’t wait to watch you become President soon. You have the most generous, giving heart and continue to spoil your people with love and gifts at all times. I love your adventurous spirit who is always willing to trek to the far corners of the earth with me, and your confidence in who you are and what you strive for. Watching you finish your own doctorate degree and advance forward in your career at lightning speed has been awe-inspiring. I never cease to be amazed by you and all you accomplish.

To my brother-in-law: Mike Tyska. What a joy it has been to welcome you into our family this year. You are so easy to love and get along with, and you always find ways to relate to anyone you are talking to. I have loved traveling with you and look forward to hopefully another Fasnacht with you in Konstanz in the post-COVID era (this remains one of my favorite life memories of all time). As you cheer my sister on towards her dreams, you also cheer me on as well.

To my mom: Shirley Giles Davis. You raised my sister and I to fight for what we believe in, to pursue our passions fearlessly, to be strong and independent, to think critically, to be hospitable and generous to everyone, and to be confident in ourselves and our abilities (among so many other things). You are perhaps one of the only people besides my committee who will read every word of this dissertation. In fact, you already have read and reviewed much of it, with your excellent journalism skills. You listened to my highs and lows throughout graduate school, fervently helping me re-focus when I was discouraged and always letting me know how proud of me you are. You taught me to strive for my dreams, never once telling me how outlandish “studying wild primates in the jungle” could be.

To my dad: Robert Davis. Growing up watching you devote your skills in leadership, teaching, administration, and research to CU Boulder was remarkable. You dedicate enormous energy to your collaborators, students, and staff at the university and I know they all benefit from your commitments to diversity, high-standards, and ambitious visions. I have undeniably been inspired by your career path in academia, and aspire that someday I can become even a portion of the exceptional advisor and researcher that you are. You taught Allie and I to lead our lives with integrity, generosity, dedication, hard-work, and humility. I am proud to call myself your daughter.

Thank you to the many organizations and institutions who provided generous funding for my research, none of which would have been possible without your support: The National Science Foundation, National Geographic, The Leakey Foundation, The Smithsonian Institution, The Smithsonian Tropical Research Institute, The Anthropology Department at the University of California, Davis, The Max Planck Institute of Animal Behavior, The Hemispheric Institute of the Americas, Peet's Coffee, The Rodman-Mitani Award, The Animal Behavior Society, The Explorer's Club, The Institute for Social Sciences at UC Davis, The Provost's Fellowship at UC Davis, and The Tinker Foundation.

DEDICATION

To my Grandma, Marjorie Irvine Giles

Educator. Traveler. Pray-er. Independent woman.

Your unconditional love and encouragement have irrevocably formed my life for the better.

ABSTRACT

Living in a group means not necessarily being able to do what you want, when you want. Social animals regularly confront consensus decisions where group members must collectively choose between mutually exclusive actions, such as where to go and when to move. Reaching consensus is often particularly difficult when group members have different needs and capabilities, leading to conflicts of interest over what to do and when to do it. In cohesive, heterogeneous social groups that must come consensus decisions to avoid group dissolution, some individuals ultimately have to compromise their preferred patterns of behavior, presumably at a cost to themselves. Making consensus decisions is a primary challenge of group-living, and how social species come to consensus is central to understanding the evolution of complex social systems like our own. A key challenge to studying how group decisions are made in the wild is determining the motivations driving individuals' decisions, and thus the link between individual needs and collective action. In this dissertation, I present a novel integration of two influential fields in behavioral ecology—optimal foraging theory and collective decision-making—to seek to overcome this challenge and understand how group-level actions emerge from the behavioral decisions of individuals. In chapter 1, I present a theoretical framework for using optimal foraging theory, specifically the marginal value theorem, as a tool for understanding individual preferences about when to leave a food patch, against which the behavior of groups can be compared under different decision-making regimes. Then, in chapters 2 and 3, I use empirical studies of cohesive social groups of wild white-faced capuchin monkeys (*Cebus capucinus*) on Barro Colorado Island, Panama to understand the drivers behind divergent foraging behaviors and preferences of group members, how these groups resolve conflicts of interest to come to consensus decisions, and who pays the costs of compromise. In chapter 2, I examine aspects of

social and individual predictors of foraging behavior, showing that dominance rank, age class, and timing of access to a foraging patch all influence patterns of foraging behavior and efficiency. In chapter 3, I illustrate how foraging theory models can be applied to my empirical data on capuchin monkey collective foraging—very simply and with standard observational data collection techniques—to understand how social groups resolve conflict and reach consensus over foraging decisions. My dissertation demonstrates the benefit of taking a theory-driven approach to generate predictions about emergent collective phenomena that can be tested with simple field and experimental data across a range of systems. In doing so, foraging theory can help the field of collective behavior become a more predictive science.

INTRODUCTION

To obtain the benefits of sociality, group-living animals coordinate important daily activities such as foraging and reach (or fail to reach) consensus decisions about where to go, when to move, and what to do (Reina et al. 2021, Mann 2018, Herbert-Read et al. 2019, King & Cowlishaw 2009, Couzin et al. 2005, Conradt & Roper 2005). Making consensus decisions is a primary challenge of group-living, and how social species come to consensus is central to understanding the evolution of complex social systems, including our own (Dyer et al. 2009, Conradt & Roper 2005). In heterogeneous social groups, dissimilar preferences or motivations of group members for a particular decision outcome can pose an obstacle to consensus decision-making by causing the interests of group members to diverge (Jolles et al. 2020, Conradt 2012, Conradt & Roper 2009). When conflicts arise about what to do, conflicts can often be resolved by sharing decisions across group members or by a despotic individual exerting their choice on behalf of the group (Conradt & Roper 2009). Under either decision-making regime, group members must come to a consensus decision or risk group dissolution. When group members have different needs and capabilities, some individuals have to compromise their preferred patterns of behavior, presumably at some cost to themselves (consensus costs—Conradt & Roper 2010).

A key challenge to studying how group decisions are made in the wild is determining the motivations driving individuals' decisions, and thus the link between individual needs and collective action. Determining how consensus decisions are reached is remarkably difficult in natural systems, as we do not have the luxury of asking what an animal prefers to do and when. As such, studies have often assessed group decision-making and which individuals contribute by observing the decision outcome (i.e., where or when groups move). For instance, studies have considered individuals who move first or are in front of the group to be leaders of group movements from place to place (Papageorgiou et al. 2020, Strandburg-Peshkin et al. 2018, Amornbunchornvej et al. 2018, King et al. 2011, Stueckle et al. 2008). Other studies have observed instances of group members communicating (i.e., "voting") for a decision outcome (Black 1988), through vocalizations (Sankey et al. 2021, Radford 2004, Boinski & Campbell 1995) or body orientations (Prins 1996). However, research has yet to directly link individuals' contributions to group decision outcomes to the preferences underlying their actions.

While the study of collective behavior has been focused on how groups come to collective decisions, it has yet to make use of the extensive body of knowledge provided by the wealth of classical models in behavioral ecology, such as optimal foraging theory. To date, theory has explored foraging decisions of individuals and social aggregations (DiGiogio et al. 2020, Palacios-Romo et al. 2019, Davidson et al. 2019, Falcón et al. 2017, Frank et al. 2017, Kolling et al. 2017). In this dissertation, I show how these models are easily re-cast for social animal groups to examine (i) individual preferences and conflicts of interest between group members, (ii) how collective foraging decisions in cohesive groups can emerge from individual strategies and preferences, and (iii) if and how the relative costs and benefits of group foraging decisions can be balanced across group members (Davis et al. 2022).

In Chapter 1, I present a novel theoretical framework for using optimal foraging theory as a tool for understanding group decision-making processes by reviewing and combining several existing social formulations of optimality models (the marginal value theorem, in particular, Charnov 1976). Then, in Chapters 2 and 3 I use empirical studies of cohesive social groups of wild white-faced capuchin monkeys (*Cebus capucinus*) on Barro Colorado Island, Panama to understand the drivers behind divergent foraging behaviors and preferences of group members, how these groups resolve conflicts of interest to come to consensus decisions, and who pays the costs of compromise. In Chapter 2, I examine aspects of both social dynamics and individual predictors of foraging behavior, showing that dominance rank, age class, and timing of access to a foraging patch all influence patterns of foraging behavior and efficiency. In Chapter 3, I illustrate how foraging theory models can be applied to my empirical data on capuchin monkey collective foraging—very simply and with standard data collection techniques—to understand how social groups reach consensus over foraging decisions. Overall, in this dissertation, I demonstrate that formally linking collective decision-making processes to optimal foraging theory models provides a powerful theoretical framework for making predictions about individual animals' preferences, allowing us to link their individual motivations to their actions, and ultimately to collective outcomes. Further, the great strength of making such clear quantitative predictions is that they make the methods available to all empiricists, without requiring expensive technology.

The capuchin monkeys that live on Barro Colorado Island (BCI) represent an ideal study system for investigating collective foraging behavior and group decision-making in a number of ways. These monkeys live in multi-male, multi-female cohesive social groups, such that they remain in proximity together all day every day and thus must come to consensus choices about what to do and when to do it (Perry 1997). The social groups of capuchins are also relatively stable in membership over short time periods (excluding rare dispersal events, Perry 1997). The capuchin groups on BCI live in home ranges of approximately 90-160 hectares and are xenophobic with mutually agonistic relationships with their neighbors (Crofoot 2007). Social groups usually average between 17-19 individuals (Fedigan et al. 2001), although the study groups on BCI tend to have fewer individuals averaging around 11 group members (ranging from 9-25 individuals in a study published by Crofoot 2007).

Even in the smallest social groups of capuchins, group members differ in age, social status, experience, size, and sex, amongst many other variables. Capuchins are long-lived animals that live about 30 years in the wild and have a prolonged juvenile period (Harvey et al. 1987). Females are philopatric (i.e., stay in their natal group), whereas males migrate one to a few times during their lifetime into new neighboring groups (Fedigan 1993). As such, adult females presumably have increased knowledge of their home ranges compared to other group members. There is a dominance hierarchy within males and females, such that dominant individuals tend to gain priority access to important resources and mates (Jack & Fedigan 2006, Vogel 2004). The dominant male, in particular, has a central role in capuchin groups (Di Bitetti 1997) and can monopolize access to resources through aggressive behaviors, including displacing other group mates off of feeding patches (Janson 1985). As a result of the wide range of heterogeneity amongst capuchin group members, I could reliably examine how differences between group members translate into dissimilar foraging behaviors and preferences.

The foraging patterns of the capuchin monkeys on BCI also exemplify an ideal study system to test optimal foraging theory models in the wild, especially over collective departures of when to leave food patches. Capuchins rely heavily on ripe fruiting trees for food (comprising between 60-80% of their diet, Fragaszy et al. 2004), an ephemeral resource in the seasonal tropical forest of Barro Colorado Island that are typically distributed in discrete, depletable patches (fruit trees) across their home ranges. I focus my data collection in this dissertation on capuchin foraging in *Attalea butyracea* palm trees, a keystone resource for the monkeys throughout June-September. The capuchin groups spend >75% of their total feeding time during these months in these trees (Davis unpublished data). *A. butyracea* fruits grow in large clumps, or infructesences, that suspend off a single stem of the palm plant (Bernal et al. 2010). Due to this structure, palm fruits are easily monopolizable for high-ranking individuals who can exclude their group-mates from the infructescence. Furthermore, palm fruits in an infructescence ripen asynchronously (Bernal et al. 2010), such that the monkeys must discriminate between ripe versus unripe fruits. The edible pulp of palm fruits is covered by a hard exterior shell, requiring the monkeys to open the shell to access the pulp inside. These characteristics of *A. butyracea* trees allow me to quantify the ways in which individuals vary in their abilities to process and consume food items (fruits). By collecting observational data on capuchin group foraging on *A. butyracea* palm trees, I examine how group members differ in their foraging strategies and preferences and ultimately how groups reach consensus over when to leave trees.

In chapter 1 (Davis et al. 2022), I first demonstrate how the study of collective decision-making is rich in predictions about how decision-making can resolve conflicts of interests among group members, but weak in empirical evidence to match these predictions. I then review the body of theoretical work that forms the framework of optimal foraging theory and how these can apply to group-living animals. I subsequently illustrate how optimal foraging theory, and in particular the marginal value theorem, can generate testable predictions about the processes underlying collective foraging decisions, specifically how groups coordinate departure decisions (when to go). The tools developed in optimal foraging theory allow researchers to quantify the degree of within-group conflict for observed collective decisions and investigate how observed patterns of behavior deviate from individual- and/or group-level optima (i.e., which group members pay consensus costs). From these data, it is then possible, and simple, to evaluate whether collective decisions are underpinned by a threshold number of individuals having passed their optimal choice (i.e., a quorum process), whether departures are dictated by the optimal choice for a specific individual or individuals (i.e., an unshared or partially shared process), or whether groups can optimize decisions to benefit the majority of their members (i.e., an emergent process). I further utilize foraging theory to make predictions about the distribution of consensus costs across group members and under what environmental conditions shared decision-making may be favored or disfavored.

In chapter 2, I evaluate the extent of variation in foraging behavior and efficiency across group members in capuchin monkey groups and how this variation is shaped by important determinants of social status and experience such as age, a measure of an individual's experience, abilities, and strength, and social rank, a measure of an individual's competitive ability. While optimal foraging theory models provide clear currencies from which to compare inter-individual foraging efficiencies (energy and time, Stephens & Krebs 1986, Mangel & Clark 1986), they do not always provide concurrent information about the specific foraging behaviors that result in foraging efficiency, such as when a group member gets access to a feeding patch, how long it takes them to search for a food item, how long it takes to handle and consume that food item, etc. Hence, I measure foraging behavior of capuchin monkey group members across multiple levels in *A. butyracea* feeding patches to provide an in-depth and comprehensive analysis of the specific behavioral strategies that individuals use to maximize their foraging success. Specifically, I calculate foraging behaviors across group members in a patch during both the search phase of finding food items to consume and the active feeding phase of processing and consuming food items. Alongside the timing of access to a patch, these behaviors are important components of the ultimate foraging success outcome. For animals who forage in social groups like capuchin monkeys, I illustrate how variation in foraging underlies disparities between the way group members experience their environment, creating a range of individual needs, preferences, and capabilities. Ultimately, such heterogeneity between group members can translate into conflicts between individuals over their foraging preferences.

In chapter 3, I empirically test the theoretical framework developed in chapter 1 of this dissertation (Davis et al. 2022) in wild capuchin monkey groups. I utilize the marginal value theorem to quantify the degree of within-group conflict for observed collective decisions over when to leave foraging patches. I then investigate how observed patterns of group departure behavior deviate from individual- and group-level optima (i.e., which group members contribute to group decisions and which group members pay consensus costs by leaving at suboptimal times). From these data, I then determine the process of collective departure decisions of when to go, whether they be underpinned by an unshared, shared, or group-level optimal process. I also compare my foraging theory results with more conventional methods of assessing who has influence over group decisions by observing the outcomes of group departure decisions (i.e., which individual(s) successfully initiate group movements). Finally, I evaluate which group members paid consensus costs to collective decisions, by leaving patches at a suboptimal time. Together, this captures important elements of group decision-making in cohesive social groups like capuchin monkeys: when to leave food patches, how such decisions are made, and who pays consensus costs.

In this dissertation, I present a novel integration of two influential fields in behavioral ecology—optimal foraging theory and collective decision-making—to understand how group-level actions emerge from the behavioral decisions of individuals. Despite major advances in the study of collective behavior, how groups of animals decide when and where to forage remains a central question for understanding the evolution of group-living and the diversification of animal societies. While I apply optimal foraging theory to cohesive social groups with stable membership, I maintain that foraging models can similarly be used for other species that nevertheless benefit from collective behaviors (such as open societies and fission-fusion groups that forage socially and individuals must decide whether to maintain cohesion with others versus maximize their own energy gain). My work demonstrates the benefit of taking a theory-driven approach to generate predictions about emergent collective phenomena that can be tested with simple field and experimental data across a range of systems. In doing so, foraging theory can help the field of collective behavior become a more predictive science.

REFERENCES

Amornbunchornvej, C., Brugere, I., Strandburg-Peshkin, A., Farine, D. R., Crofoot, M. C., & Berger-Wolf, T. Y. (2018). Coordination event detection and initiator identification in time series data. *ACM Transactions on Knowledge Discovery from Data (TKDD)*, *12*(5), 1-33.

Bernal, R., Galeano, G., García, N., Olivares, I. L., & Cocomá, C. (2010). Uses and commercial prospects for the wine palm, Attalea butyracea, in Colombia. *Ethnobotany Research and Applications*, *8*, 255-268.

Black, J. M. (1988). Preflight signalling in swans: a mechanism for group cohesion and flock formation. *Ethology*, *79*(2), 143-157.

Boinski, S. & Campbell, A. F. (1995). Use of trill vocalizations to coordinate troop movement among white-faced capuchins: a second field test. *Behaviour*, *132*(11-12), 875-901.

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical population* *biology*, *9*(2), 129-136.

Conradt, L. (2012). Models in animal collective decision-making: information uncertainty and conflicting preferences. *Interface focus*, *2*(2), 226-240.

Conradt, L., & Roper, T. J. (2005). Consensus decision making in animals. *Trends in ecology & evolution*, *20*(8), 449-456.

Conradt, L., & Roper, T. J. (2009). Conflicts of interest and the evolution of decision sharing. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1518), 807-819.

Conradt, L., & Roper, T. J. (2010). Deciding group movements: where and when to go. *Behavioural Processes*, *84*(3), 675-677.

Couzin, I. D., Krause, J., Franks, N. R., & Levin, S. A. (2005). Effective leadership and decision-making in animal groups on the move. *Nature*, *433*(7025), 513-516.

Crofoot, M. (2007). Mating and feeding competition in white-faced capuchins (Cebus capucinus): the importance of short-and long-term strategies. *Behaviour*, *144*(12), 1473-1495.

Davidson, J. D., & El Hady, A. (2019). Foraging as an evidence accumulation process. *PLoS computational biology*, *15*(7), e1007060.

Davis, G. H., Crofoot, M. C., & Farine, D. R. (2022). Using optimal foraging theory to infer how groups make collective decisions. *Trends in Ecology & Evolution*, 37(11): 942-952.

di Bitetti, M. S. (1997). Evidence for an important social role of allogrooming in a platyrrhine primate. *Animal behaviour*, *54*(1), 199-211.

DiGiorgio, A. L., Upton, E. M., Susanto, T. W., & Knott, C. D. (2020). Wild Bornean orangutan

(Pongo pygmaeus wurmbii) feeding rates and the Marginal Value Theorem. *American Journal of Primatology*, *82*(10), e23183.

Dyer, J. R., Johansson, A., Helbing, D., Couzin, I. D., & Krause, J. (2009). Leadership, consensus decision making and collective behaviour in humans. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1518), 781-789.

Falcón-Cortés, A., Boyer, D., & Ramos-Fernández, G. (2019). Collective learning from individual experiences and information transfer during group foraging. *Journal of the Royal Society Interface*, *16*(151), 20180803.

Fedigan, L. (1993). Sex differences and intersexual relations in adult white-faced capuchins (Cebus capucinus). *International Journal of Primatology*, *14*(6), 853-877.

Fragaszy, D. M., Visalberghi, E., & Fedigan, L. M. (2004). *The complete capuchin: the biology of the genus Cebus*. Cambridge University Press.

Frank, E. T., & Linsenmair, K. E. (2017). Individual versus collective decision making: optimal foraging in the group-hunting termite specialist Megaponera analis. *Animal Behaviour*, *130*, 27-35.

Harvey, P., Martin, R. D., and Clutton-Brock, T. H. (1987). Life histories in comparative perspective. In Smuts, B., Cheney, D., Seyfarth, R., Wrangham, R., and Struhsaker, T. (eds.), *Primate Societies*, University of Chicago Press, Chicago, pp. 181–196.

Herbert-Read, J. E., Wade, A. S. I., Ramnarine, I. W., & Ioannou, C. C. (2019). Collective decision-making appears more egalitarian in populations where group fission costs are higher. *Biology letters*, *15*(12), 20190556.

Jack, K. M., & Fedigan, L. M. (2006). Why be alpha male? Dominance and reproductive success in wild white-faced capuchins (Cebus capucinus). In *New perspectives in the study of Mesoamerican primates* (pp. 367-386). Springer, Boston, MA.

Janson, C. (1985). Aggresive competition and individual food consumption in wild brown capuchin monkeys (Cebus apella). *Behavioral Ecology and Sociobiology*, *18*(2), 125-138.

Jolles, J. W., King, A. J., & Killen, S. S. (2020). The role of individual heterogeneity in collective animal behaviour. *Trends in ecology & evolution*, *35*(3), 278-291.

King, A. J., & Cowlishaw, G. (2009). All together now: behavioural synchrony in baboons. *Animal behaviour*, *78*(6), 1381-1387.

King, A. J., Sueur, C., Huchard, E., & Cowlishaw, G. (2011). A rule-of-thumb based on social affiliation explains collective movements in desert baboons. *Animal Behaviour*, *82*(6), 1337-1345.

Kolling, N., & Akam, T. (2017). (Reinforcement?) Learning to forage optimally. *Current opinion in neurobiology*, *46*, 162-169.

Mangel, M., & Clark, C. W. (1986). Towards a unifield foraging theory. *Ecology*, *67*(5), 1127-1138.

Mann, R. P. (2018). Collective decision making by rational individuals. *Proceedings of the National Academy of Sciences*, *115*(44), E10387-E10396.

Palacios-Romo, T. M., Castellanos, F., & Ramos-Fernandez, G. (2019). Uncovering the decision rules behind collective foraging in spider monkeys. *Animal Behaviour*, *149*, 121-133.

Papageorgiou, D., & Farine, D. R. (2020). Shared decision-making allows subordinates to lead when dominants monopolize resources. *Science advances*, *6*(48), eaba5881.

Perry, S. (1997). Male-female social relationships in wild white-faced capuchins (Cebus capucinus). *Behaviour*, *134*(7-8), 477-510.

Prins, H. H. T. (1996). Selecting grazing grounds: A case of voting. In *Ecology and behaviour of the African buffalo* (pp. 218-236). Springer, Dordrecht.

Radford, A. N. (2004). Vocal coordination of group movement by green woodhoopoes (Phoeniculus purpureus). *Ethology*, *110*(1), 11-20.

Reina, A., Ferrante, E., & Valentini, G. (2021). Collective decision-making in living and artificial systems. *Swarm Intelligence*, *15*(1), 1-6.

Sankey, D. W. E., O'Bryan, L. R., Garnier, S., Cowlishaw, G., Hopkins, P., Holton, M., ... & King, A. J. (2021). Consensus of travel direction is achieved by simple copying, not voting, in free-ranging goats. *Royal Society open science*, *8*(2), 201128.

Stephens, D. W., & Krebs, J. R. (1986). *Foraging theory*. Princeton University Press.

Strandburg-Peshkin, A., Farine, D. R., Couzin, I. D., & Crofoot, M. C. (2015). Shared decision-making drives collective movement in wild baboons. *Science*, *348*(6241), 1358-1361.

Stueckle, S., & Zinner, D. (2008). To follow or not to follow: decision making and leadership during the morning departure in chacma baboons. *Animal Behaviour*, *75*(6), 1995-2004.

Vogel, E. R. (2004). *The ecological basis of aggression in white-faced capuchin monkeys, Cebus capucinus, in a Costa Rican dry forest*. State University of New York at Stony Brook.

CHAPTER 1

Using optimal foraging theory to infer how groups make collective decisions[1]

ABSTRACT

Studying animal behavior as collective phenomena is a powerful tool for understanding social processes, including group coordination and decision-making. However, linking individual behavior during group decision-making to the preferences underlying those actions poses a considerable challenge. Optimal foraging theory, and specifically the marginal value theorem (MVT), can provide predictions about individual preferences, against which the behavior of groups can be compared under different models of influence. A major strength of formally linking optimal foraging theory to collective behavior is that it generates predictions that can easily be tested under field conditions. This opens the door to studying group decision-making in a range of species; a necessary step for revealing the ecological drivers and evolutionary consequences of collective decision-making.

---

[1] Adapted from: Davis, G. H., Crofoot, M. C., & Farine, D. R. (2022). Using optimal foraging theory to infer how groups make collective decisions. *Trends in Ecology & Evolution*, 37(11): 942-952.

HIGHLIGHTS

A growing body of evidence emerging from the analysis of advanced animal tracking data shows that moving groups make shared decisions about where to go, with each group member influencing the outcome. How groups coordinate departure decisions (when to go), however, remains poorly understood.

Classic models from optimal foraging theory, specifically the marginal value theorem (MVT), are well-established tools that can generate quantitative predictions about when individuals should prefer to leave a food patch, given patch quality and the distribution of patches in the environment.

Integrating optimal foraging theory into studies of animal collectives provides rich opportunities for gaining new insights from both empirical and theoretical studies.

Specifically, the MVT can be used to make predictions about conflict of interests among group members, how consensus costs vary under different models of collective decision-making, and under what environmental conditions shared decision-making may be favored or disfavored.

GLOSSARY

Conflicts of interest

differences in optimal behaviors among individuals, such as their individual optimal patch departure times.

Consensus cost

the cost incurred by an individual foregoing its optimal action to comply with the group decision outcome, thereby leaving a patch earlier or later than the optimal departure time. Consensus costs can be measured as the difference in the energy gained when departing relative to the possible energy gain based on the average environmental intake rate.

Consensus decisions

the outcome of a group choosing between two or more mutually exclusive actions, such that the group can maintain cohesion and coordinate actions. When decisions are shared, these are often referred to as collective decisions.

Fission–fusion dynamics

a social system where groups are variable in size and composition both spatially and temporally, such that these groups frequently form, split apart, and reform.

Gain curve

the cumulative energy an individual gains (or the number of prey items it consumes) as a function of time spent foraging in a patch.

Group-level consensus costs

the sum of consensus costs across all group members combined.

Group-level gain curve

the cumulative energy gained (or number of prey items consumed) by all group members as a function of time spent foraging in a patch. This is simply the sum of all group members' gain curves.

Handling time

the time an individual spends processing and consuming a distinct prey item from the moment it encounters the prey item until it is ready to search for the next prey item.

Harvest rate

the rate at which prey items, or energy, are gained over time.

Observed group departure time

the observed outcome of the group consensus decision of when to leave a patch; when the group is actually observed to depart. Groups can depart patches cohesively, or have staggered observed departure times (hence the observed group departure time could be represented by the last, or the mean of, group members' observed departure times). In some cases, observations on each group member's distinct departure times can be useful (e.g., when measuring consensus costs).

Optimal patch departure time

the predicted time an individual (or the group overall) should leave a patch to maximize its energy intake rate across the environment. The MVT defines this as the time point when the current rate of energy gain falls below the average rate of energy gain for the habitat. The optimal patch departure time provides a quantifiable prediction of an individual's or group's preference for when to leave a patch.

Patch

foraging areas that can contain one or more resource(s) distributed over an area that is encompassed by the group dispersion. Patches deplete over time with continued foraging effort and harvest rates reduce (show diminishing returns) with an increase in time and foraging effort. The discrete nature of patches introduces travel time when moving between them.

Prey

individual food items, which can represent anything from a single blade of grass to an individual animal.

Sub-majority

a quorum whereby the threshold for activating a (change in) behavior is less than 50% of group members.

Travel time

the time it takes an animal (or animal group) to travel from one foraging patch to the next.

OPTIMAL FORAGING THEORY AND COLLECTIVE ANIMAL BEHAVIOR

Collective behaviors are remarkable natural phenomena in social organisms, and how interactions between individuals produce emergent patterns of behavior has received considerable attention [1-5]. A central question in the study of collective behavior is how individuals in groups coordinate their behavior and reach (or fail to reach) **consensus decisions** (see Glossary) about where to go, when to move, and what to do [6-11]. However, a key challenge to studying how such decisions are made in wild animals is the difficulty of establishing the link between individual preferences and the resulting collective outcome(s). While the outcomes of consensus decisions can be documented [12-16], determining the processes by which decisions are made requires the ability to predict, and empirically assess, the preferences of each group member [17].

The strong theoretical basis that exists for studying individual foraging decisions provides a rare opportunity to elucidate the dynamics of collective decision-making. In particular, the existence of clear and measurable currencies – energy and time – facilitates comparison of individual preferences and decision outcomes across collective foraging scenarios. Optimal foraging theory [18,19] can predict animals' decisions, including diet choice [20,21], where to eat [22], and how to move between resources [23,24]. The marginal value theorem (MVT) [25], for example, can be used to predict when individuals should leave a resource **patch** based on their current intake rate and the distribution of resources in the landscape (Box 1). A rich body of theory [26-31] and empirical work [32-38] have explored such foraging decisions within aggregations of individuals. However, in animals that form cohesive groups with stable membership, decisions are socially contingent [32-34]. For example, costs and benefits of foraging decisions can differ among group-mates [12,39], and different-sized groups can vary in how rapidly they exploit patches [27,40]. Formulating the MVT for cohesive social groups – whereby individuals all leave patches together – can reveal the conflicting preferences between group members, how groups make decisions (i.e., who has influence), and the costs that individuals pay to achieve consensus.

Here, we lay out a framework for integrating optimal foraging theory – specifically the MVT – into studies of collective decision-making of cohesive groups with stable membership.

We show that making consensus decisions results in **consensus costs**, and that the MVT can combine empirical data on rates of **prey** acquisition (to estimate individuals' **gain curves**) together with the **observed group departure time** to infer who has influence and how groups make decisions.

APPLICATIONS OF THE MARGINAL VALUE THEOREM TO COHESIVE SOCIAL GROUPS

Beyond deciding where and how to search for food [41,42], foragers must also decide how long to feed on one resource patch before leaving to find a new patch. The MVT predicts that these decisions should be based on the instantaneous rate of energy gain. As an animal starts to deplete a patch, the rate at which energy is gained decreases, reaching a point where it is more profitable to search for a new food source than to remain. Foragers are therefore expected to leave when their current rate of energy gain falls below the average rate of energy gain for the habitat (their **optimal patch departure time**) [25]. Although the MVT is an over-simplification of animals' decision-making processes [43,44], its predictions nonetheless continue to be supported across a diverse set of organisms (e.g., birds*,* [45,46]; hunter-gatherers, [38,47]; non-human primates*,* [35,48]; rodents, [49]; insects, [33]).These studies also demonstrate how the MVT can be tested using field data. Specifically, the number of prey items individuals consume per unit time can then be fitted with negative exponential models, from which their optimal departure times can be estimated.

The MVT can be readily extended to social foraging contexts where animals travel and exploit resources as groups. These include troops of primates [50-53]; bird flocks, including old world babblers (Family Timaliidae) [54,55], cooperative breeders (e.g., superb fairy-wrens *Malurus cyaneus* [56], white-winged choughs *Corcorax melanorhamphos* [57]), family groups (e.g., black-capped chickadees *Poecile atricapillus* [58]), and species forming multilevel bird societies (e.g., vulturine guineafowl *Acryllium vulturinum* [59]); stable groups of bats (e.g., Spix's disk-winged bat *Thyroptera tricolor* [60]); cetacean pods [61], and mongoose groups [62,63]. Whether highly cohesive or more distributed (the MVT is scale insensitive), group daily movements extend much farther than their spread, with members switching from local foraging movements to directed movement. Thus, to effectively exploit foraging resources across their range – infructescences, schools of bait fish, open grassy areas, masting trees – group members must coordinate their activities and reach consensus over not only where to move [12,14,64], but also when to move [65].

While several social formulations of the MVT exist [28,66], these assume group members are identical. They predict that all group members share the same optimal patch departure time, also matching the optimal departure time given by the **group-level gain curve** (the sum of all the individual gain curves; see Figure1A in Box 1). Current social implementations (Box 1) already highlight tradeoffs arising from foraging as (larger) groups versus foraging alone or in smaller groups, and how tradeoffs are impacted by the distribution of patches across the environment, the types of food available within patches, and the foraging performance of groups. Thus, even in its simplest forms, the MVT already makes useful predictions when applied to social groups.

BOX 1. BASIC SOCIAL PATCH EXPLOITATION MODELS

The gain curve of a forager in a patch, as a function of the time since entering the patch (*t*), can be modeled as a negative exponential function:

$$W(t) = 1 - exp(-\lambda t) \qquad [I]$$

where the cumulative energy gained by an individual over time ($W(t)$) increases faster as a function of harvest rate (λ), but has an exponentially decreasing rate leading to an asymptote. An individual is expected to leave a foraging patch when its current rate of food capture falls below the average capture rate for the habitat [25], which is given by the point maximizing $\frac{W(t)}{\mu+t}$, with μ being the average travel time between patches. However, some prey items require handling time (*h*), reducing the rate of energy gain. In such cases, the time taken to extract the *g*th prey item from a patch containing *G* prey items (the inverse of the gain curve) is given as [99]:

$$t(g) = \frac{1}{\lambda} log \frac{G}{G-g} + hg. \qquad [II]$$

The simplest extension of the solitary patch model to social groups considers depletable patches that are exploited by *N* foragers that arrive and leave the patch simultaneously. The model [28]:

$$W(Nt) = 1 - exp(-\lambda Nt), \qquad [III]$$

assumes that all group members have the same instantaneous patch exploitation rate. It predicts that all individuals should have the same patch residency time, which is equal to the group-level optimal patch residency time (Figure1A, $T_G = T_{i'}$). The MVT generally predicts that individuals should live in small rather than large groups because the *per capita* energy gain over time ($\frac{1}{N} \cdot \frac{W(t)}{\mu+t}$) is typically greater in smaller groups. However, if larger group size enables greater individual harvest rates (λ), for example, due to reduced vigilance or enhanced group performance [40], then the foraging favors larger groups, but only if the travel time between patches is short (not shown). If travel time is also affected by group size (e.g., larger groups move more slowly [100]), this could yield an optimal group size for optimal foraging.

The MVT further predicts that (larger) groups should leave patches sooner (due to more foragers encountering and consuming prey items) and deplete resources to a greater extent (due to having a higher overall harvest rate), than individuals (Figure 1B) or smaller groups (Figure 1C). Food items that involve handling time reduce the per capita intake rate, leading to greater patch residency times. This has a stronger impact on individuals living in large (Figure 1D) versus small groups (Figure 1E).

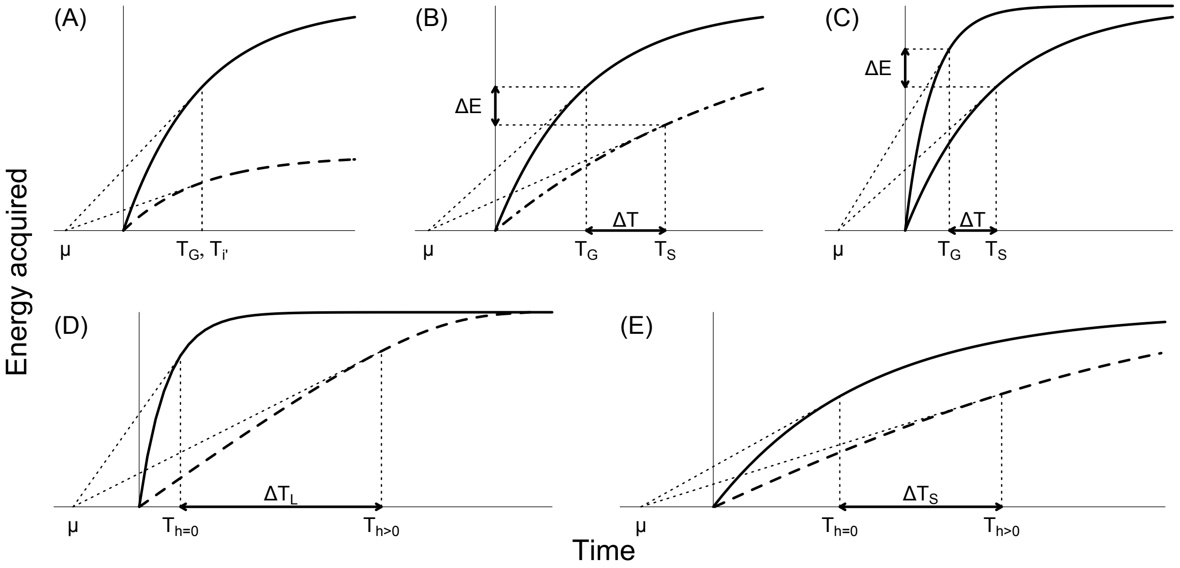

Figure 1. Social patch model where groups of individuals deplete patches. The unbroken gain curves, *W*(*Nt*), represent the cumulative energy acquired (intake) for a group as a function of patch exploitation time. The dotted lines drawn tangent to each curve provide the optimal patch departure time for each curve given the average travel time between patches, μ. (A) The group-level ($N = 3$) optimal residency time (T_G) and optimal residency time of identical group members ($T_{i'}$ given by the individual-level gain curve–broken line) are equal. (B) Groups (here $N = 3$) have shorter optimal patch residency times (ΔT) and acquire more overall energy (ΔE) relative to solitary foragers (dotted–broken line, with an optimal departure time of T_S). (C) Larger groups (top curve, $N = 10$) acquire more overall energy with shorter patch residency (T_L) than smaller groups (lower curve, $N = 3$). (D,E) With handling time (h > 0, broken lines), individuals acquire the same amount of energy as without handling times (h = 0, unbroken lines), but have longer optimal patch residency times ($T_{h>0} > T_{h=0}$). This effect is true for groups of all sizes, although the increase in patch residency times is greater for larger groups (D) than for smaller groups (E), that is, $\Delta T_L > \Delta T_S$ given the same environment.

PREDICTING CONFLICTS OF INTEREST OVER WHEN TO LEAVE

When applied to stable social groups, the MVT can capture variation between group members in their foraging behavior and ultimately their preferences over when to leave a patch. In most species, groups contain individuals that differ in size, dominance status, experience, and abilities [67-69]. Such characteristics can correspond to differences in abilities at extracting resources from the environment (e.g., intake rates, processing times), distinct gain curves, and therefore, within-group differences in optimal patch departure times. Thus, collective departures (the observed group departure time) will deviate from the optimal departure time of some group members, introducing opportunity costs relative to lone foraging [65]. Here, we show that extending the MVT to such group-foraging contexts is relatively straightforward (Box 2), and provides a way to predict, and quantify, **conflicts of interest** over the timing of group departures.

In heterogeneous groups that move together, group members will differ in their ability to extract energy from the patch, as well as the total quantity obtained. Such differences can alter the environment experienced by different group members, thereby introducing variation in the rate of energy gain. Unequal access to the patch alone will not generate conflict over the timing of movements, as the MVT predicts that otherwise identical individuals will have the same optimal patch departure times despite interindividual differences in overall energy gain (see Figure 2A in Box 2). However, if resources are heterogeneously distributed in the patch, individuals with access to better parts of the patch (e.g., dominants [12,70-72]) experience a richer environment than those relegated to the poorer parts, generating within-group variation in optimal patch departure times. Specifically, individuals with a higher **harvest rate** are predicted to have earlier optimal patch departure times than other group members (see Figure 2B in Box

2). Foragers also vary in their ability to process and consume prey. For instance, individuals can become more proficient at handling food items as they accumulate experience [73-75]. The MVT predicts that longer **handling times** lead to later optimal patch departure times (see Figure 2C in Box 2). Thus, unequal access to the best foraging sites and variation in foraging ability, but not differences in the total amount of energy extracted from a patch, will introduce conflicts of interest within groups over the timing of departures.

Individuals can simultaneously differ across multiple dimensions, such as experience, dominance, and personality, leading to some unexpected, and perhaps counterintuitive, predictions. For example, scenarios exist where better foragers are predicted to have later optimal departure times (e.g., see Figure 2E in Box 2). Such predictions illustrate the value of formal modeling for generating predictions about the conflicts of interest that arise in groups of heterogeneous foragers, including species that do not maintain strictly cohesive groups with stable membership but that benefit from collective behaviors, with individuals balancing the need to depart with the risk of moving alone (e.g., leaving before the group, or remaining after the group leaves).

BOX 2. HETEROGENEITY IN GROUPS CAN GENERATE CONFLICTS IN OPTIMAL PATCH DEPARTURE TIMES

When groups have heterogeneous membership, differences in gain curves among group-mates can lead to conflicts of interest over the timing of patch departures (i.e., differences in the predicted optimal departure time among group members). Only when individuals vary solely in the total amount of energy they can extract from the patch (the asymptote of their gain curve, where $W(t) = 0$) will all individuals have the same optimal departure time as each other and as the group (Figure 2A). If individuals differ in their harvest rate (λ varies), those with a higher λ can extract their share of the energy from the patch faster, and are predicted to have an earlier optimal patch departure time than individuals with a lower λ (Figure 2B). More efficient individuals also extract more energy from the patch at their optimal departure time than less efficient individuals. Individuals can also vary in their handling time for each prey item. In this scenario, individuals with shorter handling times are predicted to have earlier optimal departure times than individuals with longer handling times, but all individuals will acquire the same energy at their optimal departure times (Figure 2C).

In natural populations, individuals often vary across several parameters simultaneously. Individuals that obtain a greater portion of the total energy and harvest resources faster can have longer optimal patch residency times (Figure 2D), as do those gaining a greater portion of total energy with shorter handling times (Figure 2E). However, having a greater harvest rate and shorter handling times (Figure 2F) lead to earlier optimal departure.

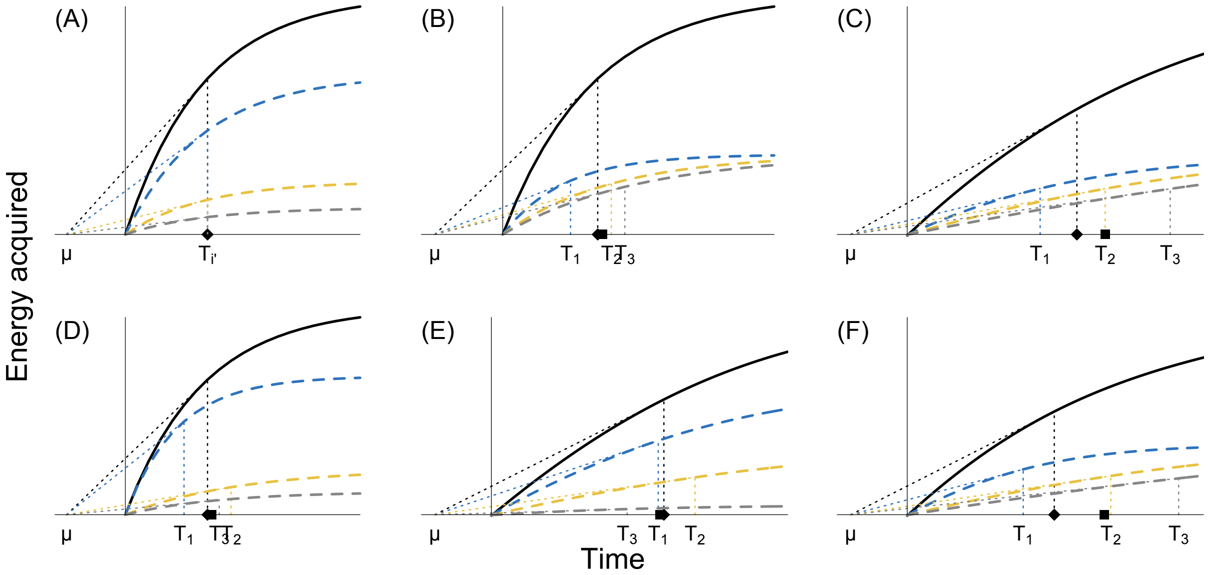

Figure 2. Interindividual differences in foraging behavior can lead to variation in the shape of the energy gain curves for group-foraging animals, and thus differences in optimal patch departure times of group-mates. (A–F) Six examples of how individuals can differ in their foraging strategies and abilities, resulting in conflicting departure times. The top black unbroken gain curve in each image represents the cumulative energy acquired by the group as a whole ($N = 3$). The lower colored broken gain curves are the cumulative energy acquired by each group member. Dotted lines capture the optimal patch departure times for each individual (T_1–T_3) and for the group as a whole (T_G, diamonds). Squares represent the mean of the group members' optimal departure times (if not shown, this equals T_G). Individuals can vary in: (A) the total amount energy they can extract from the patch, (B) harvest rate, (C) handling time, (D) the total amount energy they can extract from the patch and harvest rate, (E) the total amount energy they can extract from the patch and handling time, and (F) harvest rate and handling time. In all cases, individual 1 (blue line) has the 'best' parameters (highest energy gain, greatest efficiency, and shortest handling time), followed by individuals 2 (yellow broken line) and 3 (gray broken line).

TESTING HOW GROUPS RESOLVE CONFLICTS OF INTEREST TO REACH CONSENSUS

Taking research on leadership and influence in animal groups out of the laboratory and into ecologically, socially, and evolutionarily relevant field settings has proven remarkably challenging [76]. While aided by technological advances [3], studies focusing on observations of movement initiations (attempts to lead the group away from a patch) have not been able to directly link individuals' contributions to group decisions to the preferences underlying their actions [12,14,77-79] (but see [15]). Optimal foraging theory can provide a deeper mechanistic understanding of how group-living animals resolve conflicts of interest.

One challenge for studies of collective decision-making is to identify who has influence [17]. By comparing observed group departure times with the predicted optimal departure times of group members, the MVT can reveal influence without making assumptions about mechanisms. Influential individuals (e.g., despots) could be identified by a tendency for their group to leave foraging patches at or close to their optimal departure time (Box 3, D_D, where T_1 is a despot) as opposed to the group-level optimum (T_G) or the optimal departure times of other group members (T_2, T_3). Decisions that are shared equally across group members are expected to have a departure time matching the average time for all, which groups might approximate as the time when a majority (or **sub-majority**) of individuals have reached their optimal departure times (D_S). This approach avoids relying on observations of initiators, potentially revealing the long-hypothesized role of followers on the timing of departures [80].

Comparing when groups depart to predictions from the MVT can then be used to quantify individual consensus costs [10]. Consensus costs can be measured in terms of the energetic (foraging) loss as a result of leaving either earlier or later than the predicted optimal patch departure time for each individual (an opportunity cost, Figure 3A) [65]. Consensus costs can also be estimated under different decision-making processes, and can be used in a range of analyses, including comparative and evolutionary studies.

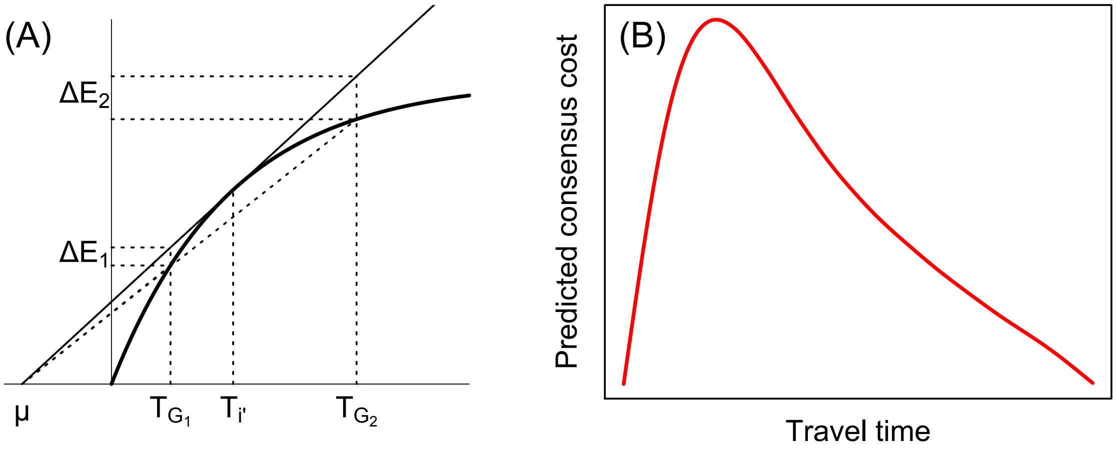

Figure 3. Using the marginal value theorem to make predictions about consensus costs across different ecological conditions. (A) Illustration of the energetic consensus cost (ΔE_1, ΔE_2) paid by an individual that leaves earlier than (T_{G1}) or later than (T_{G2}) their optimal departure time ($T_{i'}$), which is calculated as the opportunity cost (energetic loss relative to the average intake rate for the environment, represented by the unbroken line starting at μ). (B) Predicted sum of consensus costs for a group of three foragers that vary in their intake rates across different ecological conditions. Consensus costs initially increase as the environment becomes patchier (increasing travel time from low to medium), but then decrease as the environment becomes harsher (increasing to long travel times).

BOX 3. USING OPTIMAL FORAGING THEORY TO REVEAL COLLECTIVE DECISION-MAKING PROCESSES

By comparing the discrepancy between individual optimal departure times ($T_1 \ldots T_N$) versus the group's observed departure time from the patch (D), we can understand how groups of individuals come to decisions about when to leave, and who exerts the most influence. We use the MVT to predict when groups should leave patches under three common collective decision-making situations: shared (or quorum-based) decisions (D_S), despotic decisions (D_D), and globally optimal decisions (D_G).

When decisions are shared, all (or a representative proportion) of the group contributes to the group-level decision. Shared decisions are often represented by a fixed threshold or a quorum (a probabilistic threshold of group members or a 'majority rule'). In the context of social foraging, we predict that groups will leave food patches once a certain number of individuals in the group (or the median individual given a majority rule) have met their optimal patch departure times (Figure 4, $D_S = T_2$). In very large groups, the median of all individuals' departure times will be closely aligned with the group-level optimal departure time, highlighting a potential selective driver for shared decision-making.

At the opposite end of the decision-making spectrum [96] are despotic, or unshared, decisions. In a foraging context, a single individual has sole influence over the group decision about when to leave a foraging patch, and the observed departure of the group is predicted to align with the predicted optimal departure time of the despot (Figure 4, $D_D = T_1$).

Finally, individual-level energy gain could potentially be optimized by departing at the optimal departure time based on the overall group gain function (Figure 4, $D_G = T_G$). For example, if individuals vary unpredictably in their harvest rates from one patch to the next, then their individual-level energy gain over multiple patches could be maximized if they depart at the group-level optimal departure time. Thus, taking an optimal foraging view of collective decision-making reveals an alternative mechanism for reaching decisions that have not been previously considered.

Under both shared or despotic mechanisms, the group departure time can be either earlier or later than the group-level optimal departure time, which could have implications for the group's performance relative to other groups in the same habitat (e.g., if they exploit fewer resources relative to their travel time). Exploring the relative group-level gains under different levels of individual variation (Box 2), in groups with different decision-making mechanisms, and across different habitats (Figure 3) in a selection framework will yield novel insights into what type of decision-making mechanisms should evolve.

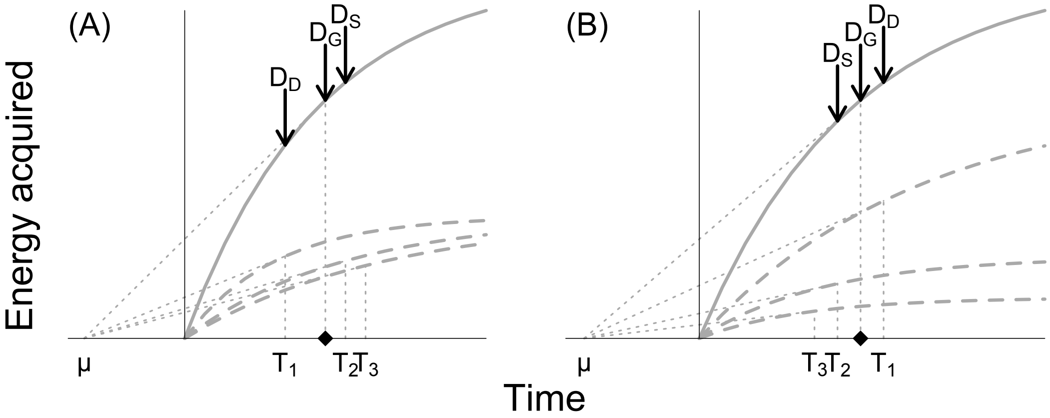

Figure 4. Conflicts of interest about optimal departure times can arise as a function of individual variation, such as when individuals differ in their (A) harvest rate or (B) total energy gain and harvest rate. Here, we demonstrate how conflicts can lead to different predictions about when groups should leave under three models of group decision-

making: shared (D_S), despotic (D_D), and group optimal (D_G). Diamonds represent the group-level optimal departure time (T_G).

ECOLOGICAL DRIVERS AND EVOLUTIONARY IMPLICATIONS OF COLLECTIVE DEPARTURES

Consensus costs are a central mechanism underpinning the social structure of animal social groups [81], and animals can respond to changes in the magnitude of consensus costs by modifying the structure of their societies [82]. For example, if compromise is too costly for individuals (relative to the benefits of remaining in a group), then **fission–fusion dynamics** emerge in lieu of consensus decision-making [83]. The magnitude of the costs borne by individuals (or the total cost experienced by a group) may be shaped by the environment itself—specifically the **travel time** between patches. Consider the simplest case where individuals vary in their harvest rates (λ; see Figure 2B in Box 2), causing a spread in the optimal foraging times of group members ($T_1 \ldots T_N$). The size of this spread will not only be dictated by the variation in harvest rates, but also by the travel time. At very short travel times, the energy intake rate trajectories among individuals have had little opportunity to diverge before they should each choose to move on, yielding a small variation in optimal departure times. Similarly, as travel times become very long, all individuals should exploit as much of the patch as possible, causing the energy intake trajectories to converge. Thus, at intermediate travel times, individuals experience the greatest spread in their energy acquisition curves, resulting in more divergent optimal departure times.

Examining the relationship between ecological conditions (variation in travel time) and the resulting consensus costs that emerge from individuals diverging from their optimal departure times (Figure 4B) confirms that **group-level consensus costs** are minimized in both resource-rich (shorter travel times between patches) and resource-poor (longer travel times between patches [68]) environments, and maximized in environments with intermediate resource availability (Figure 4B). This suggests that maintaining social cohesion entails increasing costs when transitioning from high-quality environments, but that these costs shrink again as conditions become even less favorable. By predicting a decrease in consensus costs in environments when conditions become harsher, the MVT might therefore help to explain the apparent paradox that environmental harshness (low rainfall combined with seasonal unpredictability that increase travel time as groups forage over larger areas [56,84]) can result in greater social cohesiveness, such as in the evolution of cooperation [85,86] or the fusion of groups within mammalian and avian multilevel societies [59,87-91]. This demonstrates how integrating the MVT with models of collective decision-making and collective movement has significant potential to generate predictions about the evolution of group-living under different ecological conditions.

A final question is whether cohesive groups can maximize the rate of energy extracted from the environment by leaving patches at the optimal time predicted by the group-level gain curve (Box 1, Box 2, Box 3, T_G). This could be beneficial if, for example, the group member(s) that access better parts of a patch varies (unpredictably) from one patch to the next as it maximizes the average rate of harvest from the environment across group members. Several examples demonstrate how collectives can produce such higher-level optimization. One classic example is the ideal free distribution [92], whereby individuals maximize their fitness by spreading themselves across heterogeneous resources in such a way that maximizes their individual harvest rates, thereby also maximizing the harvest rate of the group or population. Thus, animals could have evolved fine-tuned collective decision-making mechanisms that benefit them via optimal performance of their group (see Outstanding questions).

Finally, two intriguing predictions of the MVT are that the mean of the departure times across group members can be equal to, earlier, or later than the group-level optimal departure time (Box 2), and that the predicted optimal departure time for a given group does not always match the optimal departure time based on a majority-based decision (i.e., $T_2 \neq T_G$ in Box 3). Future studies could investigate the consequences of these mismatches. For example, if individual optimal departure times are long-tailed, then decisions could be made by a sub-majority [10]. Such sub-majority decisions were observed in group-living vulturine guineafowl, where subordinates that are displaced from patches initiate movements away on reaching ~13 individuals, irrespective of group size [12] (which can range from 15 to 65 [59]).

USING THE MARGINAL VALUE THEOREM IN EMPIRICAL STUDIES OF COLLECTIVE DECISION-MAKING

Group decision-making processes can be inferred by collecting foraging data from group members, estimating harvest rates and how these change over time, and observing group departure times. There are many ways to collect foraging data, including recording intake rates for all group members in the patch concurrently using observations or video recordings (e.g., [12]), collecting short repeated foraging observations from group members asynchronously (e.g.,

[35]), or focusing on two group members at once to quantify conflicts of interest dyadically (e.g., between a dominant and a subordinate). Two potentially useful ways to facilitate observational data collection are to create experimental patches where the amount of food is known *a priori* [49] or to estimate foraging return rates by weighing food items acquired by group members [38]. Foraging time could also be inferred from behavioral classification of biologging data, such as detecting prey encounters from accelerometer data [93] or detecting chewing from microphones [94]. Importantly, all of these approaches can allow data collection across repeated foraging patches (see Outstanding questions).

From the foraging data, individual harvest rates (and how these change over time) can be modeled by fitting negative exponential models. Models allow individual gain curves to be extended beyond when they leave the patch to calculate the theoretical individual-level optimal departure times. This calculation is done by combining gain curves with data on travel time, which is readily available in studies that follow groups while collecting global positioning signal (GPS) data (e.g., [51,88]) or in the increasing number of studies that fit GPS loggers to at least one group member (e.g., [12,14]). Finally, the energetic consensus cost can be calculated for each individual as the difference between the actual rate of energy gained relative to the theoretical maximum energy the individual could have extracted from the environment had it left at its optimal departure time (per Figure 4A). These four simple steps – obtaining foraging data over time, fitting individual-level curves, estimating individual-level optimal departure times, and calculating consensus costs – are readily achievable in most field systems.

CONCLUDING REMARKS

Despite a wealth of theoretical models of collective decision-making in animals [9,83,95-98], few empirical studies have moved beyond asking ‘who leads’ to explicitly testing how groups make decisions [17]. This is largely because determining how consensus decisions are reached in natural systems is significantly more challenging than observing the decision outcomes (i.e., where or when groups move). We highlighted that the MVT helps us understand collective decision-making by: (i) predicting when each individual should want to leave a patch, (ii) quantifying conflicts of interest for any given decision, (iii) precisely predicting when groups should depart a patch under different models of collective decision-making, (iv) quantifying consensus costs in ecologically meaningful currencies (energy, time) and identifying who pays them, and (v) predicting under what ecological conditions stable groups should pay greater versus fewer costs. In doing so, the MVT will help the field of collective behavior become a more predictive science by providing predictions that can readily be tested under field conditions. Further, while we have focused on animals that form cohesive groups with stable membership, the model is also applicable to open societies, where animals forage socially but vary in when they access patches and must decide whether to optimize their departures to maintain cohesion or maximize energy gain. Finally, the MVT and other models from optimal foraging theory can readily be integrated into evolutionary models of collective decision-making, potentially providing a rich framework for studying the evolution of collective decision-making under different social (e.g., group size, competitive regimes, and composition) and ecological (e.g., habitat type or predation risk) conditions (see Outstanding questions).

OUTSTANDING QUESTIONS

Broader contexts

Can optimal foraging models inform other aspects of group decision-making, such as where to go next or what resources to favor?

How do consensus costs and within-patch competitive dynamics among group members impact the foraging strategies used by individuals (e.g., whether they are generalist foragers or specialist foragers in heterogeneous patches, or whether they invest in learning how to better handle prey items)? Such questions could be addressed by applying a game-theoretic approach to optimal foraging theory, which can better integrate frequency-dependent processes that arise when group members compete for prey items.

Repeated decisions

Do departures matching the group's optimal departure time also maximize individual performance over repeated foraging events, given other processes such as satiation or accessing patches with different food types?

How are consensus costs accumulated or averaged over the course of sequential decisions?

How does within-group variation in patch quality experienced by individuals over sequential patches (e.g., stochasticity in which individuals access better parts of patches) shape the evolution of decision-making processes?

How does asynchrony in access to the patch affect consensus costs? Does waiting for access to patches or while initiating departures from patches reduce conflicts among group members, for example, by delaying initiators' optimal departure time as a result of increasing their inter-patch access time (waiting plus travel times)?

Consensus costs

Can the mechanisms of collective decision-making favor departures that match the optimal time for the group?

When do the mean of group members' optimal departure times differ from the group-level optimal departure time?

What is the magnitude of the consensus costs – in terms of foraging efficiency – of living in a group?

How do different axes of individual variation in foraging (e.g., personality, producer-scrounger roles, foraging abilities) impact conflicts of interest within a group?

Ecological implications

Do groups change how they make collective decisions to optimize departure times, or minimize consensus costs, under different environmental conditions?

How do habitat conditions and the challenges of moving as a collective combine to affect travel costs for moving groups?

How does predation risk affect consensus costs, given differences in risk and predator detection across group sizes, and does the effect of predation on collective decisions vary depending on whether risk is greater in patches or when traveling between patches? In the case of predation risk within patches, it should increase vigilance and reduce the harvest rate (λ). In the case of predation risk between patches, it should favor strategies that minimize the proportion of time individuals (and their groups) spend moving between patches (e.g., by delaying group departures).

REFERENCES

1. Biro, D. *et al.* (2016) Bringing a Time-Depth Perspective to Collective Animal Behaviour. *Trends Ecol Evol* 31 (7), 550-562.

2. Gordon, D.M. (2016) The Evolution of the Algorithms for Collective Behavior. *Cell Syst* 3 (6), 514-520.

3. King, A.J. *et al.* (2018) Re-wilding Collective Behaviour: An Ecolocical Perspective. *Trends Ecol Evol* 33 (5), 347-357.

4. Westley, P.A.H. *et al.* (2018) Collective movement in ecology: from emerging technologies to conservation and management. *Philos T R Soc B* 373 (1746).

5. Couzin, I.D. and Krause, J. (2003) Self-organization and collective behavior in vertebrates. *Adv Stud Behav* 32, 1-75.

6. Reina, A. *et al.* (2021) Collective decision-making in living and artificial systems: editorial. *Swarm Intell-Us* 15 (1-2), 1-6.

7. Mann, R.P. (2018) Collective decision making by rational individuals. *P Natl Acad Sci USA* 115 (44), E10387-E10396.

8. Herbert-Read, J.E. *et al.* (2019) Collective decision-making appears more egalitarian in populations where group fission costs are higher. *Biol Letters* 15 (12).

9. Couzin, I.D. *et al.* (2005) Effective leadership and decision-making in animal groups on the move. *Nature* 433 (7025), 513-516.

10. Conradt, L. and Roper, T.J. (2005) Consensus decision making in animals. *Trends Ecol Evol* 20 (8), 449-456.

11. King, A.J. and Cowlishaw, G. (2009) All together now: behavioural synchrony in baboons. *Anim Behav* 78 (6), 1381-1387.

12. Papageorgiou, D. and Farine, D.R. (2020) Shared decision-making allows subordinates to lead when dominants monopolize resources. *Sci Adv* 6 (48).

13. Kadak, K. and Miller, N. (2020) Follow the straggler: zebrafish use a simple heuristic for collective decision-making. *P Roy Soc B-Biol Sci* 287 (1940).

14. Strandburg-Peshkin, A. *et al.* (2015) Shared decision-making drives collective movement in wild baboons. *Science* 348 (6241), 1358-1361.

15. King, A.J. *et al.* (2008) Dominance and Affiliation Mediate Despotism in a Social Primate. *Curr Biol* 18 (23), 1833-1838.

16. Smith, J.E. *et al.* (2015) Collective movements, leadership and consensus costs at reunions in spotted hyaenas. *Anim Behav* 105, 187-200.

17. Strandburg-Peshkin, A. *et al.* (2018) Inferring influence and leadership in moving animal groups. *Philos T R Soc B* 373 (1746).

18. Stephens, D.W. and Krebs, J.R. (1986) Foraging theory, Princeton University Press.

19. Mangel, M. and Clark, C.W. (1986) Towards a unifield foraging theory. *Ecology* 67 (5), 1127-1138.

20. Macarthur, R.H. and Pianka, E.R. (1966) On Optimal Use of a Patchy Environment. *Am Nat* 100 (916), 603-+.

21. Winterhalder, B. (1986) Diet Choice, Risk, and Food Sharing in a Stochastic Environment. *J Anthropol Archaeol* 5 (4), 369-392.

22. Smith, J.N. and Dawkins, R. (1971) The hunting behaviour of individual great tits in relation to spatial variations in their food density. *Anim Behav* 19 (4), 695-706.

23. Cody, M.L. (1974) Optimization in Ecology. *Science* 183 (4130), 1156-1164.

24. Pyke, G.H., Studies in the foraging efficiency of animals, University of Chicago, 1974.

25. Charnov, E.L. (1976) Optimal Foraging, Marginal Value Theorem. *Theor Popul Biol* 9 (2), 129-136.

26. Caraco, T. and Giraldeau, L.A. (1991) Social Foraging - Producing and Scrounging in a Stochastic Environment. *J Theor Biol* 153 (4), 559-583.

27. Clark, C.W. and Mangel, M. (1986) The Evolutionary Advantages of Group Foraging. *Theor Popul Biol* 30 (1), 45-75.

28. Giraldeau, L.A. and Caraco, T. (2000) Social foraging theory, Princeton University Press.

29. Ranta, E. *et al.* (1993) Competition Versus Cooperation - Success of Individuals Foraging Alone and in Groups. *Am Nat* 142 (1), 42-58.

30. Sorato, E. *et al.* (2012) Effects of predation risk on foraging behaviour and group size: adaptations in a social cooperative species. *Anim Behav* 84 (4), 823-834.

31. Giraldeau, L.A. and Livoreil, B. (1998) Game theory and social foraging. In Game theory and animal behavior (Dugatkin, L.A. and Reeve, H.K. eds), Oxford University Press.

32. Falcon-Cortes, A. *et al.* (2019) Collective learning from individual experiences and information transfer during group foraging. *J R Soc Interface* 16 (151).

33. Frank, E.T. and Linsenmair, K.E. (2017) Individual versus collective decision making: optimal foraging in the group-hunting termite specialist Megaponera analis. *Anim Behav* 130, 27-

35. DiGiorgio, A.L. *et al.* (2020) Wild Bornean orangutan (Pongo pygmaeus wurmbii) feeding rates and the Marginal Value Theorem. *Am J Primatol* 82 (10).

34. Palacios-Romo, T.M. *et al.* (2019) Uncovering the decision rules behind collective foraging in spider monkeys. *Anim Behav* 149, 121-133.

35. DiGiorgio, A.L. *et al.* (2020) Wild Bornean orangutan (Pongo pygmaeus wurmbii) feeding rates and the Marginal Value Theorem. *Am J Primatol* 82 (10).

36. Davidson, J.D. and El Hady, A. (2019) Foraging as an evidence accumulation process. *Plos Comput Biol* 15 (7).

37. Kolling, N. and Akam, T. (2017) (Reinforcement?) Learning to forage optimally. *Curr Opin Neurobiol* 46, 162-169.

38. Venkataraman, V.V. *et al.* (2017) Hunter-gatherer residential mobility and the marginal value of rainforest patches. *P Natl Acad Sci USA* 114 (12), 3097-3102.

39. Vogel, E.R. (2005) Rank differences in energy intake rates in white-faced capuchin monkeys, Cebus capucinus: the effects of contest competition. *Behav Ecol Sociobiol* 58 (4), 333-344.

40. Cantor, M. *et al.* (2020) A primer on the relationship between group size and group performance. *Anim Behav* 166, 139-146.

41. Polansky, L. *et al.* (2015) Elucidating the significance of spatial memory on movement decisions by African savannah elephants using state-space models. *P Roy Soc B-Biol Sci* 282 (1805).

42. The Modelling Animal Decisions Group (2014) The evolution of decision rules in complex environments. *Trends Cogn Sci* 18 (3), 153-161.

43. Pierce, G.J. and Ollason, J.G. (1987) Eight reasons why optimal foraging theory is a complete waste of time. *Oikos* May, 111-118.

44. Sih, A. and Christensen, B. (2001) Optimal diet theory: when does it work, and when and why does it fail? *Anim Behav* 61, 379-390.

45. Watanabe, Y.Y. *et al.* (2014) Testing optimal foraging theory in a penguin-krill system. *P Roy Soc B-Biol Sci* 281 (1779).

46. Pyke, G.H. (1978) Optimal Foraging in Hummingbirds - Testing the Marginal Value Theorem. *Am Zool* 18 (4), 739-752.

47. Pacheco-Cobos, L. *et al.* (2019) Nahua mushroom gatherers use area-restricted search strategies that conform to marginal value theorem predictions. *P Natl Acad Sci USA* 116 (21), 10339-10347.

48. Turrin, C. *et al.* (2017) Social resource foraging is guided by the principles of the Marginal Value Theorem. *Sci Rep* 7 (1), 1-13.

49. Brown, J.S. (1988) Patch Use as an Indicator of Habitat Preference, Predation Risk, and Competition. *Behav Ecol Sociobiol* 22 (1), 37-47.

50. Petit, O. *et al.* (2009) Collective decision-making in white-faced capuchin monkeys. *P Roy Soc B-Biol Sci* 276 (1672), 3495-3503.

51. Razafindratsima, O.H. *et al.* (2014) Patterns of Movement and Seed Dispersal by Three Lemur Species. *Am J Primatol* 76 (1), 84-96.

52. Houle, A. *et al.* (2006) Testing mechanisms of coexistence among two species of frugivorous primates. *J Anim Ecol* 75 (4), 1034-1044.

53. Houle, A. *et al.* (2010) Intratree vertical variation of fruit density and the nature of contest competition in frugivores. *Behav Ecol Sociobiol* 64 (3), 429-441.

54. King, B.R. (1980) Social-Organization and Behavior of the Grey-Crowned Babbler Pomatostomus-Temporalis. *Emu* 80 (Apr), 59-76.

55. Ostreiher, R. *et al.* (2021) On the self-regulation of sentinel activity among Arabian babbler groupmates. *Anim Behav* 173, 81-92.

56. Camerlenghi, E. *et al.* (2022) Cooperative breeding and the emergence of multilevel societies in birds. *Ecol Lett*.

57. Rowley, I. (1978) Communal Activities among White-Winged Choughs Corcorax-Melanorhamphus. *Ibis* 120 (2), 178-&.

58. Smith, S.M. (1991) The black-capped chickadee: behavioral ecology and natural history, Cornell University Press.

59. Papageorgiou, D. *et al.* (2019) The multilevel society of a small-brained bird. *Curr Biol* 29 (21), R1120-R1121.

60. Chaverri, G. *et al.* (2013) A call-and-response system facilitates group cohesion among disc-winged bats. *Behav Ecol* 24 (2), 481-487.

61. Christal, J. and Whitehead, H. (2001) Social affiliations within sperm whale (Physeter macrocephalus) groups. *Ethology* 107 (4), 323-340.

62. Doolan, S.P. and Macdonald, D.W. (1996) Diet and foraging behaviour of group-living meerkats, Suricata suricatta, in the southern Kalahari. *J Zool* 239, 697-716.

63. Rood, J.P. (1986) Ecology and social evolution in the mongooses. In Ecological Aspects of Social Evolution (Rubenstein, D.R. and Wrangham, R.W. eds), Princeton University Press.

64. King, A.J. and Cowlishaw, G. (2009) Leaders, followers, and group decision-making. *Commun Integr Biol* 2 (2), 147-150.

65. Conradt, L. and Roper, T.J. (2010) Deciding group movements: Where and when to go. *Behav Process* 84 (3), 675-677.

66. Lague, M. *et al.* (2012) The effects of facilitation and competition on group foraging in patches. *J Theor Biol* 310, 88-96.

67. Perry, S.E. *et al.* (2017) Older, sociable capuchins (Cebus capucinus) invent more social behaviors, but younger monkeys innovate more in other contexts. *P Natl Acad Sci USA* 114 (30), 7806-7813.

68. Altmann, J. and Alberts, S.C. (2005) Growth rates in a wild primate population: ecological influences and maternal effects. *Behav Ecol Sociobiol* 57 (5), 490-501.

69. Heyes, C.M. (1994) Social-Learning in Animals - Categories and Mechanisms. *Biol Rev* 69 (2), 207-231.

70. Isbell, L.A. (1991) Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behav Ecol* 2 (2), 143-155.

71. Sterck, E.H.M. and Steenbeek, R. (1997) Female dominance relationships and food competition in the sympatric Thomas langur and long-tailed macaque. *Behaviour* 134, 749-774.

72. Pruetz, J.D. and Isbell, L.A. (2000) Correlations of food distribution and patch size with agonistic interactions in female vervets (Chlorocebus aethiops) and patas monkeys (Erythrocebus patas) living in simple habitats. *Behav Ecol Sociobiol* 49 (1), 38-47.

73. Call, J. and Tomasello, M. (1994) The social learning of tool use by orangutans (Pongo pygmaeus). *Hum Evol* 9 (4), 297-313.

74. Holzhaider, J.C. *et al.* (2010) The development of pandanus tool manufacture in wild New Caledonian crows. *Behaviour* 147 (5-6), 553-586.

75. Schuppli, C. *et al.* (2016) Development of foraging skills in two orangutan populations: needing to learn or needing to grow. *Front Zool* 13 (1), 1-17.

76. Byrne, R.W. (2000) How Monkeys Find Their Way: Leadership, Coordination, and Cognitive Maps of African Baboons. In On The Move: How and Why Animals Travel in Groups (Boinski, S. and Garbor, P.A. eds), p. 811, University of Chicago Press.

77. King, A.J. and Sueur, C. (2011) Where Next? Group Coordination and Collective Decision Making by Primates. *Int J Primatol* 32 (6), 1245-1267.

78. Stueckle, S. and Zinner, D. (2008) To follow or not to follow: decision making and leadership during the morning departure in chacma baboons. *Anim Behav* 75, 1995-2004.

79. Amornbunchornvej, C. *et al.* (2018) Coordination Event Detection and Initiator Identification in Time Series Data. *Acm T Knowl Discov D* 12 (5).

80. Strum, S. (2001) Almost human: A journey into the world of baboons, Chicago University Press.

81. Conradt, L. and Roper, T.J. (2000) Activity synchrony and social cohesion: a fission-fusion model. *P Roy Soc B-Biol Sci* 267 (1458), 2213-2218.

82. Prox, L. and Farine, D.R. (2020) A framework for conceptualizing dimensions of social organization in mammals. *Ecol Evol* 10 (2), 791-807.

83. Conradt, L. and Roper, T.J. (2007) Democracy in animals: the evolution of shared group decisions. *P Roy Soc B-Biol Sci* 274 (1623), 2317-2326.

84. Papageorgiou, D. *et al.* (2021) Seasonality impacts collective movements in a wild group-living bird. *Mov Ecol* 9 (1).

85. Jetz, W. and Rubenstein, D.R. (2011) Environmental Uncertainty and the Global Biogeography of Cooperative Breeding in Birds. *Curr Biol* 21 (1), 72-78.

86. Downing, P.A. *et al.* (2020) Group formation and the evolutionary pathway to complex sociality in birds. *Nat Ecol Evol* 4 (3), 479-486.

87. Schreier, A.L. and Swedell, L. (2012) Ecology and sociality in a multilevel society: Ecological determinants of spatial cohesion in hamadryas baboons. *Am J Phys Anthropol* 148 (4), 580-588.

88. Sugiura, H. *et al.* (2011) Variation in Spatial Cohesiveness in a Group of Japanese Macaques (Macaca fuscata). *Int J Primatol* 32 (6), 1348-1366.

89. Wittemyer, G. *et al.* (2005) The socioecology of elephants: analysis of the processes creating multitiered social structures. *Anim Behav* 69, 1357-1371.

90. Hart, E.E. *et al.* (2022) Static and dynamic methods in social network analysis reveal the association patterns of desert-dwelling giraffe. *Behav Ecol Sociobiol* 76 (5).

91. Spikins, P. *et al.* (2021) Theoretical and Methodological Approaches to Ecological Changes, Social Behaviour and Human Intergroup Tolerance 300,000 to 30,000 BP. *J Archaeol Method Th* 28 (1), 53-75.

92. Milinski, M. (1979) An evolutionarily stable feeding strategy in sticklebacks. *Z Tierpsychol* 51 (1), 36-40.

93. Kokubun, N. *et al.* (2011) Penguin head movement detected using small accelerometers: a proxy of prey encounter rate. *J Exp Biol* 214 (22), 3760-3767.

94. Andriamandroso, A.L.H. *et al.* (2016) A review on the use of sensors to monitor cattle jaw movements and behavior when grazing. *Biotechnol Agron Soc* 20, 273-286.

95. Conradt, L. *et al.* (2013) Swarm Intelligence: When Uncertainty Meets Conflict. *Am Nat* 182 (5), 592-610.

96. Conradt, L. and Roper, T.J. (2003) Group decision-making in animals. *Nature* 421 (6919), 155-158.

97. Conradt, L. and Roper, T.J. (2009) Conflicts of interest and the evolution of decision sharing. *Philos T R Soc B* 364 (1518), 807-819.

98. Sueur, C. *et al.* (2012) From Social Network (Centralized vs. Decentralized) to Collective Decision-Making (Unshared vs. Shared Consensus). *Plos One* 7 (2), e32566.

99. Bettinger, R.L. and Grote, M.N. (2016) Marginal value theorem, patch choice, and human foraging response in varying environments. *J Anthropol Archaeol* 42, 79-87.

100. Papageorgiou, D. and Farine, D.R. (2020) Group size and composition influence collective movement in a highly social terrestrial bird. *Elife* 9, e59902.

CHAPTER 2

Rank- and age-related differences in patch exploitation and foraging behavior in white-faced capuchin monkeys[2]

ABSTRACT

In this study, I assess aspects of social dynamics and individual predictors of foraging behavior in wild white-faced capuchin monkeys living on Barro Colorado Island, Panama. Using an observational study of capuchin groups feeding on *Attalea butyracea* palm trees, I evaluate the extent of variation in foraging efficiency across group members and how this is predicted by important determinants of social status and experience in a group including age, a measure of a group member's experience, abilities, and strength, and social rank, a measure of a group member's competitive ability. To provide a more holistic picture of the specific behavioral strategies that individuals use to maximize their foraging success, I measure foraging behaviors of group members during both the search phase of finding food items in a patch (like how long it takes to locate a ripe fruit to eat and what search behaviors a monkey performs to find fruit) and the consumption phase of processing and eating those food items (the handling time to eat a fruit and how much fruit pulp is consumed). I also evaluate whether the timing of access to trees is a strategy individuals use to increase their foraging returns by receiving a finder's share portion of fruit. Across all the foraging parameters I calculate, I consistently observe within and between

---

[2] Adapted from: Davis, G.H. & Crofoot, M.C. (In review). Rank- and age-related differences in patch exploitation and foraging behavior in white-faced capuchin monkeys.

individual differences. My results suggest that higher ranking individuals obtain preferential access to *A. butyracea* patches by displacing others more often on the fruit and receiving more food overall (especially dominant males). I also find that adults are more efficient foragers than juveniles, whereby they test fewer fruits before finding a ripe one to eat and consume greater proportions of fruits in shorter amounts of time (handling time) when compared to juveniles. Adults also take longer to find a fruit to eat than juveniles, indicating they may be more discriminatory of which fruits to select. Finally, I find that individuals who arrive first into patches receive a finder's share portion of the patch that ultimately boosts their intake when compared to non-finder group members. Taken together, these results suggest that dominance rank, age class, and timing of access to a foraging patch all influence patterns of foraging behavior and efficiency, leading to inter-individual differences in the foraging preferences of group mates.

INTRODUCTION

Finding and processing food is a vital part of daily activity for all animals; so vital, in fact, that survival and reproductive success directly depend upon the intake of resources (Schoener 1987, Stephens & Krebs 1986). The fitness consequences of food intake for an animal even cascade down to the survival and quality of that individual's own offspring (Warner et al. 2015, Karell et al. 2009, Rotem et al. 2003). Animals need to decide what kinds of food to eat, locate where that food is, determine how to process that food for consumption, and, if food is located in discrete patches, decide when to leave a food patch and move on to the next (Stephens et al. 2008, Charnov 1976). For animals who live in groups (or forage with other individuals), individuals must also navigate the social dynamics of foraging, including who gets access to food and how much food each individual receives (Giraldeau & Caraco 2000). Thus, being an "efficient" forager requires a number of cognitive, technical, and social skills that animals must acquire and learn, often early on during their lifetimes.

Substantial theory has postulated on what signifies efficiency in foraging behavior (Giraldeau & Caraco 2000, Perry & Pianka 1997, Mangel & Clark 1986, Pyke 1984, Charnov 1976). At its simplest, foraging efficiency is a measure of an animal's ability to acquire energy and nutrients in the least costly manner, i.e., with the least amount of energy expended acquiring food and/or with the least amount of risk from predation. Our understanding about efficient foraging has greatly increased through optimal foraging theory (OFT) models that use time and energy intake as currencies. These models show that an efficient forager is one who maximizes their energetic intake, often measured in caloric gain, while minimizing their energetic loses while searching for and consuming food (Parker & Maynard Smith 1990, Stephens & Krebs 1986, Charnov 1976, MacArthur & Pianka 1966). Furthermore, OFT models predict that when food items occur in discrete patches in the environment, like fruit trees or clusters of prey, an efficient forager optimally travels between food patches in a short amount of time relative to distance (i.e., they travel directly from patch to patch without unnecessary meandering, Bartumeus & Catalan 2009). Once food patches are located, an efficient forager then faces a number of challenges to maximizing their energy intake. They must select which food items in the patch are the best to consume, such as the ripest fruits that hold the highest caloric value, and locate these food items as efficiently as possible. Once the forager has selected an appropriate food item, they need to process that food item to extract the largest amount of energy in the shortest time (often referred to as "handling time" in foraging theory, Stephens & Krebs 1986). Animals who forage alongside other individuals (social foragers) must also compete for access to the food patch itself and the food items within it (Giraldeau & Caraco 2000). These measures of foraging efficiency all influence the rate of energy intake and are important determinants of how long an individual should spend eating in a food patch before moving on.

However, the perfectly-efficient forager of theoretical models rarely, if ever, exists in nature. Individuals of the same species, and even members of the same social group, typically vary substantially in their abilities to find and consume food. Individual variation in foraging efficiency can be shaped by a number of factors, including an animal's expertise in foraging (Kamil & Roitblat 1985), their strength and intrinsic skills to feed on hard-to-process food items (Eadie 2015), and their competitive abilities to access the best portions of a feeding patch and exclude others while feeding (also called their susceptibility to interference: the detrimental effect of competitors on their intake rate, Sutherland & Parker 1992, Goss-Custard & Durell 1987).

For long-lived species with an extended juvenile period, learning is key to efficient foraging. As they mature, the foraging efficiency of juvenile primates, for example, improves as they accumulate experience (i.e., individual learning) and as they are exposed to and sometimes adopt the foraging strategies of older, more experienced group mates (i.e., social learning, Schuppli et al. 2016, Thornton et al. 2011, Rendell et al. 2010, Rapaport & Brown 2008, Galef et al. 2005, Giraldeau et al. 2002). Indeed, learning how to properly forage is one of the proposed explanations for long juvenile periods, and even larger-brain sizes, in primates (Walker et al. 2006, Gibson 1986, Harvey et al. 1980). The "needing to learn hypothesis" postulates that complex and unpredictable niches select for longer juvenile periods (and an increase in brain size), because this allows young individuals more time, and a greater ability, to learn how to exploit resources in their environments before they reach critical reproductive age (Schuppli et al. 2012, Johnson & Bock 2004). In species that primarily feed on food items that require technical skills to process (like a fruit with a hard shell that must be opened and pealed to reveal the edible pulp inside), it can take substantial time to learn how to successfully obtain the necessary energy and nutrients to survive (this version of the needing to learn hypothesis is often referred to as the "difficult diet hypothesis", Kaplan et al. 2000, Gibson 1986). Beyond acquiring the technical skills about how to forage, older individuals are usually more capable of performing well in foraging tasks purely based on greater strength and size when compared to young (Bird & Bird 2002). As such, studies often report that juvenile individuals are less efficient foragers when compared to adults (Franks & Thorogood 2018, Schuppli et al. 2016, Agostini et al. 2005). Alternatively, other studies see little or no difference between adult and juvenile foraging efficiency (MacKinnon 2006, Boinski & Fragaszy 1989). Ultimately, further research is needed to illuminate how age correlates with foraging efficiency and if juvenile individuals need time to accumulate expertise to become efficient foragers.

For animals who forage alongside other individuals, another essential predictor of efficient foraging is competitive ability, or the ability to compete with fellow foragers for a share of the food patch and/or the best food items to maximize energy intake rates (Goss-Custard & Sutherland 1997, Sutherland 1996, Goss-Custard & Durell 1987). Competition between group members is often quite substantial and plays a role in foraging payoffs for individuals (De la Fuente et al. 2019, Ranta et al. 1993, Clark & Mangel 1986). Competition between group mates can arise in two primary ways: simply as a result of more individuals being present such that access to food is divided among group members (scramble competition) or due to active competition between individuals over food that often involves aggression (contest competition) (Isbell 1991, Nicholson 1954).

Competition is particularly exacerbated when food resources are can be monopolized, for example when they are clumped (Koenig 2002). Under these conditions, access to food is limited and some individuals can exclude others from feeding. When one, or a few, group members can monopolize resources, some individuals may seek to increase their foraging advantage by arriving to feeding patches first (Ranta et al. 1996, Vickery et al. 1991, Barnard & Sibly 1981). By being the first to arrive, an individual may obtain a “finder’s share” of the food resource; that is, the amount of food consumed by the first individual into the patch before the arrival of others (Giraldeau & Caraco 2000). In groups with hierarchical dominance structures, a “finder’s” strategy is predicted to be efficient for lower-ranking individuals who can increase their food intake by arriving at patches early and consuming the available food rapidly, before they are displaced by more dominant group mates (Hirsch et al. 2020, Di Bitetti & Janson 2001, Barta & Giraldeau 1998). Higher-ranking individuals are predicted to have priority access to resources, such that they can defend resources from others, often benefiting from increased energy intake rates as a result (Koenig 2002, Janson 1985, Vehrencamp 1983). Ultimately, dominance status has been shown to directly influence the energy intake rate of individuals and is an important predictor of foraging efficiency.

Here, I evaluated the extent of variation in foraging behavior across individuals in a group and how this was influenced by important determinants of social status and experience in a group, including *age*, a measure of an individual’s experience, abilities, and strength, and *social rank*, a measure of an individual’s competitive ability. While age and dominance rank have been shown to influence foraging success (Vogel 2005), these two are rarely considered in parallel.

Furthermore, the majority of studies that have examined interindividual variation in foraging efficiency use energy intake rates or total energy gained as the principal, and often only, measure to compare foraging success across different individuals. While energy intake provides a clear currency from which to compare the outcome of foraging tasks, it does not provide information about the specific foraging behaviors that result in foraging efficiency, such as when an individual gets access to a feeding patch, how long it takes them to search for a food item, how long it takes to handle and consume that food item, etc. To provide a more holistic picture of the specific behavioral strategies that individuals use to maximize their foraging success, I measured foraging efficiency across multiple levels. These levels included: access to the food patch (when an animal entered a patch), searching behaviors to find food items, how long it took an animal to search for a food item, the time it took an animal to process and consume a food item, how much of each food item an animal consumed, and the estimated amount of food available to an animal calculated as a measure of how large the foraging patch is relative to the number of foragers feeding together.

To capture the influence of both age and rank on interindividual variation in foraging, I used social groups of white-faced capuchin monkeys living on Barro Colorado Island, Panama. Capuchin monkeys live in structured social groups with dominance hierarchies that contain individuals of all age and rank classes, providing an ideal study system to compare foraging efficiency between juveniles versus adults and subordinates versus dominants. Additionally, capuchins predominantly feed on fruiting trees that provide discrete food patches in their environment that can be monopolized by certain group members to exclude others from feeding. These fruit items typically require complex handling techniques to process, like the peeling of a hard shell to access the ripe pulp inside.

I hypothesized that individuals in a capuchin group vary in their foraging abilities as a result of social rank and age and thus have consistent differences in their foraging behaviors. As social dominance is known to influence access to resources, I predicted that in capuchin monkey groups, high ranking individuals would: (a) displace others more often on the foraging patch, (b) be displaced less frequently, and (c) have a higher overall intake when compared to lower ranking group members. Older individuals are often more efficient foragers due to experience accumulated during their lifetimes and increased strength to handle hard-to-process food items. Therefore, I predicted that in comparison to juveniles, adult capuchin monkeys would: (a) test fewer fruits before finding a ripe one to consume, (b) take less time to find a ripe fruit, (c) take less time to consume a ripe fruit (shorter handling time), and (d) consume more of the fruit pulp when compared to juveniles. Finally, I hypothesized that the timing of access to the patch influences foraging behavior and efficiency. I predicted that individuals who arrive first into foraging patches obtain a finder's share portion of the patch which increases their foraging efficiency. This study evaluates two key sources of individual variation (age and rank) and how they relate to multiple measures of foraging efficiency.

METHODS

Study Site: For this study, four field observers conducted behavioral observations of two well-studied capuchin groups (Tórrez-Herrera et al. 2020, Crofoot et al. 2008, Crofoot 2007) at the Smithsonian Tropical Research Institute field site on Barro Colorado Island (BCI) in Panama. Data collection occurred during the months of June to September in 2015 and 2016. BCI (9°9'N, 79°51’W) is a 1560-hectare island in the Panama Canal composed of semi-deciduous lowland tropical moist forest. The island was formed during the construction of the Panama Canal between 1911 and 1914 when the waters of the Chagres River were dammed to create Gatun Lake. The United States Government designated the island as a natural preserve in 1923, and BCI has been administered by the Smithsonian Tropical Research Institute since 1946. As one of the most studied tropical forests on earth, research on BCI has been at the forefront of measuring diversity of plant and animal life in the tropics. BCI has two primary seasons: a wet season from April to November and a dry season from December to May (Windsor 1990). Distinct seasonality in the availability of fruiting trees on the island occurs, an important resource for many species, including the resident primate populations. Fruit availability tends to be high during the dry season and into the early wet season and is lowest during the late wet season (Leigh 1999). Five resident primate species live on BCI, including the white-faced capuchin monkeys.

Primate study species: This study examines foraging behavior in white-faced capuchin monkeys. This species is an arboreal, New World monkey that is native to the forests of Central America and the extreme north-west portion of Colombia. White-faced capuchins are part of the family Cebidae, subfamily Cebinae. Capuchins rely heavily on ripe fruiting trees for food (Fragaszy et al. 2004), an ephemeral resource in the seasonal tropical forest of BCI that are typically distributed in discrete patches (trees) across their home ranges. A population of between 15-20 capuchin social groups lives on BCI (Crofoot, Davis, and Torrez, unpublished data).

White-faced capuchins are long-lived animals that live about 30 years in the wild and have a prolonged juvenile period (Harvey et al. 1987). Capuchins live in multi-male, multi-female, cohesive social groups that remain in proximity together all day every day of their lives (excluding rare dispersal events, Perry 1997). Females are philopatric (i.e., stay in their natal group), whereas males migrate one to a few times during their lifetime into new neighboring groups (Fedigan 1993). Social groups usually average between 17-19 individuals (Fedigan et al. 2001), although the study groups on BCI tend to have fewer individuals averaging around 11 group members (ranging from 9-25 individuals in a study published by Crofoot 2007). There is a dominance hierarchy within males and females, such that dominant individuals tend to gain priority access to important resources and mates (Jack & Fedigan 2006; Vogel 2004). The dominant male, in particular, has a central role in capuchin groups (Di Bitetti 1997) and can monopolize access to resources through aggressive behaviors, including displacing other group mates off of feeding patches (Janson 1985).

Capuchins are omnivorous animals who eat a varied diet, although they rely heavily on fruit, which comprises between 60-80% of their diet (Fragaszy et al. 2004). The capuchin groups on BCI live in home ranges of approximately 90-160 hectares and are xenophobic with mutually agonistic relationships with their neighbors (Crofoot 2007). I focused my observations on two groups of capuchins: FC (composed of 12 individuals), and TOP (composed of 18 individuals, see Figure 5 for an aerial view of BCI and the home ranges of the two study groups). Both groups have a single adult male, and FC group has 3 adult females and TOP has 5 adult females. There were 7 juvenile individuals in FC and 1 infant, and 10 juveniles and 2 infants in TOP. During my study period there were no subadult individuals (potentially a result of a mass mortality event in years prior, Milton & Giacalone 2014). Members of each of the primary primate study groups were fitted with GPS and radio telemetry collars, and their movements and activity patterns were tracked throughout the duration of the study.

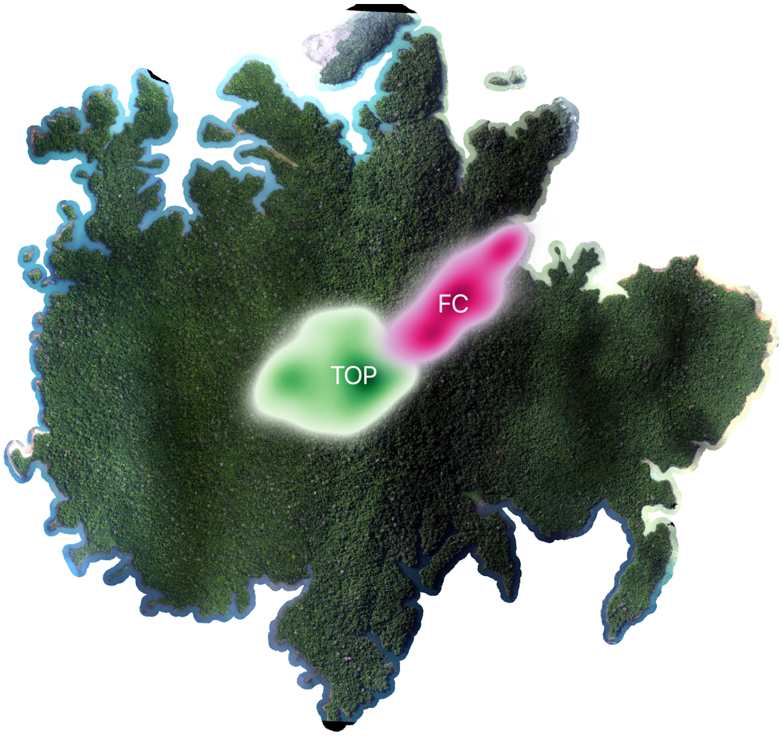

Figure 5. Home ranges for white-faced capuchins (*Cebus capucinus*) belonging to FC (pink) and TOP (green) groups on Barro Colorado Island, Panama from June to August, 2016. Home ranges were calculated using continuous time movement models implemented in the ctmm package in R (Calabrese et al. 2016) using handheld GPS data, where observers recorded GPS points of the group centroid every 5 minutes during daily follows. The color gradient represents the probability mass for the home range (darker colors reflect higher intensity of use).

Foraging tree study species: I focused my data collection on *Attalea butyracea* palm trees, a keystone tree species during June-September of 2015 and 2016. The capuchin groups spend >75% of their total feeding time during these months in these trees. *A. butyracea* fruits grow in large clumps, or infructesences, that suspend off a single stem of the palm plant (Figure 6). Due to this structure, palm fruits are easily monopolizable for high-ranking individuals who can exclude their group-mates from the infructescence. Furthermore, palm fruits in an infructescence ripen asynchronously, such that the monkeys must discriminate between ripe versus unripe fruits. The edible pulp of palm fruits is covered by a hard exterior shell, requiring the monkeys to open the shell to access the pulp inside. These characteristics of *A. butyracea* trees allowed me to quantify the ways in which individuals vary in their abilities to process and consume food items (fruits). Four observers collected data on the two capuchin study groups, focusing on foraging behavior in *A. butyracea* trees.

Figure 6. Photographs of *A. butyracea* palm infructescences, without monkeys feeding, with multiple group members feeding together, and with the dominant male feeding.

<u>*Observational daily follows:*</u> Capuchin monkeys are diurnal primates, and activities begin at or just after dawn. In order to track both study groups, I used radio telemetry. One member in

each of the capuchin study groups was equipped with a radio collar. Each collar transmited a unique frequency signal. Using a hand-held antenna and receiver radio, I and my field assistants could reliably locate the study group in the early morning. Daily follows lasted for 5-12 contact hours with the selected study group. We alternated daily between study groups to obtain behavioral data on each group each week throughout the study season.

Once visual contact was made with the study group in the morning, we recorded the identities and age/sex classes of all group members present. We identified individuals within each social group using differences in size, facial fur patterns, and other distinctive markings (e.g., spots, scars, freckles, missing or broken appendages). Because there was more than one observer collecting data for this project, we conducted periodic inter-observer reliability checks to assure agreement in identification of group members, behavioral activity categories, and identification of fruit trees. As these groups are habituated to human observers, we could successfully follow underneath the monkeys during the day as they move and forage in the trees. When the group was traveling from place to place, one observer positioned themself at the front of the troop, looking for any feeding trees with ripe fruits the group might visit. We recorded ad libitum observations of significant events during the daily observation time period, such as predation threats, intergroup encounters with other monkey groups, etc., as these can significantly impact behavior.

Social dominance interactions: I and my field assistants recorded subtle and active aggressive encounters on an all-occurrence basis throughout daily follows of the monkey groups. Subtle encounters included cowers, avoids, facial or vocal threats whereas active encounters referred to active fighting that included behaviors such as chases, bites, slaps, and lunges. We noted all observations of aggressive interactions between all group members except dependent infants (see ethogram for specific behavioral information in supplementary materials, Altmann 1974).

Focal tree method: To quantify variation in foraging behaviors among group members, I and my field assistants used an adaptation of Vogel & Janson's focal tree method (Vogel & Janson 2007). For each foraging visit in *A. butyracea* trees, the field observers recorded the tree's location (using a hand-held GPS) and determined the order of individuals' arrivals and departures, recording the identity and time each member of the focal group entered and left the fruit tree. The time between the first arrival and last departure represented the "total group feeding time". If there were gaps in feeding during the feeding bout such that no animals were feeding, the amount of time in which monkeys were not feeding was subtracted from the total group feeding time. To obtain foraging rates and feeding behaviors, three to four observers collected data in the field. Because of the size and shape of *A. butyracea* infructescences, it was possible to record each time any and all members of the monkey group entered the food patch and removed fruit. When a group entered a palm, the observers positioned themselves on either side of the palm to get the complete view of all fruiting clumps within the palm (occasionally, palms have more than one fruiting raceme). The primary observer responsible for data collection called out the behaviors and the secondary observers inputted the behaviors using the iOS app "Animal Behaviour Pro" on an iPhone or iPad (version 1.2, Newton-Fisher 2012). Using this app, we generated specific buttons with the identification names of the monkeys and all behaviors in our ethogram. The start of the sampling bout occurred when the first individual entered a palm tree, and the primary observer said aloud the date and exact time. The primary observer also noted the number of fruit clumps in the palm. Using the Animal Behaviour Pro app, we recorded the time (to the second), direction of entry, identification of the first monkey arrival to the palm, each successive arrival, and the identification and direction of exit of each departing monkey from the palm. We also recorded displacement events in palm trees, including the initiator and receiver of the displacement.

To calculate individual foraging behaviors, we recorded the identity of each monkey that removed fruit, the amount of fruit pulp taken and eaten, and the time each fruit is harvested and subsequently discarded for each monkey that fed. The following foraging behaviors, in particular, were recorded on an all-occurrence basis for all monkeys who entered and fed in each palm. Each behavior was associated with the actor (the identity of the monkey who performed the behavior) and the time stamp to the second when it was inputted into the Animal Behaviour Pro app. 1) *Patch entry time:* when a monkey descended onto the fruiting raceme. The direction of entry was also recorded using 45-degree increments corresponding to N, NE, E, SE, S, SW, W, and NW. 2) *Patch exit time:* when a monkey left the fruiting raceme. The direction of exit from the patch was recorded like above in 45-degree increments. 3) *Search behaviors* while a monkey was attempting to find a ripe fruit to consume. These included behaviors where a monkey *touches*, *bites*, or *drops* a fruit without consuming the fruit. A touch was defined as when an individual used its hands to test and squeeze fruits on the fruiting clump, without pulling them off the clump. A bite occurred when an individual used its teeth to bite into a fruit, without ultimately eating it. A drop was recorded when an individual removed a fruit from the fruiting clump and discarded it without eating. 4) *Start time of eating a fruit*: the time, to the second, a monkey started to process and eat a fruit (from the moment the monkey took the fruit off the raceme and began to manipulate and peal it for consumption). 5) *End time of eating a* *fruit:* the time, to the second, a monkey stopped eating a fruit and discarded it to the forest floor. 6) *Percent of the fruit consumed*: once a monkey stopped eating a fruit and discarded it, we recorded approximately how much of the fruit pulp the monkey ate. The approximate amount of pulp consumed was recorded in four categories: >25% eaten, 25-50% eaten, 50-75% eaten, and 75-100% eaten. These categories were chosen because the monkeys typically peal the fruit up to four times to consume the entire pulp (i.e., if a monkey ate only about 25% of the fruit pulp, it was readily observable because the monkey would peal a fourth of the hard outer shell and then consume the pulp and discard the fruit). If, because of visual constraints, the amount of pulp consumed was not visible, we recorded "unknown" for the percent of fruit consumed.

These observations provided information for each individual monkey on: entry times into trees, fruit intake rates, searching behaviors for fruits, searching rates for ripe fruits, handling times for consumption of a ripe fruit, how much of each food item (a fruit) was consumed, and competitive interaction data for all individual monkeys in the tree. We collected data on capuchin foraging in a total of 231 *Attalea butyracea* focal trees (166 trees for FC group and 66 trees for TOP group).

<u>Data analyses</u>

To assess the impact of social dominance on access to resources, I first computed dominance hierarchies within each capuchin monkey group. Dominance hierarchies were calculated based on subtle (i.e., cowers, avoids, facial or vocal threats) and active (i.e., chases, bites, slaps, fights, lunges) aggressive outcomes. To avoid circularity in my assessment of dominance ranks and displacement events on focal trees, I calculated dominance hierarchies using data from my all-occurrence sampling of aggressive encounters during continuous daily observations and I excluded displacement events from my calculations. I only assessed dominance status for adult individuals. The hierarchical dominance relationships were determined on the basis of direction of agonistic dyadic interactions where I could determine a clear aggressor (winner) and clear receiver (loser) of the threat. I used these winner-loser interactions to calculate and rank each individual in each monkey group for each study year by Elo scores (Neumann et al. 2011). Because my study periods for each year were short (3-4 months long), I assumed dominance ranks to be stable during each study period. To achieve a more robust estimate of dominance rank, I generated 1000 replicated datasets of interactions by randomizing the order of interactions (timing). I calculated the mean and 95% confidence intervals of ranks of individuals based on Elo score, using the R package aniDom (Farine & Sanchez-Tojar 2022).

Prior to statistical analyses, I calculated the following foraging parameters relevant to my predictions by processing the raw data output from the Animal Behavior Pro app. 1) *Total intake*. To assess if higher ranking individuals had a higher overall intake rate when compared to lower ranking group members, I summed the total amount of fruit pulp (the percent of pulp eaten per fruit) each monkey had consumed by the end of the foraging bout for each palm tree. 2) *Number of search behaviors before finding a ripe fruit to consume.* To compare if older individuals were more adept at finding a ripe fruit to consume versus younger individuals, I calculated the number of searching behaviors for all adults and juveniles. This included the number of touches, bites, and drops a monkey performed before every ripe fruit that it ate. I predicted adults would test fewer fruits before finding a ripe one to eat. 3) *Inter-fruit search time.* To assess if adult individuals were also faster at finding a ripe fruit when compared to juveniles, I calculated how long it took each monkey to find each ripe fruit that it ate. This time interval was calculated by recording the time, to the second, each monkey completed eating one fruit by dropping it to the forest floor and started to process and eat the next ripe fruit. 4) *Handling time*. If older individuals were also more efficient foragers, I further predicted they would take less time to consume each fruit when compared to younger individuals. I calculated this measure of handling time from when the monkey started to peel open the outer fruit shell until the monkey discarded that fruit to begin searching for the next fruit to consume. 5) *Percent of the fruit consumed*. As I expected adults to ingest a greater proportion of the fruit pulp when compared to juveniles (an additional measure of foraging efficiency), I compared approximately how much of the fruit pulp a monkey ate for adults versus juveniles. 6) *Patch entry time and delay to patch entry*. As I anticipated that the timing of access to the patch influences foraging behavior and efficiency, I calculated what time each monkey entered the tree relative to the first monkey who entered. The first monkey who entered the fruit raceme had a start time of zero, marking the beginning of the group foraging bout. All subsequent individuals who entered into the tree and fed had a start time relative to that first individual, which can also be considered their delay to patch entry time. 7) *Finder's share.* I predicted that the first individual to enter foraging patches would receive a boost in foraging return, marked as the amount of fruit pulp they consumed before the arrival of the second individual into the fruit raceme (the "finder's share").

Statistical analyses

All analyses and plots were done using R (R Development Core Team, 2022). Data were analyzed using generalized linear mixed models (GLMM) using glmmTMB as implemented in the package glmmTMB (Brooks et al. 2017). These models are fitted using maximum likelihood estimation via Template Model Builder. I calculated standardized model coefficients (β), their

95% confidence intervals (CIs), and report categorical effect sizes in my results. I used the ggeffects package (Lüdecke 2018) to calculate the marginal effects and 95% CIs for each of my models, and then plotted these using the ggplot2 (Wickham 2016) and cowplot (Wilke 2020) packages.

For analyses involving dominance rank as a predictor variable, I assessed rank in two ways: 1) as a continuous variable where each individual was assigned a numeric dominance rank corresponding with their Elo Rating status (with the most dominant monkey being "1" and so on), and 2) a categorical variable whereby I pulled out the dominant male and dominant female and compared to all other subordinate adults. I note that I conducted my analyses of dominance only with respect to all adult individuals in the two groups. In both monkey groups during my study, there were no subordinate adult males so my category of subordinate adults comprises only subordinate adult females. For analyses involving age class as a predictor variable, I assessed this categorically with two classes: adults and juveniles. As neither of the capuchin monkey groups contained any sub-adult monkeys during my study periods, it was straightforward to classify each monkey as either adult or juvenile.

My statistical models assess how age class (adult or juvenile) and dominance rank (either ordered or categorical, as above) influence interindividual variation in foraging across multiple parameters (described above). I also ran a GLMM to evaluate if finder individuals (those first into focal trees) obtained greater foraging returns when compared to non-finder group members. To assess if dominance rank could predict whether an individual would successfully displace another individual during a displacement event, I ran a GLMM with a binary response variable (1: successful at displacing, 0: unsuccessful at displacing) and the predictor variable of dominance rank. For questions concerning count data (e.g., the number of displacements given/received, and the number of touches, bites, and drops a monkey did prior to finding a ripe fruit to feed), I fit either Poisson or negative binominal GLMMs in accordance with overdispersion in the data. For questions concerning the time spent engaging in a behavior (e.g., inter-fruit search time, handling time, patch entry time and delay to patch entry time), I fit gamma GLMMs (with log link functions). For questions involving the total amount of fruit consumed in a tree (measured as the sum of fruit pulp consumed at the end of a focal tree follow), I fit gamma GLMMs (with log link functions). I fit beta GLMMs (to deal with my proportional data, with logit link functions) to assess the proportion of fruit pulp consumed per fruit. In all models, I included individual monkey identity, study group identity, study year, and bout identity (the specific focal tree follow for each observation) as random effects to control for repeated measures in the dataset. Statistical significance of the fixed effects in the GLMMs (either dominance rank, age class, or finder/non-finder individual) were assessed using the report package (Makowski et al. 2020). Significance for all tests was set a $\alpha = 0.05$.

RESULTS

I obtained data from 231 focal tree follows in *A. butyracea* palms across my two field seasons. This included 66 tree follows for the TOP group and 166 tree follows for the FC group. During these focal tree follows, I recorded 29,546 discrete instances of the foraging and social behaviors listed in my ethogram. On average, the capuchin monkey groups spent 16.63 minutes in a focal tree (mean, 95% CI [9.12, 19.15]). An individual monkey consumed, on average, 4.04

fruits in a focal tree (mean, 95% CI [3.65, 4.43]), measured as the sum of the total fruit pulp consumed.

Observations of 233 all-occurrence dominance interactions across both monkey groups revealed a distinct social hierarchy, with a dominant male as the highest-ranked individual in both groups (Figures 7A and 7C). Supporting my hypothesis that social dominance rank confers access to resources, observations of 92 displacement events in focal trees suggested that higher-ranking group members are much more successful at displacing lower-ranking group members to access the fruit (Generalized linear mixed model (GLMM): $\chi^2 = 8.244$, $p < 0.001$, Figures 7B and 7D). Note that social rank was determined via interactions outside *A. butyracea* trees excluding displacement events to avoid circularity.

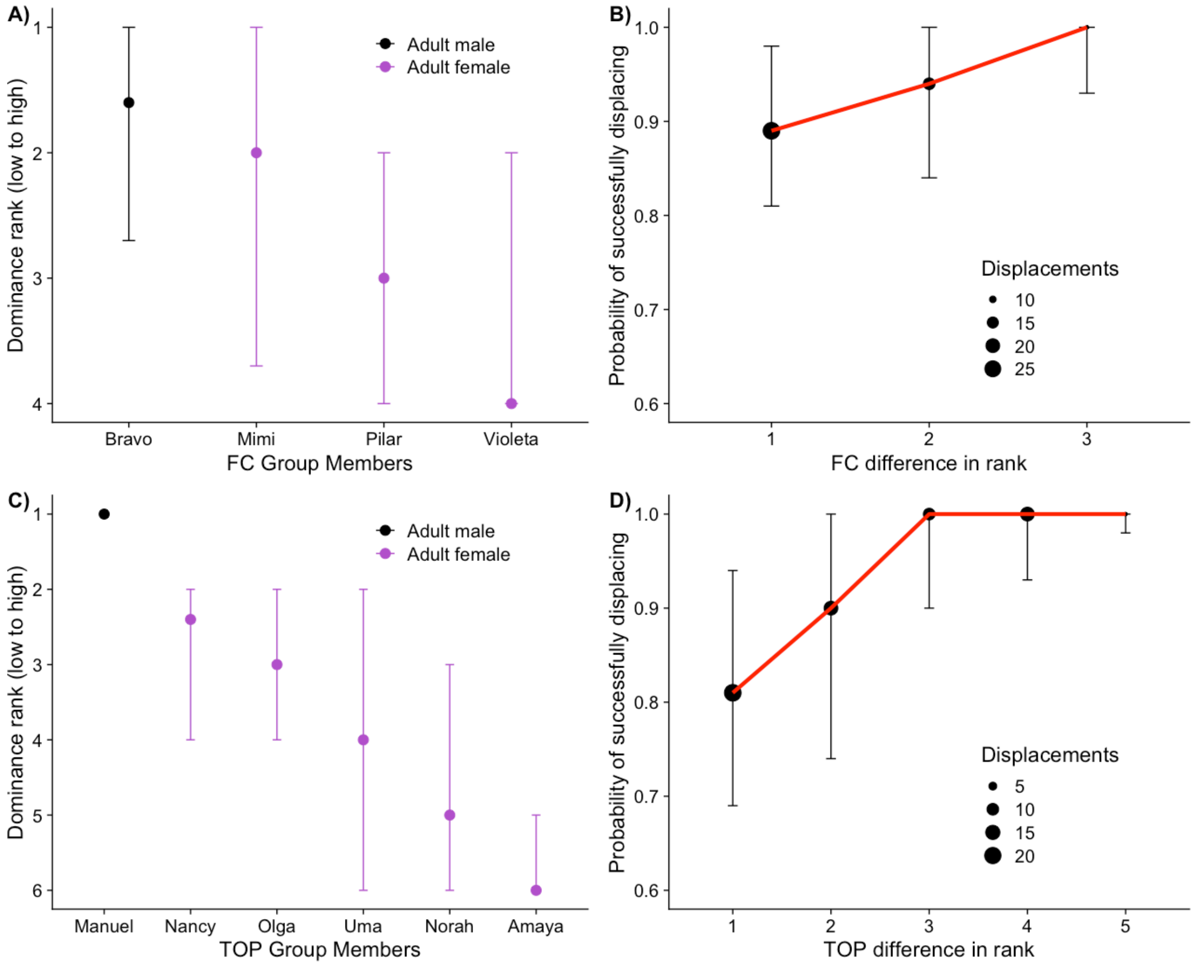

Figure 7. Both capuchin monkey groups exhibited a within-group dominance hierarchy, and higher-ranking individuals were more likely to displace others on foraging patches. Whiskers represent 95% confidence intervals of rank estimates based on 1000 randomizations (Farine & Sanchez-Tojar 2022). (A, C) The dominance hierarchy of each capuchin group in this study (A for FC and C for TOP). Individuals are colored by sex class, with black for adult male and purple for adult female. (B, D) The probability of an individual successfully displacing another individual on a foraging patch, according to the difference in dominance rank for FC and TOP respectively. The size of points relates to the number of displacement observations.

I found that my prediction that dominant individuals would consume more fruit in a tree was somewhat supported in my analyses. Continuous rank order was not a significant predictor of the total intake in a tree (measured as total amount of fruit pulp a monkey consumed in a focal tree) (GLMM: $\chi^2 = 0.311$, $p = 0.577$). However, categorical rank order was a significant predictor of the total intake in a tree, such that dominant male monkeys consumed, on average, more than double the amount of fruit in a tree compared to dominant females and all subordinates (GLMM: $\chi^2 = 9.755$, $p = 0.008$, dominant male: $\bar{x} = 7.666$ total fruits consumed in a focal tree, 95% CI [4.670, 12.582], dominant female: $\bar{x} = 3.345$ total fruits consumed in a focal tree, 95% CI [2.200, 5.086], subordinate adults: $\bar{x} = 3.144$ total fruits consumed in a focal tree, 95% CI [2.276, 4.345]; Figure 8).

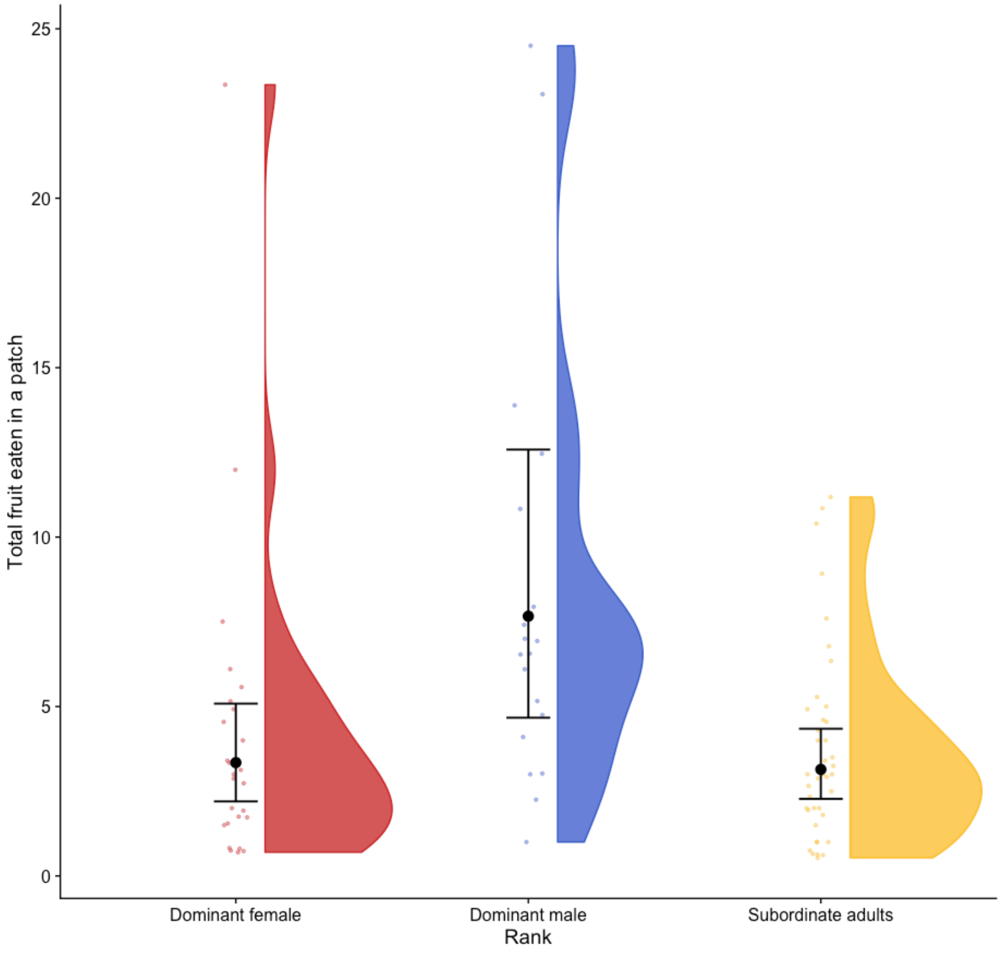

Figure 8. Dominant males ate more than twice as much fruit in focal trees compared to adults of other social ranks. The total amount of fruit eaten in an *A. butyracea* palm tree compared across the rank categories of dominant female (red), dominant male (blue), and subordinate adults (yellow). Total fruit eaten was measured as the cumulative sum of fruit pulp consumed by an individual in a focal palm tree. Solid black dots represent the predicted mean amount of fruit pulp eaten in a tree, with error bars showing 95% confidence intervals. Colored points represent the raw data values. Colored half-violin distributions denote the density distributions of the raw data values.

I also hypothesized that older individuals would be more efficient foragers due to experience accumulated during their lifetimes and increased strength to handle hard-to-process food items, predicting that adult monkeys would be more efficient at finding and processing ripe fruits when compared to juveniles. I found that handling time, when measured as the time interval it took a monkey to process and consume one fruit item, was not predicted significantly by age class (GLMM: $\chi^2 = 0.433$, $p = 0.510$, adults: $\bar{x} = 0.445$ minutes to consume one fruit item, 95% CI [0.345, 0.573], juveniles: $\bar{x} = 0.375$ minutes to consume one fruit item, 95% CI [0.226, 0.621]). However, I found that adults consumed significantly more of the fruit pulp than juveniles, consistent with my prediction (GLMM: $\chi^2 = 77.334$, $p < 0.001$, adults: $\bar{x} = 0.906$ proportion of a fruit pulp eaten, 95% CI [0.867, 0.935], juveniles: $\bar{x} = 0.730$ proportion of a fruit pulp eaten, 95% CI [0.698, 0.759]; Figure 9a). Correcting handling time by the proportion of fruit pulp consumed (instead of for just one fruit item), then these results suggest that juveniles did indeed have longer handling times to consume the same amount of fruit pulp as adults.

I predicted that adult monkeys would be better at finding ripe fruits to eat, by locating fruits faster and with fewer searching behaviors when compared to juveniles. Contrary to my predictions, adults took significantly more time to find a fruit to consume (their inter-fruit search time) when compared to juveniles (GLMM: $\chi^2 = 14.103$, $p < 0.001$, adults: $\bar{x} = 0.430$ minutes to find a fruit to consume, 95% CI [0.377, 0.490], juveniles: $\bar{x} = 0.343$ minutes to find a fruit to consume, 95% CI [0.313, 0.375], Figure 9b). When examining searching behaviors prior to consumption, I notably found that only the number of fruits bitten (and not fruits touched or dropped) aligned with my predictions whereby juveniles bit more fruits than adults. My models specifically indicated that the number of fruits touched before finding a fruit to consume was not predicted significantly by age class (GLMM: $\chi^2 = 0.756$, $p = 0.394$, adults: $\bar{x} = 0.764$ fruits touched, 95% CI [0.593, 0.985], juveniles: x̄ = 0.819 fruits touched, 95% CI [0.652, 1.029]). The number of fruits dropped before finding a fruit to eat was also not significantly different between adults and juveniles (GLMM: $\chi^2 = 0.784$, $p = 0.376$, adults: x̄ = 0.112 fruits dropped, 95% CI [0.080, 0.157], juveniles: x̄ = 0.097 fruits dropped, 95% CI [0.077, 0.121]). However, juveniles bit more fruits before finding a ripe one to eat when compared to adults (GLMM: $\chi^2 = 48.803$, $p < 0.001$, adults: x̄ = 0.080 fruits bitten, 95% CI [0.057, 0.113], juveniles: x̄ = 0.205 fruits bitten, 95% CI [0.161, 0.262], Figure 9c).

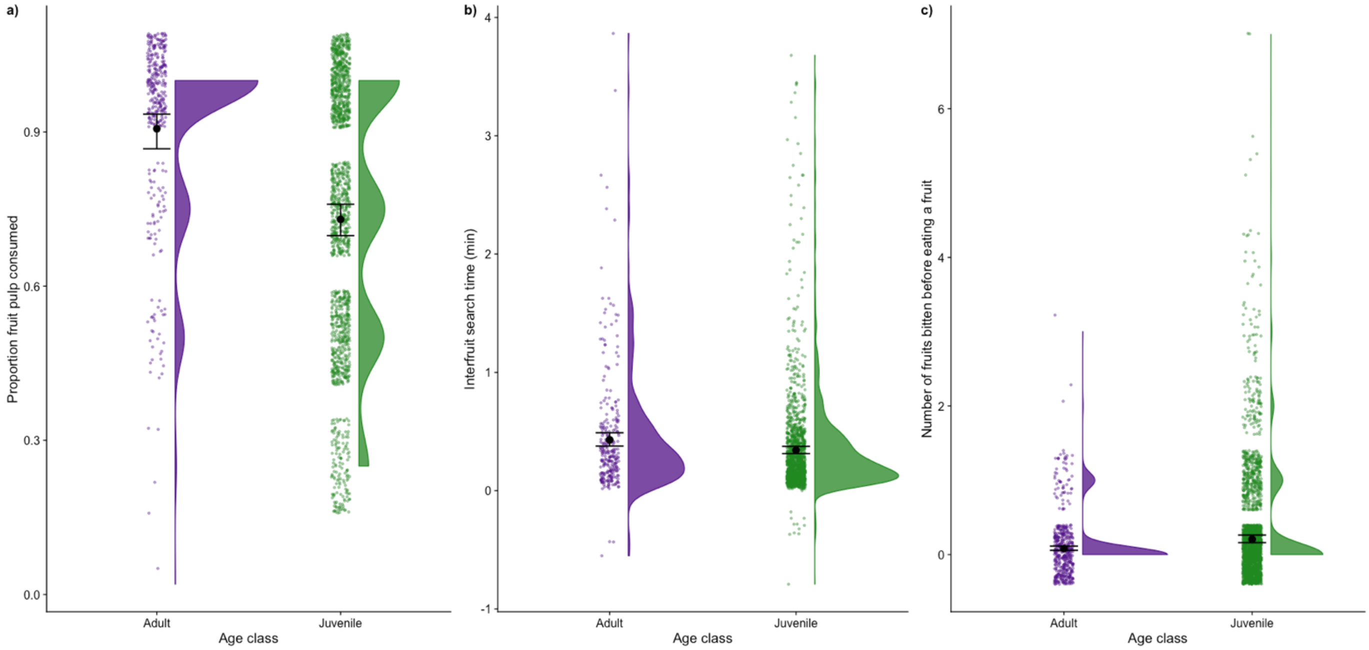

Figure 9. Adult individuals consumed more of the fruit pulp when processing a fruit, had a longer inter-fruit search time to find a fruit to eat, and bit fewer fruits when searching for which fruit to select. Comparison of foraging parameters significantly predicted by age class: a) proportion of fruit pulp consumed in a focal tree, b) inter-fruit search time in minutes (the time it took an individual to find a fruit to consume), and c) the number of fruits an individual bit before eating a fruit. Adults are represented in purple and juveniles are represented in green. Solid black

dots represent the predicted mean amount of fruit pulp eaten in a tree, with error bars showing 95% confidence intervals. Colored points represent the raw data values. Colored half-violin distributions denote the density distributions of the raw data values.

Finally, I hypothesized that the timing of access to the patch influences foraging behavior and return. I first assessed if dominance rank or age class predicted the delay to patch entry time into the fruiting raceme, and I found that neither age class nor rank was a significant predictor of this measure (GLMM rank order: $\chi^2 = 0.09$, $p = 0.765$; GLMM rank categorical: $\chi^2 = 0.110$, $p = 0.946$, dominant male: $\bar{x} = 8.304$ minute delay into a focal tree, 95% CI [3.765, 18.316], dominant female: $\bar{x} = 9.969$ minute delay into a focal tree, 95% CI [4.299, 21.865], subordinate adults: $\bar{x} = 9.055$ minute delay into a focal tree, 95% CI [4.299, 21.865]; GLMM age class: $\chi^2 = 0.142$, $p = 0.706$, adults: $\bar{x} = 4.449$ minute delay into a focal tree, 95% CI [3.167, 6.252], juveniles: $\bar{x} = 4.701$ minute delay into a focal tree, 95% CI [3.669, 6.023]). I then calculated how much fruit pulp, on average, the first individual into a focal tree received prior to the entry of the second individual (the “finder’s share”) which amounted to 2.4 fruits (mean, 95% CI [4.15, 0.65]). Consistent with my prediction, finder individuals consumed significantly more total fruit in focal trees, eating on average 40% more than non-finder individuals (measured as the sum of the fruit pulp consumed for all fruits throughout the duration of the focal tree follow, GLMM: $\chi^2 = 6.855$, $p = 0.009$, finders: $\bar{x} = 4.307$ fruits, 95% CI [2.772, 6.689], non-finders: $\bar{x} = 3.073$ fruits, 95% CI [2.001, 4.7185], Figure 10).

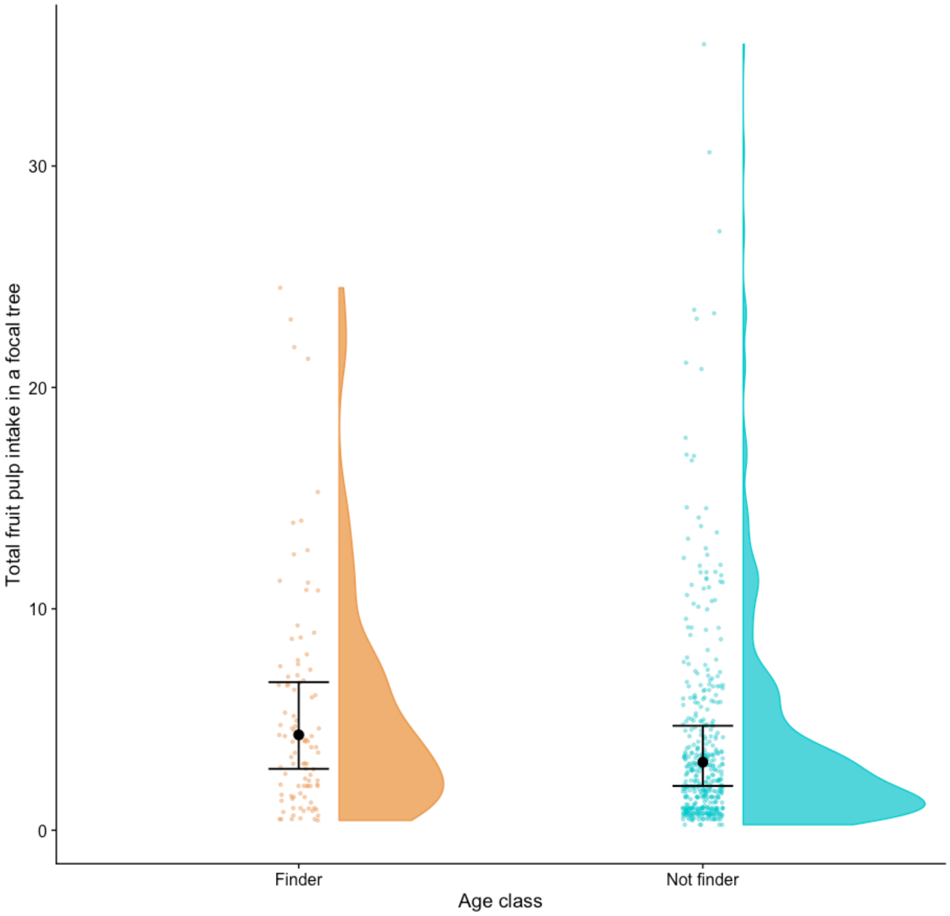

Figure 10. Finder individuals who are the first into focal trees obtained more fruit overall when compared to non-finder group members. The total fruit pulp consumed in a focal tree for finder (orange) and non-finder (turquoise) individuals. Solid black dots represent the predicted mean amount of fruit pulp eaten in a tree, with error bars showing 95% confidence intervals. Colored points represent the raw data values. Colored half-violin distributions denote the density distributions of the raw data values.

DISCUSSION

In my study, I assessed aspects of both social dynamics and individual predictors of foraging behavior, showing that dominance rank, age class, and timing of access to a foraging patch all influence patterns of foraging behavior and efficiency. I measured foraging efficiency across multiple levels to provide in-depth and comprehensive analyses of the specific behavioral strategies that individuals use to maximize their foraging success. Specifically, I calculated foraging behaviors in a patch during the search phase of finding food to consume (like how long it takes to locate a ripe fruit to eat and what searching behaviors a monkey performs to find fruit) and during the active feeding phase (the handling time to eat a fruit and how much fruit pulp is consumed). Alongside the timing of access to a patch, these behaviors are important components of the ultimate foraging success outcome (how much total food is obtained in a patch).

If social dominance influences access to resources, I predicted that high-ranking individuals would displace others more often on a patch, be displaced less frequently, and have a higher overall intake when compared to lower ranking group members. Consistent with my predictions, I found that more dominant individuals displaced others more often and experienced fewer displacements. I used displacements as a proxy for access to a patch, and my results indicate that dominant individuals have a competitive advantage over a monopolizable resource like *A. butyracea* fruit racemes. While the total intake (amount of fruit pulp consumed in a focal tree) was not predicted solely by dominance status, I did find that dominant alpha males consumed significantly more fruit when compared to all other adults (Figure 8). This effect was substantial, such that alpha males obtained more than double the amount of food in a tree versus their subordinates.

If age confers elevated experience and increased strength to process hard-to-handle food items (like *A. butyracea* fruits), I predicted that adult monkeys would test fewer fruits before finding a ripe one to consume, take less time to locate a fruit to eat, consume fruits faster (shorter handling time), and eat more of the fruit pulp when compared to juveniles. Of the three searching behaviors the capuchins exhibited while testing which fruits to eat (touch, bite, and drop), only biting was predicted significantly by age class such that juveniles bite more fruits than adults (Figure 9c). Interestingly, contrary to my predictions, adults took longer than juveniles to find a fruit to eat (inter fruit search time, Figure 9b). When I assessed handling time measured as the amount of time it took a monkey to process and eat one fruit item, there was no significant difference between age classes. However, once I controlled for the amount of fruit pulp eaten, then adults had shorter handling times than juveniles as predicted. Supporting my predictions, adults ate more of the fruit pulp, consuming on average over 90% of the fruit pulp (Figure 9a). Juveniles consumed just over 70% of the fruit pulp in comparison. The majority of these results support the hypothesis that adults are more efficient foragers and age has a significant impact on foraging behavior.

If the timing of access into a patch is a strategy individuals use to increase their foraging returns, I predicted that the first individual into a patch (the finder) would receive a finder's share portion of the patch that ultimately boosted their intake when compared to non-finder group members. As expected, I found that the first monkey into a tree did obtain a finder's share amounting to an average of 0.75 fruits (median) before the second individual entered the tree. Since individuals averaged about 2.52 fruits (median) per tree, this finder's share amounts to 30% of that total fruit pulp consumption, a substantial amount of extra food. My results further indicated that at the end of a focal tree follow, finder individuals had consumed significantly more total fruit, eating on average 40% more than non-finder individuals (Figure 10). These findings suggest that the behavioral strategy of being the first into a tree confers a distinct and measurable foraging advantage. When examining who may be a finder individual into trees, I did not find that certain dominance ranks or age classes were more (or less) likely to be finders.

Several studies have demonstrated the pattern whereby dominant individuals experience an increased food intake relative to subordinate group members (Vogel 2005, Janson 1985, Whitten 1983, Robinson 1981). This foraging benefit for dominants is particularly true for food resources that occur in defensible (or monopolizable) clumps, like *A. butyracea* fruiting racemes. Higher-ranking individuals may secure priority access to resources and gain greater overall energy intake by aggressively excluding their subordinates from parts of feeding trees (Vogel & Janson 2007, Vogel 2005). Further, if resources are heterogeneously distributed in the patch, dominant individuals may gain differential access to high value areas, where food is easier to acquire and consume. I found that only dominant adult males experienced a greater intake compared to other group members, likely indicating that in our groups alpha males have critical competitive advantage to control priority access to the patch.

Each of the three search behaviors monkeys use in *A. butyracea* palms could indicate different ways a monkey locates the best possible edible fruit. The best possible fruit could be a fruit that is the easiest to find and pull off the raceme, a fruit with the highest caloric value, a ripe fruit that is easier to digest because of fewer nitrogenous organic compounds, and/or a fruit that is easy to peel and consume yielding a shorter handling time. Touching a fruit may give a monkey an indication of the ripeness stage, as fruits are shown to soften during the ripening process by converting starches into sugars and breaking down cell walls (Seymour et al. 2013). Biting a fruit could also give an indication of ripeness level through the sweetness of taste. As these palm fruits have an inedible hard outer shell that must be removed to eat the pulp instead, biting a fruit may also signal how easily the outer shell can be removed (likely an important component influencing handling time). Dropping a fruit suggests the monkey has rejected that fruit, perhaps because it looks or feels inadequate. Capuchin monkeys likely use sight to discriminate ideal fruits to eat, as fruits change from green in color to yellow and orange as chlorophyll is degraded and other pigments are revealed, although measuring how many fruits a monkey looks at was infeasible in this study (Tucker et al. 2013). While smell has been shown to be an important way in which capuchins select fruits (Melin et al. 2019), I did not observe the monkeys actively smelling *A. butyracea* fruits. I note that there were many instances, across all group members, where the monkeys did not perform any testing behaviors before selecting a fruit to eat. In these cases, perhaps a monkey does not need to perform a test behavior if it is otherwise obvious that fruit is ideal, say from the color of the fruit and/or how easily the fruit was plucked from the raceme. All individuals in both capuchin monkey groups displayed searching behaviors that involved tactile, gustatory, and likely visual and olfactory senses, suggesting that capuchins use multiple senses to choose fruit to eat.

Although my results suggested that the only search behavior significantly different between adults and juveniles is biting, I found that for all three search behaviors, juvenile monkeys exhibited a greater spread in the observed number of fruits they tested compared to adults. This maximum number of fruits tested by juveniles was more than two-fold the number tested for adults for touching and biting behaviors, such that I observed juveniles touching up to 19 fruits (adults a maximum of 9) and biting up to 7 fruits (adults maximum 3) before finding one to eat. Such a difference in spread could indicate that some younger individuals do touch, bite, and drop more fruits to find ripe ones. It is possible that juveniles improve their foraging abilities incrementally with age (Schuppli et al. 2016), and future studies could track foraging behaviors across juvenile development as I was unable to ascertain exact ages of the juvenile monkeys in this study. This difference in spread could also occur if there are certain trees where it is easier to figure out which fruits are ripe versus some trees where it is more challenging.

The only result that went against my predictions for age class was that adults took longer than juveniles to find a fruit to eat (inter fruit search time). While I expected that adults would be more experienced foragers and thus able to locate a ripe fruit to eat faster than their younger counterparts, this result could instead indicate that adults are more discriminatory in the fruits that they will select to eat. By investing extra time into finding the best fruit, adults may actually increase their foraging success by only choosing fruits which have the highest energetic return value (caloric, for instance) and the shortest handling time. Optimal foraging theory has a similar prediction at its core: that an animal should maximize their energetic intake while minimizing their foraging costs (like time, Stephens & Krebs 1986). This possibility is supported by my findings that adults consistently consume almost the entirety of the fruit pulp at a shorter handling time than juveniles (more energetic intake at a shorter time cost). Indeed, I found it to be extremely rare that adults would consume only 25% or 50% of the fruit pulp (this only occurred for 1% and 8% of all eaten fruits observed, respectively), meaning once they have selected a ripe fruit to consume, they consume it to near entirety. Further research that investigates the caloric and nutritional value of the fruits that adults versus juveniles select to consume would advance our knowledge of whether older individuals reliably select fruits of the highest energetic value.

Both experience and strength have been shown to be two important factors influencing why adults may be more efficient foragers than juveniles (Schuppli et al. 2016). Complex diets often require a naïve individual to learn how to properly forage, and the needing to learn (or difficult diet) hypothesis is one of the proposed reasons for extended juvenile periods in primates (Johnson & Bock 2004, Schuppli et al. 2012, Kaplan et al. 2000, Gibson 1986). Certain foraging parameters in my study indicate the impact of experience on foraging success, namely the searching behaviors to find a ripe fruit and inter-fruit search time. Other foraging parameters I measured imply increased strength or ability to handling hard-to-process food items like *A. butyracea* fruits that must be peeled prior to consumption, such as the handling time it takes to consume a fruit.

When calculating how timing of access to a patch influences foraging success, I found that finder individuals first into trees received a finder's share and ultimately consumed considerably more food in a tree than all other group members (finders ate 40% more total fruit pulp). Previous studies have highlighted how the finder's share influences social foraging behavior, and this type of social foraging has been modeled both as information-sharing models and producer-scrounger games (di Bitetti & Janson 2001, Ranta et al. 1996, Vickery et al. 1991, Barnard & Sibley 1981). One possible reason for why an individual would act as a finder is to receive a boost in foraging payoff that offsets possible later decreases in foraging efficiency as a result of being displaced off the patch. In this way, being a finder can be a strategy to mitigate later drops in foraging returns because of competition for access to the patch. To investigate this further, I could assess foraging return rates for a finder before and after other individuals arrive into a patch and before and after displacement events.

While focusing on one fruit tree species in my study allowed for repeated measures of foraging behaviors across individuals and groups, expanding data collection to include different foraging tree species would further advance our understanding of the foraging strategies of group-living animals. Examining foraging behavior for easier- versus harder-to-process food items would provide additional information on the ontogeny of foraging behaviors (Eadie 2015). More replicates of capuchin monkey groups would offer more statistical power for my analyses, and allow comparisons of social foraging across groups. Further research could also assess additional axes of inter-individual variation in foraging, such as personality. Risk tolerance can also play an important role in creating heterogeneity in resource acquisition rates in groups (Ward et al. 2004). More energetically needy, bolder, or larger individuals often prefer to travel at the front of their group, trading-off increased risk of encountering predators to gain priority access to the best parts of food patches (Sueur et al. 2010, Sibbald et al. 2009, Di Bitetti et al. 2001, Krause 1993, Robinson 1981). In these cases, individuals who get access to more profitable portions of the patch will consume more food at a faster rate, exemplifying another axis of inter-individual variation that can produce differences in foraging efficiency.

While differences between group members translates into a diversity of foraging strategies, from the perspective of group-level outcomes, it is clear that heterogeneity among group members can generate positive impacts for social organisms (Jolles et al. 2020, del Mar Delgado et al. 2018, Herbert-Read et al. 2013, Croft et al. 2009, Giardina 2008). Groups with greater variation in individual personality forage more efficiently (Aplin et al. 2014), and microbiome communities with greater diversity in composition are more successful at processing nutrients in the mammalian gut (McFall-Ngai et al. 2013). In humans, groups with greater diversity (differences in race, gender, religion, background, and/or differences in the approaches used to solve problems) can perform better at problem solving given they communicate effectively (Mathieu et al. 2008, Jackson et al. 2003, Mohammed & Angell 2003, Neuman et al. 1999). Such effects are likely widespread, as many species that live in stable social groups are characterized by high degrees of individual variation (Montiglio et al. 2013, Bergmüller & Taborksy 2010). For example, social stratification and dominance hierarchies are central to the organization of primate societies (Mitani et al. 2012), while species with long developmental periods can live in groups containing individuals of different sizes, experiences, and abilities (Perry et al. 2017, Altmann & Alberts 2005, Heyes 1994). Ultimately, observing and quantifying how, when, and why groups members differ from each other will provide us with knowledge of the dynamics of social foraging and how individuals learn to become efficient foragers.

Across all the foraging parameters I calculated, I consistently observed within and between individual differences in behavior. While these individual differences in foraging are likely caused by a variety of factors beyond my assessments of age, rank, and timing of access to a patch, these inter-individual differences ultimately led to variation in the foraging efficiency and success of individuals. For animals who forage in social groups like capuchin monkeys, variation in foraging underlies disparities between the way group members experience their environment, creating a range of individual needs, preferences, and capabilities. Ultimately, such heterogeneity between group members can translate into conflicts between individuals over their foraging preferences.

REFERENCES

Agostini, I., & Visalberghi, E. (2005). Social influences on the acquisition of sex-typical foraging patterns by juveniles in a group of wild tufted capuchin monkeys (Cebus nigritus). *American Journal of Primatology: Official Journal of the American Society of Primatologists*, *65*(4), 335-351.

Altmann, J., & Alberts, S. C. (2005). Growth rates in a wild primate population: ecological influences and maternal effects. *Behavioral Ecology and Sociobiology*, *57*(5), 490-501.

Aplin, L. M., Farine, D. R., Mann, R. P., & Sheldon, B. C. (2014). Individual-level personality influences social foraging and collective behaviour in wild birds. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1789), 20141016.

Barnard, C. J., & Sibly, R. M. (1981). Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Animal behaviour*, *29*(2), 543-550.

Barta, Z., & Giraldeau, L. A. (1998). The effect of dominance hierarchy on the use of alternative foraging tactics: a phenotype-limited producing-scrounging game. *Behavioral Ecology and Sociobiology*, *42*(3), 217-223.

Bartumeus, F., & Catalan, J. (2009). Optimal search behavior and classic foraging theory. *Journal of Physics A: Mathematical and Theoretical*, *42*(43), 434002.

Bergmüller, R., & Taborsky, M. (2010). Animal personality due to social niche specialisation. *Trends in ecology & evolution*, *25*(9), 504-511.

Bird, R. B., & Bird, D. W. (2002). Constraints of knowing or constraints of growing?. *Human Nature*, *13*(2), 239-267.

Boinski, S., & Fragaszy, D. M. (1989). The ontogeny of foraging in squirrel monkeys, Saimiri oerstedi. *Animal Behaviour*, *37*, 415-428.

Calabrese, J. M., Fleming, C. H., & Gurarie, E. (2016). ctmm: An R package for analyzing animal relocation data as a continuous-time stochastic process. *Methods in Ecology and Evolution*, *7*(9), 1124-1132.

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical population biology*, *9*(2), 129-136.

Clark, C. W., & Mangel, M. (1986). The evolutionary advantages of group foraging. *Theoretical population biology*, *30*(1), 45-75.

Crofoot, M. (2007). Mating and feeding competition in white-faced capuchins (Cebus capucinus): the importance of short-and long-term strategies. *Behaviour*, *144*(12), 1473-1495.

Crofoot, M. C., Gilby, I. C., Wikelski, M. C., & Kays, R. W. (2008). Interaction location outweighs the competitive advantage of numerical superiority in Cebus capucinus intergroup contests. *Proceedings of the National Academy of Sciences*, *105*(2), 577-581.

Croft, D. P., Krause, J., Darden, S. K., Ramnarine, I. W., Faria, J. J., & James, R. (2009). Behavioural trait assortment in a social network: patterns and implications. *Behavioral Ecology and Sociobiology*, *63*(10), 1495-1503.

De la Fuente, M. F., Schiel, N., Bicca-Marques, J. C., Caselli, C. B., Souto, A., & Garber, P. A. (2019). Balancing contest competition, scramble competition, and social tolerance at feeding sites in wild common marmosets (Callithrix jacchus). *American Journal of Primatology*, *81*(4), e22964.

del Mar Delgado, M., Miranda, M., Alvarez, S. J., Gurarie, E., Fagan, W. F., Penteriani, V., ... & Morales, J. M. (2018). The importance of individual variation in the dynamics of animal collective movements. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1746), 20170008.

di Bitetti, M. S. (1997). Evidence for an important social role of allogrooming in a platyrrhine primate. *Animal behaviour*, *54*(1), 199-211.

di Bitetti, M. S., & Janson, C. H. (2001). Social foraging and the finder's share in capuchin monkeys, Cebus apella. *Animal Behaviour*, *62*(1), 47-56.

Eadie, E. C. (2015). Ontogeny of foraging competence in capuchin monkeys (Cebus capucinus) for easy versus difficult to acquire fruits: A test of the needing to learn hypothesis. *PloS one*, *10*(9), e0138001.

Farine, D. R., & Sánchez-Tójar, A. (2022). aniDom: inferring dominance hierarchies and estimating uncertainty. *R package version 0.1*, *2*.

Fedigan, L. (1993). Sex differences and intersexual relations in adult white-faced capuchins (Cebus capucinus). *International Journal of Primatology*, *14*(6), 853-877.

Fedigan, L. M., & Jack, K. (2001). Neotropical primates in a regenerating Costa Rican dry forest: a comparison of howler and capuchin population patterns. *International Journal of Primatology*, *22*(5), 689-713.

Fragaszy, D. M., Visalberghi, E., & Fedigan, L. M. (2004). *The complete capuchin: the biology of the genus Cebus*. Cambridge University Press.

Franks, V. R., & Thorogood, R. (2018). Older and wiser? Age differences in foraging and learning by an endangered passerine. *Behavioural processes*, *148*, 1-9.

Galef, B. G., & Laland, K. N. (2005). Social learning in animals: empirical studies and theoretical models. *Bioscience*, *55*(6), 489-499.

Giardina, I. (2008). Collective behavior in animal groups: theoretical models and empirical studies. *HFSP journal*, *2*(4), 205-219.

Giraldeau, L. A., & Caraco, T. (2018). Social foraging theory. In *Social Foraging Theory*.

Princeton University Press.

Giraldeau, L. A., Valone, T. J., & Templeton, J. J. (2002). Potential disadvantages of using socially acquired information. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *357*(1427), 1559-1566.

Goss-Custard, J. D., & Durell, S. L. V. D. (1987). Age-related effects in oystercatchers, Haematopus ostralegus, feeding on mussels, Mytilus edulis. I. Foraging efficiency and interference. *The Journal of Animal Ecology*, 521-536.

Goss-Custard, J. D., & Sutherland, W. J. (1997). Individual behaviour, populations and conservation. *Behavioural ecology: an evolutionary approach*, *4*, 373-395.

Harvey, P. H., Clutton-Brock, T. H., & Mace, G. M. (1980). Brain size and ecology in small mammals and primates. *Proceedings of the National Academy of Sciences*, *77*(7), 4387-4389.

Herbert-Read, J. E., Krause, S., Morrell, L. J., Schaerf, T. M., Krause, J., & Ward, A. J. W. (2013). The role of individuality in collective group movement. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1752), 20122564.

Heyes, C. M. (1994). Social learning in animals: categories and mechanisms. *Biological Reviews*, *69*(2), 207-231.

Hirsch, B. T., Malpass, E., & Di Blanco, Y. E. (2020). Interindividual spacing affects the finder's share in ring-tailed coatis (Nasua nasua). *Behavioral Ecology*, *31*(1), 232-238.

Isbell, L. A. (1991). Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behavioral ecology*, *2*(2), 143-155.

Jack, K. M., & Fedigan, L. M. (2006). Why be alpha male? Dominance and reproductive success in wild white-faced capuchins (Cebus capucinus). In *New perspectives in the study of*

Mesoamerican primates (pp. 367-386). Springer, Boston, MA.

Jackson, S. E., Joshi, A., & Erhardt, N. L. (2003). Recent research on team and organizational diversity: SWOT analysis and implications. *Journal of management*, *29*(6), 801-830.

Janson, C. (1985). Aggresive competition and individual food consumption in wild brown capuchin monkeys (Cebus apella). *Behavioral Ecology and Sociobiology*, *18*(2), 125-138.

Johnson, S. E., & Bock, J. (2004). Trade-offs in skillacquisition and time allocation among juvenile chacma baboons. *Human Nature*, *15*(1), 45-62.

Jolles, J. W., King, A. J., & Killen, S. S. (2020). The role of individual heterogeneity in collective animal behaviour. *Trends in ecology & evolution*, *35*(3), 278-291.

Kamil, A. C., & Roitblat, H. L. (1985). The ecology of foraging behavior: implications for animal learning and memory. *Annual review of psychology*, *36*(1), 141-169.

Kaplan, H., Hill, K., Lancaster, J., & Hurtado, A. M. (2000). A theory of human life history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews*, *9*(4), 156-185.

Karell, P., Pietiäinen, H., Siitari, H., Pihlaja, T., Kontiainen, P., & Brommer, J. E. (2009). Parental allocation of additional food to own health and offspring growth in a variable environment. *Canadian Journal of Zoology*, *87*(1), 8-19.

Koenig, A. (2002). Competition for resources and its behavioral consequences among female primates. *International Journal of Primatology*, *23*(4), 759-783.

Leigh, E. G. (1999). *Tropical forest ecology: a view from Barro Colorado Island*. Oxford University Press on Demand.

Lüdecke, D. (2018). ggeffects: Tidy data frames of marginal effects from regression models. *Journal of Open Source Software*, *3*(26), 772.

MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. *The American Naturalist*, *100*(916), 603-609.

MacKinnon, K. C. (2006). Food choice by juvenile capuchin monkeys (Cebus capucinus) in a tropical dry forest. In *New perspectives in the study of Mesoamerican primates* (pp. 349-365). Springer, Boston, MA.

Makowski, D., Ben-Shachar, M. S., Patil, I., & Lüdecke, D. (2020). Methods and algorithms for correlation analysis in R. *Journal of Open Source Software*, *5*(51), 2306.

Mathieu, J., Maynard, M. T., Rapp, T., & Gilson, L. (2008). Team effectiveness 1997-2007: A review of recent advancements and a glimpse into the future. *Journal of management*, *34*(3), 410-476.

McFall-Ngai, M., Hadfield, M. G., Bosch, T. C., Carey, H. V., Domazet-Lošo, T., Douglas, A. E., ... & Wernegreen, J. J. (2013). Animals in a bacterial world, a new imperative for the life sciences. *Proceedings of the National Academy of Sciences*, *110*(9), 3229-3236.

Melin, A. D., Nevo, O., Shirasu, M., Williamson, R. E., Garrett, E. C., Endo, M., ... & Kawamura, S. (2019). Fruit scent and observer colour vision shape food-selection strategies in wild capuchin monkeys. *Nature communications*, *10*(1), 1-9.

Milton, K., & Giacalone, J. (2014). Differential effects of unusual climatic stress on capuchin (Cebus capucinus) and howler monkey (A louatta palliata) populations on Barro Colorado Island, Panama. *American Journal of Primatology*, *76*(3), 249-261.

Mitani, J. C., Call, J., Kappeler, P. M., Palombit, R. A., & Silk, J. B. (Eds.). (2012). *The evolution of primate societies*. University of Chicago Press.

Mohammed, S., & Angell, L. C. (2003). Personality heterogeneity in teams: Which differences make a difference for team performance?. *Small group research*, *34*(6), 651-677.

Montiglio, P. O., Ferrari, C., & Réale, D. (2013). Social niche specialization under constraints: personality, social interactions and environmental heterogeneity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1618), 20120343.

Neuman, G. A., & Wright, J. (1999). Team effectiveness: Beyond skills and cognitive ability. *Journal of Applied psychology*, *84*(3), 376.

Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., ... & Engelhardt, A. (2011). Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. *Animal Behaviour*, *82*(4), 911-921.

Newton-Fisher, N. E. (2012). Animal Behaviour Pro: 1.4. 4.

Nicholson, A. J. (1954). An outline of the dynamics of animal populations. *Australian journal of Zoology*, *2*(1), 9-65.

Parker, G. A., & Smith, J. M. (1990). Optimality theory in evolutionary biology. *Nature*, *348*(6296), 27-33.

Perry, G., & Pianka, E. R. (1997). Animal foraging: past, present and future. *Trends in Ecology & Evolution*, *12*(9), 360-364.

Perry, S. (1997). Male-female social relationships in wild white-faced capuchins (Cebus capucinus). *Behaviour*, *134*(7-8), 477-510.

Perry, S. E., Barrett, B. J., & Godoy, I. (2017). Older, sociable capuchins (Cebus capucinus) invent more social behaviors, but younger monkeys innovate more in other contexts. *Proceedings of the National Academy of Sciences*, *114*(30), 7806-7813.

Pyke, G. H. (1984). Optimal foraging theory: a critical review. *Annual review of ecology and systematics*, *15*, 523-575.

Ranta, E. S. A., Peuhkuri, N., Laurila, A., Rita, H., & Metcalfe, N. B. (1996). Producers, scroungers and foraging group structure. *Animal Behaviour*, *51*(1), 171-175.

Ranta, E., Rita, H., & Lindstrom, K. (1993). Competition versus cooperation: success of individuals foraging alone and in groups. *The American Naturalist*, *142*(1), 42-58.

Rapaport, L. G., & Brown, G. R. (2008). Social influences on foraging behavior in young nonhuman primates: learning what, where, and how to eat. *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews*, *17*(4), 189-201.

Rendell, L., Boyd, R., Cownden, D., Enquist, M., Eriksson, K., Feldman, M. W., ... & Laland, K. N. (2010). Why copy others? Insights from the social learning strategies tournament. *Science*, *328*(5975), 208-213.

Rotem, K., Agrawal, A. A., & Kott, L. (2003). Parental effects in Pieris rapae in response to variation in food quality: adaptive plasticity across generations?. *Ecological Entomology*, *28*(2), 211-218.

Schoener, T. W. (1987). A brief history of optimal foraging ecology. In *Foraging behavior* (pp. 5-67). Springer, Boston, MA.

Schuppli, C., Graber, S. M., Isler, K., & van Schaik, C. P. (2016). Life history, cognition and the evolution of complex foraging niches. *Journal of Human Evolution*, *92*, 91-100.

Schuppli, C., Isler, K., & van Schaik, C. P. (2012). How to explain the unusually late age at skill competence among humans. *Journal of human evolution*, *63*(6), 843-850.

Schuppli, C., Meulman, E. J., Forss, S. I., Aprilinayati, F., van Noordwijk, M. A., & van Schaik, C. P. (2016). Observational social learning and socially induced practice of routine skills in immature wild orang-utans. *Animal Behaviour*, *119*, 87-98.

Seymour, G. B., Østergaard, L., Chapman, N. H., Knapp, S., & Martin, C. (2013). Fruit development and ripening. *Annu Rev Plant Biol*, *64*(1), 219-241.

Sibbald, A. M., Erhard, H. W., McLeod, J. E., & Hooper, R. J. (2009). Individual personality and the spatial distribution of groups of grazing animals: an example with sheep. *Behavioural Processes*, *82*(3), 319-326.

Stephens, D. W., & Krebs, J. R. (1986). *Foraging theory*. Princeton University Press.

Stephens, D. W., Brown, J. S., & Ydenberg, R. C. (Eds.). (2008). *Foraging: behavior and ecology*. University of Chicago Press.

Sutherland, W. J. (1996). *From individual behaviour to population ecology* (Vol. 11). Oxford University Press on Demand.

Sutherland, W. J., & Parker, G. A. (1992). The relationship between continuous input and interference models of ideal free distributions with unequal competitors. *Animal Behaviour*, *44*, 345-355.

Thornton, A., & Clutton-Brock, T. (2011). Social learning and the development of individual and group behaviour in mammal societies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1567), 978-987.

Tórrez-Herrera, L. L., Davis, G. H., & Crofoot, M. C. (2020). Do monkeys avoid areas of home range overlap because they are dangerous? A test of the risk hypothesis in white-faced capuchin monkeys (Cebus capucinus). *International Journal of Primatology*, *41*(2), 246-264.

Tucker, G. A., Poole, M., Giovannoni, J., & Seymour, G. (2013). *The molecular biology and biochemistry of fruit ripening*. John Wiley & Sons.

Vehrencamp, S. L. (1983). A model for the evolution of despotic versus egalitarian societies. *Animal Behaviour*, *31*(3), 667-682.

Vickery, W. L., Giraldeau, L. A., Templeton, J. J., Kramer, D. L., & Chapman, C. A. (1991).

Producers, scroungers, and group foraging. *The american naturalist*, *137*(6), 847-863.

Vogel, E. R. (2004). *The ecological basis of aggression in white-faced capuchin monkeys, Cebus capucinus, in a Costa Rican dry forest*. State University of New York at Stony Brook.

Vogel, E. R. (2005). Rank differences in energy intake rates in white-faced capuchin monkeys, Cebus capucinus: the effects of contest competition. *Behavioral ecology and sociobiology*, *58*(4), 333-344.

Vogel, E. R., & Janson, C. H. (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: Official Journal of the American Society of Primatologists*, *69*(5), 533-550.

Walker, R., Burger, O., Wagner, J., & Von Rueden, C. R. (2006). Evolution of brain size and juvenile periods in primates. *Journal of Human Evolution*, *51*(5), 480-489.

Warner, D. A., Buckelew, A. M., Pearson, P. R., & Dhawan, A. (2015). The effect of prey availability on offspring survival depends on maternal food resources. *Biological Journal of the Linnean Society*, *115*(2), 437-447.

Wickham, H. (2016). Programming with ggplot2. In *ggplot2*(pp. 241-253). Springer, Cham.

Wilke, C. O., Wickham, H., & Wilke, M. C. O. (2019). Package ‘cowplot’. *Streamlined Plot Theme and Plot Annotations for ‘ggplot2*.

Windsor, D. M. (1990). Climate and moisture variability in a tropical forest: long-term records from Barro Colorado Island, Panama. *Smithsonian contributions to the earth sciences*.

CHAPTER 3

When to go? Conflicts of interest and consensus costs over the timing of group movements in cohesive groups of white-faced capuchins[3]

ABSTRACT

This study investigates an important, and quite common, daily decision in social animal groups: when to collectively leave one feeding patch and move on to the next. Optimal foraging theory, and in particular the marginal value theorem (MVT), provides a useful theoretical framework to predict the differences in the length of time each group member should want to spend exploiting a particular food patch. Using collective foraging data recorded on groups of wild white-faced capuchin monkeys on Barro Colorado Island, Panama, I use the MVT to examine: (1) if the optimal foraging strategies of individual group members differ, creating conflicts of interest about when the group should leave feeding trees, (2) how such group decisions are made and which group members exert influence, and (3) the costs that individuals pay when they compromise to achieve consensus. I collected data on capuchin group feedings in *Attalea butyracea* palms, and calculated exact individual feeding rates over the duration of each feeding event for all group members. I used these feeding rates to generate individual foraging gain curves that predict optimal patch departure times for each group member using the MVT. I compared predictions of when each individual monkey should prefer to leave trees to the

---

[3] Adapted from: Davis, G.H. & Crofoot, M.C. (In Prep) When to go? Conflicts of interest and consensus costs over the timing of group movements in cohesive groups of white-faced capuchins.

observed collective departure times from my field data to understand how group decisions are made and who contributes. I also compared my foraging theory results with more conventional methods of assessing who has influence over group decisions (i.e., which individual(s) successfully initiate group movements). My results indicated that conflicts of interest are ubiquitous among group members over when to leave feeding patches. I found that groups most often follow decisions that are optimized at the group-level, potentially indicating a mechanism of collective sensing whereby pooling of information from group members leads to a better estimate of the environment (i.e., the patch and the optimal time to leave it). However, I still found that occasionally unshared decision-making (especially dictated by the dominant adult male and female) and shared decision-making play a role in group departures. My results of observed movement initiations suggest that while all individuals in a group successfully initiated movements away from trees, dominant adult females were the most successful at leading the group away. I further found that dominant adult males paid the lowest time consensus costs, while juvenile individuals paid the highest time consensus costs over when to go decisions. Individuals who paid a higher time consensus cost ultimately received less food overall in feeding trees. This study illustrates how applying classic models from foraging theory, like the marginal value theorem, to empirical data from stable social groups can provide insight into how groups resolve conflicts of interest and reach consensus decisions about when to depart feeding trees.

INTRODUCTION

How do groups of individuals come to a consensus about what to do and when to do it? Social animals regularly confront consensus decisions where group members must choose between mutually exclusive actions and ultimately come to a choice collectively (Conradt & Roper 2009, Conradt 1998). Consider, for example, a group of primates that stays together as a social unit every day and must decide where to travel after a rest or foraging period (Stewart & Harcourt 1994), or how long to spend in each feeding tree (Boinski et al. 1995). Reaching consensus about where and when to move in their habitat is crucial for group members to obtain the benefits of sociality (such as reduced predation risk, increased access to mates, information sharing, see Silk 2007 and Ward & Webster 2016 for review). For a group to remain cohesive, its members must coordinate their activities; otherwise, the group will fragment as individuals pursue diverging patterns of behavior and movement (Sueur et al. 2011, King and Cowlishaw 2009).

Reaching consensus is particularly challenging in heterogeneous groups where individuals differ in their needs, abilities, prior experiences and knowledge, social rank, or even their social relationships (Strier 2015, Sueur et al. 2011, King & Cowlishaw 2009, Terborgh & Janson 1986). For instance, a single social unit can contain males and females, juveniles and adults, more experienced and less experienced individuals, and bolder and shyer personalities (Clutton-Brock et al. 1977). Animals in heterogeneous groups can differ in their nutritional requirements, physiological condition, in the information they have about the environment, and/or in their ability to monopolize resources. For example, in foraging decisions, males and females often prefer different types of food (Ruckstuhl et al. 2002). Hungry individuals often prefer to allocate more time to foraging and will exhibit conflicting destination preference compared to tired group members (Sueur et al. 2010, Dostálková et al. 2007, Krause et al. 1992). Young or vulnerable animals typically prefer safer areas than older, less vulnerable individuals (Lingle et al. 2005). Lactating females may prefer foraging areas with greater food rewards, as they have higher daily energy requirements (e.g., Fischhoff 2007, Clutton-Brock et al. 1982). Often in primates, larger, stronger, or simply higher-ranking individuals are able to exclude others from valuable food resources and benefit from higher foraging intake rates (Vogel 2005, Janson 1988, Janson & van Schaik 1988, and see Chapter 2 of this dissertation), particularly when these resources are distributed in dense, defensible patches like fruit trees (Nicholson 1954). With such variation between group members, conflicts of interest may frequently arise over what to do and when to do it (Petit et al. 2010).

When such conflicts exist, reaching a consensus decision will necessarily involve compromise for at least some group members, especially in cohesive groups that forage and travel together as social units. The group members who compromise ultimately pay a "consensus cost", defined as the fitness cost an individual incurs by foregoing its own optimal action in order to coordinate with other group members (Conradt & Roper 2003, 2005). Often, the consensus costs individuals pay depends on their ability to exert influence over group decisions (Conradt & Roper 2003). For example, if a dominant individual can dictate a decision ("despotic" decision making), it will not incur a consensus cost as it can pursue its own optimal behavior. Under such unshared decision-making regimes, subordinate group members will incur consensus costs of a magnitude that is relative to how different their own optima are from that of the dominant individual. A study by King et al. 2008 supports this concept; subordinate baboons experienced substantial consensus costs in experimental food patches by receiving less food than the dominant baboon, when led by the dominant to patches that the dominant could monopolize. Conversely, if all group members contribute equally to a collective choice ("shared" decision making), the consensus cost will be, on average, lower for all group members (although dominant individual(s) will pay larger consensus costs than they would have if they had imposed a despotic decision on the group, Rands et al. 2013, Conradt & Roper 2007).

Group decisions about when and where to forage are particularly important, as finding and exploiting food is necessary for the survival and fitness of group members (Conradt 2011, Kerth et al. 2006). Optimal foraging theory provides a useful theoretical framework for exploring how animal groups resolve conflicts of interest and come to consensus about what and when to eat (Davis et al. 2022, Stephens & Krebs 1986, Pyke et al. 1977, Schoener 1971). The marginal value theorem (MVT) in particular provides clear predictions about the differences in the length of time each member of a group should want to spend exploiting a particular food patch (Giraldeau & Caraco 2000, Charnov 1976). The decision of when to leave a patch and move on to the next, referred to as the "optimal departure time", is predictable using the MVT applied to cumulative foraging intake rates (illustrated as "gain curves", see Chapter 1 of this dissertation, Davis et al. 2022), whereby an individual should ideally depart a patch when their current rate of energy gain falls below the average rate of energy gain for the habitat (Charnov 1976). When individuals vary in the amount of food they require, and/or in the rate at which they can acquire it, this can introduce conflicts of interest over the timing of patch departures in social foragers (Davis et al. 2022). For individuals living in cohesive social groups that move together as a unit, groups must come to consensus decisions over when to collectively leave a patch, whereby some individuals may compromise their preferred behavior, presumably at a cost to themselves.

In this study, I integrate theoretical predictions from the marginal value theorem into an empirical study of social foraging behavior in cohesive groups of wild white-faced capuchin monkeys living on Barro Colorado Island, Panama. Using a focal tree method to measure simultaneous foraging behavior of group members in *Attalea butyracea* palm trees (Vogel & Janson 2007), I calculate exact individual feeding rates over time for each group member in trees, generate individual foraging gain curves, and use the marginal value theorem to predict the optimal patch departure time for each group member. Drawing upon the theoretical framework developed in Chapter 1 of this dissertation (Davis et al. 2022), I quantify the degree of within-group conflict for observed collective decisions over when to leave foraging patches. I then investigate how observed patterns of group departure behavior deviate from individual- and group-level optima (i.e., which group members contributed to group decisions and which group members paid consensus costs by leaving at suboptimal times). From these data, I then determine the process of collective departure decisions of when to go, whether they be underpinned by an unshared, shared, or group-level optimal process. I also compare my foraging theory results with more conventional methods of assessing who has influence over group decisions (i.e., which individual(s) successfully initiate group movements, Papageorgiou et al. 2020, Amornbunchornvej et al. 2018, Strandburg-Peshkin et al. 2018, King et al. 2011, Stueckle et al. 2008). Finally, I evaluate which group members paid consensus costs to collective decisions, by leaving patches at a suboptimal time.

First, I hypothesized that conflicts of interest exist between group members over when to leave foraging patches (refer to Table 1 for an overview of the hypotheses and predictions of this study). I calculated when individuals were predicted to prefer to leave foraging patches using the marginal value theorem, and evaluated the extent of conflicts of interest within the group over preferred optimal patch departure times. I predicted that the varying foraging abilities of group makes would lead to inter-individual differences in foraging gain curves (and optimal patch departure times) of group members *(Prediction*$_1$*)*. As dominant and older individuals often gain preferential access to the patch and thus have higher foraging rates (Koenig 2002, Vogel 2005), I predicted that high ranking and adult individuals would have earlier optimal patch departure times when compared to subordinates and juveniles *(Prediction*$_2$*)*. I note that in this study, I define dominant or high-ranking individuals in the conventional sense, where more dominant group members are those that more often win aggressive interactions.

Second, I hypothesized that the group decision-making process is either unshared (where a single individual leads), shared (where all or a representative proportion of the group contributes), or optimized at the level of the group (where groups leave trees based on a group-level optimal prediction, see Chapter 1, Box 3, Davis et al. 2022). Under unshared decisions, I predicted that the *observed* group departure time from a patch would most closely align with the *predicted* optimal departure time for one individual *(Prediction*$_3$*)*. As socially dominant individuals are conventionally defined as those who most often win aggressive interactions (Holekamp & Strauss 2016), I tested if the observed group departure time aligned with the optimal departure time for more aggressively dominant monkeys. I further predicted that the magnitude of each individuals' consensus cost (defined as the difference between *predicted* optimal and *observed* patch departure times, hereafter referred to as "time consensus costs") would be related to dominance rank and age under unshared decision-making regimes. I predicted that high ranking individuals and adults would have small time consensus costs, while low ranking and juvenile individuals would have high time consensus costs *(Prediction*$_4$*)*. Under shared decisions, I predicted that the *observed* patch departure time for the group would align with the median of group members' *predicted* optimal departure times, representing a majority rule where groups would leave patches once a certain threshold number of individuals have reached their optimal departure times (in this case, the median individual, *Prediction*$_5$). I also predicted that the magnitude of each individuals' time consensus cost would not be related to dominance rank or age under shared decision-making processes *(Prediction*$_6$*)*. And finally, under decisions that are optimized at the level of the group, I predicted that the *observed* group patch departure times would correspond with the *predicted* optimal patch departure time for the group as a whole (as predicted by the group cumulative gain curve, *Prediction*$_7$).

Third, I hypothesized that individuals who compromised their optimal foraging timing would pay a foraging consensus cost. I predicted that individuals who have optimal *predicted* times of patch departure deviating the farthest from the *observed* group departure time would obtain less food overall (a proxy of an energetic cost to leaving at a suboptimal time, *Prediction*$_8$).

Importantly, my study demonstrates the straightforwardness of applying classical theories to help us tackle novel research questions. By comparing individuals' optimal patch departure times with the real, observed group patch departure times, I tested hypotheses about how conflicts of interest are resolved in group-foraging primates, who exerts control over group decisions, how such decisions are made, and who pays consensus costs.

Hypothesis	Prediction
(H1) Conflicts of interest over patch departure time exist between group members.	(P_1) The varying foraging abilities of group mates lead to inter-individual differences in the foraging gain curves (and optimal patch departure times) of group members, such that: (P_2) dominant and adult individuals have earlier optimal patch departure times when compared to subordinates and juveniles.
(H2a) High-ranking individuals determine the timing of group decisions (i.e., group decisions of when to leave a patch are *despotic* or *fully unshared*, where a single individual leads).	(P_3) Under despotic conditions, the *observed* group departure time from a patch will most closely align with the *predicted* optimal departure time for high-ranking individual(s). (P_4) The magnitude of each individuals' consensus cost (defined as the difference between *predicted* optimal and *observed* patch departure times) will be related to rank and age. I predict that high ranking individuals and adults will have small consensus costs, while low ranking and juvenile individuals will have high consensus costs.
(H2b) Group decisions of when to leave a patch are *shared* such that all individuals in the group contribute equally.	(P_5) Under shared decisions, the *observed* patch departure time for the group will be the median of group members' *predicted* optimal departure times (representing a majority rule). (P_6) The magnitude of each individuals' consensus cost (defined as the difference between *predicted* optimal and *observed* patch departure times) will **not** be related to rank or age.
(H2c) Group decisions of when to leave a patch are *optimized* at the level of the group, such that decisions optimize group-level outcomes.	(P_7) Under group-level optimal decisions, the *observed* patch departure times will correspond with the *predicted* optimal patch departure time for the group as a whole (as predicted by the group cumulative gain curve).
(H3) Individuals who compromise their optimal foraging timing pay a foraging consensus cost.	(P_8) Individuals who have optimal *predicted* times of patch departure deviating the farthest from the *observed* group departure time obtain less food overall.

Table 1. Table of the hypotheses and associated predictions for this study.

METHODS

Study Site: For this study, four field observers conducted behavioral observations of two well-studied capuchin groups (Tórrez-Herrera et al. 2020, Crofoot et al. 2008, Crofoot 2007) at the Smithsonian Tropical Research Institute field site on Barro Colorado Island (BCI) in Panama. Data collection occurred during the months of June to September in 2015 and 2016. BCI (9°9’N, 79°51’W) is a 1560-hectare island in the Panama Canal composed of semi-deciduous lowland tropical moist forest. The island was formed during the construction of the Panama Canal between 1911 and 1914 when the waters of the Chagres River were dammed to create Gatun Lake. The United States Government designated the island as a natural preserve in 1923, and BCI has been administered by the Smithsonian Tropical Research Institute since 1946. As one of the most studied tropical forests on earth, research on BCI has been at the forefront of measuring diversity of plant and animal life in the tropics. BCI has two primary seasons: a wet season from April to November and a dry season from December to May (Windsor 1990). Distinct seasonality in the availability of fruiting trees on the island occurs, an important resource for many species, including the resident primate populations. Fruit availability tends to be high during the dry season and into the early wet season and is lowest during the late wet season (Leigh 1999). Five resident primate species live on BCI, including the white-faced capuchin monkeys.

Study species: This study examines foraging decisions in white-faced capuchin monkeys. This species is an arboreal, New World monkey that is native to the forests of Central America and the extreme north-west portion of Colombia. White-faced capuchins are part of the family

Cebidae, subfamily Cebinae. Capuchins rely heavily on ripe fruiting trees for food (Fragaszy 2004, Di Fiore et al. 2008), an ephemeral resource in the seasonal tropical forest of BCI. While finding and exploiting fruiting trees is inherently difficult in a seasonal forest where not all tree species fruit simultaneously, it is essential for survival in these primate groups. Thus, the capuchin monkey populations on BCI are an ideal study system to investigate how animal groups make vital decisions about what, where, and when they need to eat.

White-faced capuchins are long-lived animals, living more than 50 years in captivity (about 30 years in the wild) and having a prolonged juvenile period (Harvey et al. 1987). Females first give birth at about six to eight years of age, while males are considered sexually mature at eight years old (Freese & Oppenheimer 1981). Capuchins live in multi-male, multi-female, cohesive social groups that remain in proximity together all day every day of their lives (excluding rare dispersal events, Perry 1997). Females are philopatric (i.e., stay in their natal group), whereas males migrate one to a few times during their lifetime into new neighboring groups (Fedigan 1993). Social groups usually average between 17-19 individuals (Fedigan et al. 2001), although the study groups on BCI tend to have fewer individuals (ranging from 9-25 individuals in a study published by Crofoot 2007). There is a dominance hierarchy within capuchin group members, such that dominant individuals tend to gain priority access to important resources and mates (Jack & Fedigan 2006). Capuchins primarily feed on fruit, which comprises between 60-80% of their diet (Fragaszy 2004). Insects, other invertebrates, small vertebrates and other plant material are taken opportunistically. The capuchin groups on BCI live in home ranges of approximately 90-160 hectares and are xenophobic with mutually agonistic relationships with their neighbors (Crofoot 2007). I focused my observations on two groups of capuchins: FC (composed of 12 individuals), and TOP (composed of 18 individuals, see Figure

11 for an aerial view of BCI and the home ranges of the two study groups). Both groups had a single adult male, and FC group has 3 adult females and TOP has 5 adult females. There were 7 juvenile individuals in FC and 1 infant, and 10 juveniles and 2 infants in TOP. During my study periods there were no subadult individuals (potentially a result of a mass mortality event in years prior, Milton & Giacalone 2014). Members of each of the study groups were fitted with GPS and radio telemetry collars, and their movements and activity patterns were tracked throughout the duration of the study.

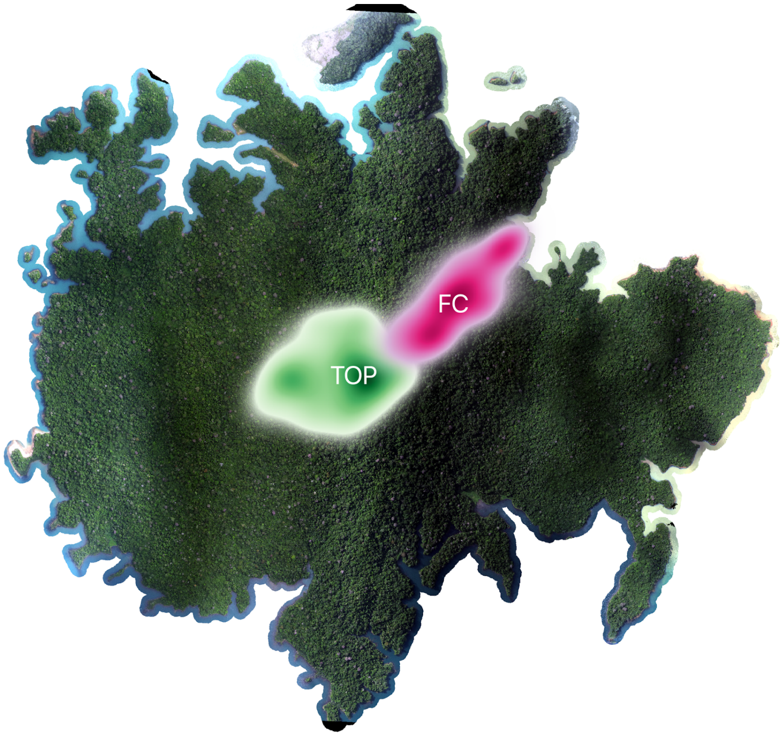

Figure 11. Home ranges of white-faced capuchins (*Cebus capucinus*) belonging to FC (pink) and TOP (green) groups on Barro Colorado Island, Panama from June to August, 2016. Home ranges were calculated using continuous time movement models implemented in the ctmm package in R (Calabrese et al. 2016) using handheld GPS data, where observers recorded GPS

points of the group centroid every 5 minutes during daily follows. The color gradient represents the probability mass for the home range (darker colors reflect higher intensity of use).

Focal tree study species: I focused my data collection on a keystone tree species during June-September of 2015 and 2016: *Attalea butyracea* palm trees. The capuchin groups spend >75% of their total feeding time during these months in these trees. *A. butyracea* fruits grow in large clumps, or infructesences, that suspend off a single stem of the palm plant (Figure 12). Due to this structure, palm fruits are easily monopolizable for high-ranking individuals who can exclude their group-mates from the infructescence. Groups of three to five observers collected data on the two capuchin study groups, focusing on foraging behavior in *A. butyracea* trees and leadership during group movements.

Figure 12. Photographs of *A. butyracea* palm infructescences, without monkeys feeding, with multiple group members feeding together, and with the dominant male feeding.

Observational daily follows: Capuchin monkeys are diurnal primates, and activities begin at or just after dawn. In order to track both study groups, I and my field assistants used radio telemetry. One member in each of the capuchin study groups was equipped with a radio collar. Each collar transmited a unique frequency signal. Using a hand-held antenna and receiver radio, we could reliably locate the study group in the early morning. Daily follows lasted for a minimum of 5 contact hours (up to 12 hours) with the selected study group. We alternated daily between study groups to obtain behavioral data on each group each week throughout the study season.

Once visual contact was made with the study group in the morning, we recorded the identities and age/sex classes of all group members present. Individuals within each social group were identified using differences in size, facial fur patterns, and other distinctive markings (e.g., spots, scars, freckles, missing or broken appendages). Because more than one observer collected data for this project, periodic inter-observer reliability checks were conducted to assure agreement in identification of group members, behavioral activity categories, and identification of fruit trees. As these groups are habituated to human observers, we could successfully follow underneath the monkeys during the day as they moved and foraged in the trees.

To obtain basic group-level activity states, we continuously recorded the activity the majority of group members during the entire day follow. There are 5 mutually exclusive activity states: foraging (group members are searching for and/or consuming food), traveling (directed movement from one place to another), vigilance (directed gaze at predators, other individuals, observers, or other objects), social (primary social activities including grooming, playing, or being aggressive), and resting (inactivity and sleeping). If the group went out of visual contact, we noted "out of sight", recording the start and end times when the group behavior was not visible.

When the group was traveling from place to place, one observer positioned themself at the front of the troop, looking for any feeding trees with ripe fruits that the group might visit. We collected written data on all observed feeding sessions on *any* fruit trees, including the start time, end time, tree species, and GPS point. We also recorded the number of individuals in the group who feed at each tree, and their identities. We noted the direction the group was moving in and what individual(s) were in front of the group from each feeding tree to the next. Directions are noted as 45-degree increments corresponding to N, NE, E, SE, S, SW, W, and NW. We recorded ad libitum observations of significant events during the daily observation time period, such as predation threats, intergroup encounters with other monkey groups, etc., as these can significantly impact behavior.

Social dominance interactions: I and my field assistants recorded subtle and active aggressive encounters on an all-occurrence basis throughout daily follows of the monkey groups. Subtle encounters included cowers, avoids, facial or vocal threats whereas active encounters referred to active fighting that includes behaviors such as chases, bites, slaps, and lunges. We noted all observations of aggressive interactions between all group members except dependent infants (see ethogram for specific behavioral information in supplementary materials, Altmann 1974).

Focal tree method: To quantify variation in feeding rates among group members, we used Vogel & Janson's focal tree method (Vogel & Janson 2007). For each foraging visit in *A.*

butyracea trees, we recorded the tree's location (using a hand-held GPS) and determined the order of individuals' arrivals and departures, recording the identity and time that each member of the focal group entered and left the fruit tree. The time between the first arrival and last departure represented the "total group feeding time". If there were gaps in feeding during the feeding bout such that no animals were feeding, the amount of time in which monkeys were not feeding was subtracted from the total group feeding time. We recorded the "observed group departure time," defined as the time when a majority of group members started directed movement (traveling) away from the focal tree (note that this may not be the exact same time as when the last monkey exits the tree). We also noted if there was a clear leader individual in front of the departing group.

When a group entered a palm, the observers positioned themselves on either side of the palm to get the complete view of all fruiting clumps within the palm (occasionally, palms have more than one fruiting raceme). If there was only one observer present, the observer recorded all behavioral observations by speaking into a hand-held recording device. If two or more observers were present, the primary observer called out the behaviors and the secondary observers inputted the behaviors using the iOS app "Animal Behaviour Pro" on an iPhone or iPad (version 1.2, Newton-Fisher 2012). Using this app, we generated specific buttons with the identification names of the monkeys and all behaviors in our ethogram. The start of the sampling bout occurred when the first individual entered a palm tree, and the primary observer said aloud the date and exact time. The primary observer also noted the number of fruit clumps in the palm. The primary observer recorded the time (to the second), direction of entry, identification of the first monkey arrival to the palm, each successive arrival, and the identification and direction of exit of each departing monkey from the palm. Because of the size and shape of *A. butyracea* infructescences, it was possible to record each time any and all members of the monkey group entered the food patch and removed fruit. Using the Animal Behaviour Pro app, we recorded the time (to the second), direction of entry, identification of the first monkey arrival to the palm, each successive arrival, and the identification and direction of exit of each departing monkey from the palm. We also recorded any and all aggressive encounters in the fruit tree, including displacements and fights (see detailed ethogram in Supplementary materials). The observers recorded data on who initiated the interaction, which individuals were involved, and who won the interaction.

To calculate individual foraging gain curves, we recorded the identity of each monkey that removed fruit, the amount of fruit taken and eaten (number of fruits as well as the proportion of each fruit that was consumed), and the time each fruit was harvested for each monkey that fed. The following foraging behaviors, in particular, were recorded on an all-occurrence basis for all monkeys who entered and fed in each palm. Each behavior was associated with the actor (the identity of the monkey who performed the behavior) and the time stamp to the second when it was inputted into the Animal Behaviour Pro app. 1) *Patch entry time:* when a monkey descended onto the fruiting raceme. The direction of entry was also recorded using 45-degree increments corresponding to N, NE, E, SE, S, SW, W, and NW. 2) *Patch exit time:* when a monkey left the fruiting raceme. The direction of exit from the patch was recorded like above in 45-degree increments. 3) *Search behaviors* while a monkey is attempting to find a ripe fruit to consume. These include behaviors where a monkey *touches*, *bites*, or *drops* a fruit without consuming the fruit. A touch was defined as when an individual used its hands to test and squeeze fruits on the fruiting clump, without pulling them off the clump. A bite occurred when an individual used its teeth to bite into a fruit, without ultimately eating it. A drop was recorded when an individual removed a fruit from the fruiting clump and discarded it without eating. 4) *Start time of eating a* *fruit*: the time, to the second, a monkey started to process and eat a fruit (from the moment the monkey took the fruit off the raceme and began to manipulate and peal it for consumption). 5) *End time of eating a fruit:* the time, to the second, a monkey stopped eating a fruit and discarded it to the forest floor. 6) *Percent of the fruit consumed*: once a monkey stopped eating a fruit and discarded it, we recorded approximately how much of the fruit pulp the monkey ate. The approximate amount of pulp consumed was recorded in four categories: >25% eaten, 25-50% eaten, 50-75% eaten, and 75-100% eaten. These categories were chosen because the monkeys typically peal the fruit up to four times to consume the entire pulp (i.e., if a monkey ate only about 25% of the fruit pulp, it was readily observable because the monkey would peal a fourth of the hard outer shell and then consume the pulp and discard the fruit). If, because of visual constraints, the amount of pulp consumed was not visible, we recorded "unknown" for the percent of fruit consumed.

These observations provided information for each individual monkey on: entry times into trees, fruit intake rates, searching behaviors for fruits, searching rates for ripe fruits, handling times for consumption of a ripe fruit, how much of each food item (a fruit) was consumed, and competitive interaction data for all individual monkeys in the tree. We collected data on capuchin foraging in a total of 231 *Attalea butyracea* focal trees (166 trees for FC group and 66 trees for TOP group).

<u>*Leadership and initiators of group movements:*</u> To understand patterns of leadership and initiation of group movements away from each feeding tree, I focused on recording leadership patterns in 'feeding-tree to feeding-tree' travel bouts. My field assistants and I recorded the time, identity, and travel direction (in 45° increments) of group members as they left each feeding tree.

An “initiation attempt” to instigate group movement away from the tree was defined as an individual who exited the tree, moving away more than 10 meters in 40 seconds in a specific direction. An unsuccessful initiator was an individual who attempted to make an initiation movement, but then returned to remain with the other group members. A successful initiator, or “leader,” was defined as an individual who (1) left the feeding tree in the direction (within 45°) of the next feeding tree the group visited, (2) did not return back towards the group, and (3) was followed by at least 1/3 of the group in the same approximate cardinal direction within 10 minutes of departure (these criteria are based on preliminary observations and comparable field studies conducted by Boinski & Campbell 1995, Petit et al. 2009).

Measurements of tree crop size: For each *A. butyracea* that the groups fed in, I estimated crop size using photographs of the fruit racemes. As soon as the primate group moved on from the tree, I took photos of all infructescences in the tree. These photos were standardized in color scheme using gray and white color cards held in front of the fruit in the photo. This allowed comparison of fruit color across photos, accounting for variation in light and shadow in the forest. Multiple photos of each fruit raceme were taken from different angles. Using these photos I then counted the fruits present in each raceme to determine the post-foraging crop size for each palm tree, using the software ImageJ. The color of the fruit provided information about fruit ripeness: orange fruits were ripe, green fruits were immature, and semi-ripe fruits were yellow. I calculated the pre-foraging crop size for each tree (how much food was available to the monkey groups when they arrived to the tree to begin foraging) by summing the number of fruits the group consumed during their time in the tree and the number of ripe fruits counted from our photos of the fruit racemes.

Data analyses

All analyses and plots were done using R (R Development Core Team, 2022). For my statistical models detailed below, I calculated standardized model coefficients (β), their 95% confidence intervals (CIs), and report categorical effect sizes in my results. I used the ggeffects package (Lüdecke 2018) to calculate the marginal effects and 95% CIs for each of my models, and then plotted these using the ggplot2 (Wickham 2016) and cowplot (Wilke 2020) packages. Statistical significance of the fixed effects in my models were assessed using the report package (Makowski et al. 2020). Significance for all tests was set a $\alpha = 0.05$.

Dominance hierarchies and age classes

To assess the impact of social dominance on access to resources, I first computed dominance hierarchies for both capuchin monkey groups. Dominance hierarchies were calculated based on subtle (i.e., cowers, avoids, facial or vocal threats) and active (i.e., chases, bites, slaps, fights, lunges) aggressive outcomes. I only assessed dominance status for adult individuals, as juvenile monkeys were more challenging to track. The hierarchical dominance relationships were determined on the basis of direction of agonistic dyadic interactions where I could determine a clear aggressor (winner) and clear receiver (loser) of the threat. I used these winner-loser interactions to calculate and rank each individual in each monkey group for each study year by Elo scores (Neumann et al., 2011). Because my study periods for each year were short (3-4 months long), I assumed dominance ranks to be stable during each study period. To achieve a more robust estimate of dominance rank, I generated 1000 replicated datasets of interactions by randomizing the order of interactions (timing). I calculated the mean and 95%

confidence intervals of ranks of individuals based on Elo score, using the R package aniDom (Farine & Sanchez-Tojar, 2017).

For analyses involving dominance rank as a predictor variable, I assessed rank in two ways: 1) as a continuous variable where each individual was assigned a numeric dominance rank corresponding with their Elo Rating status (with the most dominant monkey being “1” and so on), and 2) a categorical variable whereby I pulled out the dominant male and dominant female and compared to all other subordinate adults. In both monkey groups during my study, there were no subordinate adult males so my category of subordinate adults comprises only subordinate adult females. I note that I conducted my analyses of dominance only with respect to all adult individuals in the two monkey groups. For analyses involving age class as a predictor variable, I assessed this categorically with two classes: adults and juveniles. As neither of the capuchin monkey groups contained any sub-adult monkeys during my study periods, it was straightforward to classify each monkey as either adult or juvenile.

Marginal value theorem gain curves and optimal departure times

The original marginal value theorem model comprises two primary inputs: the average inter-patch travel time (the average time it takes to travel from one discrete feeding patch to another in the environment) and a forager’s gain function (the cumulative amount of energy acquired within a patch over time, Charnov 1976). Extensions of the MVT include handling time as well (the required time to process and consume a food item within a food patch, Bettinger & Grote 2016). Thus, I calculated these parameters to obtain the optimal patch departure times for individuals feeding in palm trees:

Inter-patch travel time: The travel time between patches (μ) is the length of time a forager spends moving from one feeding patch to another. I calculated the travel time as the average amount of time it takes the primate group to travel between feeding trees. I included *all* feeding trees in my calculations, as foraging theory requires an average across the entire environment. I also calculated an average travel time for each separate primate group. As foraging theory only approximates behavior while searching for and consuming food, I excluded times when the group was engaging in non-foraging behaviors such as vigilance, resting, and social behaviors from my analyses. To do this, I used the continuous group activity states collected throughout daily observation time. These mutually exclusive activity states included: foraging, vigilance, resting, social, and traveling. I subtracted the duration of all resting, social, and vigilance activities from the time spent travelling between feeding trees. This yielded an estimate of the time spent in directed movement. I further assessed if inter-patch travel times differed between different tree species, across the season, and/or based on time of day using gaussian generalized linear mixed models (GLMMs) with log link functions using the R package glmmTMB (Brooks et al. 2017). I included monkey group identity as a random effect to control for repeated measures.

Individual foraging gain curves: Charnov and Parker (1995) model a foraging gain function as a negative exponential function:

$$W(t) = 1 - exp(-\lambda t), \qquad \text{(equation 1)}$$

where ($W(t)$) decreases exponentially at a rate determined by the individual's foraging efficiency λ (higher λ results in a faster rise of the gain to its asymptote). Elaborating this basic model within patches, Bettinger & Grote (2016) highlight that prey items can require a distinct handling time, increasing patch residency time and reducing rate of energy gain. In this scenario, the time taken to extract the gth prey item from a patch containing G prey items (the inverse of the gain function) is given by:

$$t(g) = \frac{1}{\lambda} log \frac{G}{G-g} + hg, \qquad \text{(equation 2)}$$

where h is the handling time. As 'prey' items within *A. butyracea* palms require a distinct handling time prior to consumption (i.e., each fruit has a hard, inedible exterior peal that must be removed to access the pulp inside), I used equation 2 above that includes handling time to formulate individual gain curves for all individual monkeys feeding in each palm tree. I used my estimates of tree crop size from my photographs of *A. butyracea* infructescences as measures of G (also referred to as the "pristine patch value" in foraging theory). Note that while a change in prey abundance in the patch affects travel travel time between patches, this does not affect handling time (Bettinger and Grote 2016). Foraging that entails alternating search and handling times for discrete food items within a patch, like *A. butyracea* palm fruits, requires gain curves to be calculated using equation 2.

Group-level foraging gain curves: Much like how individual foraging gain curves are calculated, I modeled a group-level foraging gain curve for each feeding patch the monkey groups visit. This group-level curve was calculated by counting the cumulative amount of fruit pulp eaten by all group members over time (in another sense, I treated the group foraging rate as if the group was a single entity extracting resources from the patch).

Optimal patch departure times: An individual was expected to leave the foraging patch when their current rate of food capture fell below the average capture rate for the habitat (Charnov 1976), which was given by the point where $\frac{W(t)}{\mu+t}$ is maximized and μ is the average travel time between patches. Using the above calculations for individual- and group-level foraging gain curves and average travel time between patches, I found this optimal patch departure time for each individual and the group overall in each tree. These optimal patch departure times represent predictions of individual preferences over when to leave a tree.

Conflicts of interest exist between group members over when to leave

I defined a conflict of interest between group members over when to leave a foraging patch as a difference in time between the predicted optimal patch departure times for individuals. Higher conflicts of interest would be represented by larger differences between the optimal departure times for group members.

As Chapter 2 of this dissertation indicates, individuals differ in their ability to monopolize and/or exploit food resources *(P_1)*, leading to differences in the foraging efficiency, and thus foraging gain curves, of group mates. I compared individual gain curves between group members to examine if dominance rank, and relative age (adult versus juvenile) led to differences in the optimal patch departure times and, if so, if *(P_2)* optimal patch departure times of high ranking and older adult individuals preceded those of low ranking and juvenile individuals. To control for variation in the amount of time the monkey groups spent in *A*.

butyracea focal trees, I translated optimal departure times in a focal tree into ordered factors (with “1” being the earliest predicted optimal departure time, “2” being the next optimal departure time, and so on). To test if higher ranking or adult individuals have earlier optimal patch departure times, I fit ordinal logistic regression models to my ordered response, which was the order of optimal patch departure times for each group member, using the R package MASS (Venables & Ripley et al. 2002). My predictor variables were dominance rank or age class (adult or juvenile).

The process(es) of group decision-making

By comparing the *observed* group departure times with the *predicted* optimal departure times for each individual and the group overall, calculated based on their foraging gain curves, I tested whether despotism *(H2a)*, shared decisions *(H2b)*, or group-level optimal decisions *(H2c)* dominated the group decision-making process. If the observed group departure times consistently closely aligned with the predicted optimal departure time for high-ranking individuals *(P_3)*, this was evidence for despotism and support of hypothesis 2A where dominant individuals exerted disproportionate control over group decisions. Conversely, if observed group departure times did not strongly correlate with the high-ranking individual, and instead aligned with the median of all group members’ predicted optimal departure times, this suggested shared decision-making whereby groups followed a majority rule and left trees once a threshold number of individuals reached their optimal departure times (the median, *P_5)*. If the observed group departure time corresponded to the optimal departure time predicted by the group cumulative gain curve this indicated optimization of a group-level outcome *(P_7)*.

I tested whether an individual group member *(P_3)*, the “average” group member *(P_5)*, or the cumulative group overall *(P_7)* had a predicted optimal departure time that corresponded the closest to the observed group departure time for a given focal tree by running a binomial GLM with the logit link. I ran the same GLM separately for each monkey group. I converted the time differences between optimal and observed departure times into absolute values prior to analyses, and then assigned a binary response to each absolute value time difference depending on which absolute value time difference was the closest to zero (in other words, close alignment between observed and optimal departure times). The response variable was binary (1: the closest optimal departure time to the observed group departure time for a given focal tree; 0: not the closest optimal departure time to the observed group departure time), and the independent variable was identity (either individual identity, the average group member, or the cumulative group overall).

I further examined which individuals paid a *time consensus cost* when the group departure decision did not align with their preferred optimal choice. Under despotic decisions, I predicted high ranking and adult individuals would have the smallest time consensus costs in comparison to low ranking and juvenile individuals *(P_4)*. If instead group departure decisions were shared, I expected time consensus costs to not be related to rank and age *(P_6).* To test these predictions, I calculated the magnitude of each individuals' time consensus cost for when-to-leave decisions as the absolute time difference between the optimal and observed patch departure times. Then, I examined whether dominance rank and age class predicted the time consensus cost individuals paid by using gamma GLMMs with log link functions using the glmmTMB package (Brooks et al. 2017). In these models, I included individual monkey identity, study group identity, study year, and bout identity (the specific focal tree follow for each observation) as random effects to control for repeated measures in the dataset.

To compare my optimal foraging theory results with more conventional methods of studying group decision-making and leadership, I examined my data on movement initiation attempts away from feeding trees and which individuals (‘leaders’) were most successful at recruiting the group to move on to the next resource. I quantified what proportion of total initiation attempts an individual was successful at recruiting the group to follow (and what proportion an individual was not successful). I then tested whether dominance rank and age could predict whether an individual would be a successful initiator of group departures by running binomial GLMMs on group departures away from focal trees using the glmmTMB package (Brooks et al. 2017). The response variable was binary (1: successful; 0: unsuccessful) for a given initiator, and the independent variable was either dominance rank (ordered or categorial, as above) or age class. I included study group identity and study year as random effects to control for repeated measures in the dataset.

Consensus costs

Beyond my analyses of time consensus costs (as detailed above), I also tested if individuals who compromised their optimal foraging timing paid an *energetic consensus cost.* I predicted that individuals whose optimal predicted times of patch departure deviated the farthest from the observed group departure time obtained less food overall in a focal tree, a proxy for energetic consensus costs *(P_9)*. To test this, I ran a gamma GLMM with log link function using the glmmTMB package (Brooks et al. 2017). My response variable was the total amount of fruit pulp eaten by an individual in a focal tree, and my independent variable was the absolute time difference between that individual’s optimal departure time and the observed group departure time (the *time consensus cost*). I included individual monkey identity, study group identity, study year, and bout identity (the specific focal tree follow for each observation) as random effects to control for repeated measures in the dataset.

RESULTS

Dominance hierarchies

Observations of 233 all-occurrence dominance interactions across both monkey groups revealed a distinct social hierarchy, with a dominant male as the highest-ranked individual in both groups (Figures 7A and 7C, Chapter 2).

Marginal value theorem gain curves and optimal departure times

Inter-patch travel time: The estimated mean travel time from feeding tree to feeding tree was 12.79 minutes (95% CI [9.01, 14.55]) for FC group, and 10.84 minutes (95% CI [9.15, 12.54]) for TOP group (see distribution of travel times in Figure 13). Inter-patch travel times were not significantly different between different tree species, based on time of day, or across the field season (GLMM tree species: $\chi^2 = 2.21$, $p = 0.529$; GLMM time of day: $\chi^2 = 0.753$, $p = 0.385$; GLMM date in field season: $\chi^2 = 4.11$, $p = 0.150$, Figure 14).

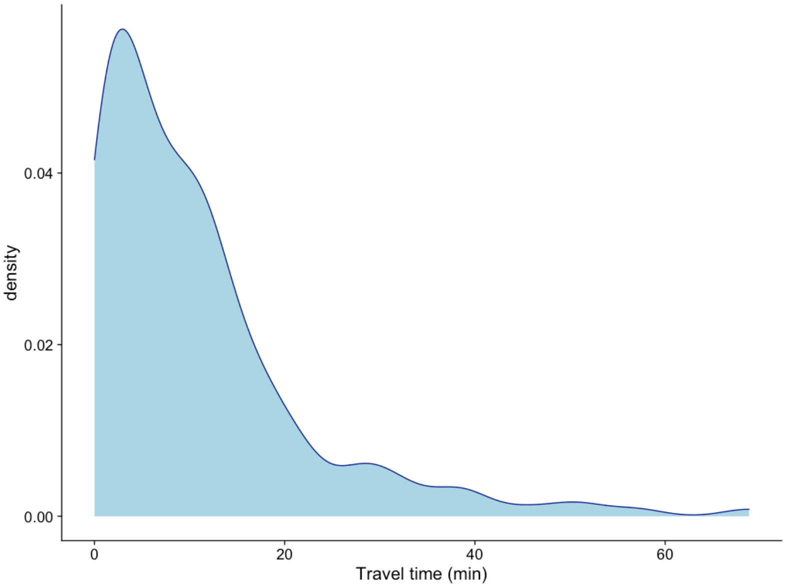

Figure 13. Density distributions of inter-patch travel times (in minutes) across all species of feeding tree for FC and TOP capuchin groups.

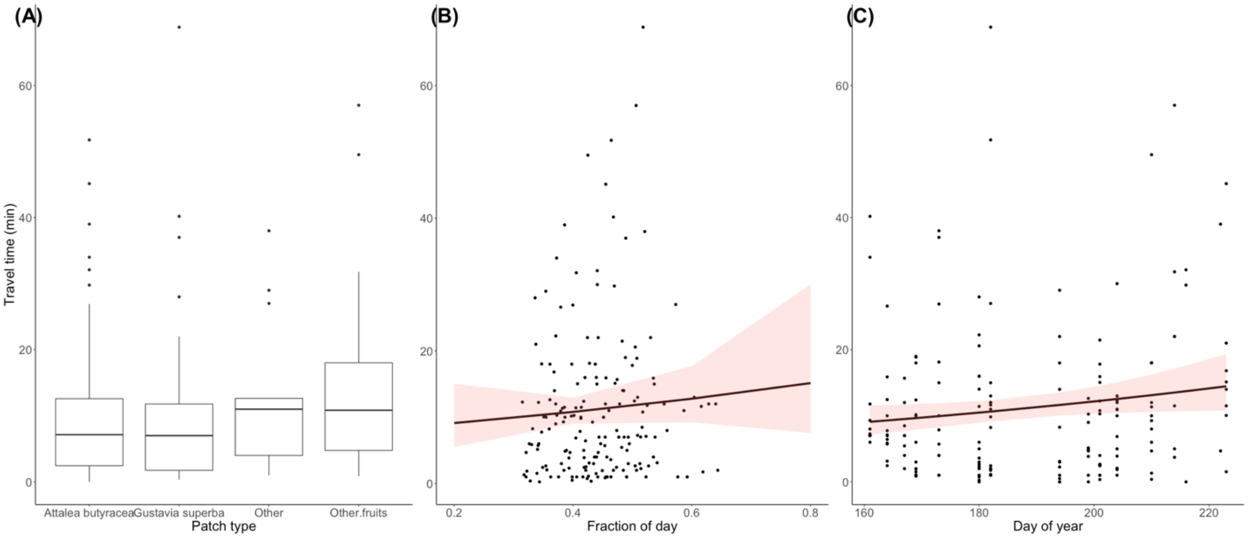

Figure 14. Inter-patch travel times were not significantly different between different tree species, based on time of day, or across the field season. (A) Box plot of the of inter-patch travel times (in minutes) to the two primary tree species during the field season months (*Attalea butyracea* and *Gustavia superba*) compared to other foraging resources (labeled as "other") and

other fruiting trees (labeled as “Other fruits’). The bolded line represents the median and the box bounds the 50% interquartile range. Whiskers represent scores outside the 50% interquartile range. Outliers are shown as solid circles. (B) Scatter plot with GLMM model prediction line and 95% confidence intervals of travel time across the fraction of the day, representing when, during the day, the travel occurred. (C) Scatter plot with GLMM model prediction line and 95% confidence intervals for the of travel time based on the day of the year. Overall, travel times between feeding patches remain consistent regardless of tree species, time of day, or day of the year (season).

Individual and group-level foraging gain curves and optimal patch departure times

I conducted focal tree follows for a total of 231 *A. butyracea* palm trees across both field seasons. Of these focal trees, 102 had an associated photograph(s) of the infructescence, such that I could accurately estimate patch size for the foraging gain curve models. Comparison of Charnov’s classical marginal value theorem model (equation 1) versus the marginal value model that incorporates handling time (equation 2) suggested that the handling time model was the most appropriate (Figure 15). These foraging gain curve models produced estimates of cumulative energy gain (represented as amount of fruit pulp consumed) for each individual and the group overall in each feeding tree (see Figure 16 for an example of the foraging gain curves produced for individuals, colored, and the group overall, black). By calculating the point where energy gain was maximized (see methods section), this produced predicted optimal patch departure times for each individual and the group overall. The time when the majority of group members began to move off in a directed manner was considered to be the observed group departure time (the collective decision of when to go).

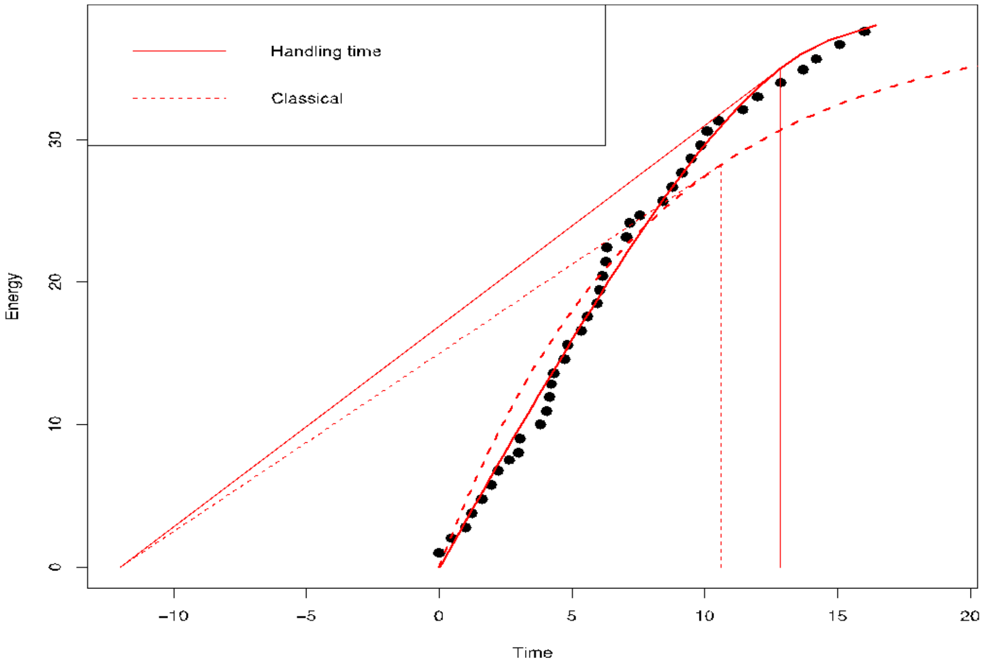

Figure 15. A visual comparison of a single monkey's foraging gain curve model fit to Charnov's classical marginal value theorem model (red dashed line) versus the marginal value theorem model with handling time (solid red line). Black dots represent observed instances of palm fruit consumption (energy gain) in a single feeding tree, cumulatively across time spent in the tree.

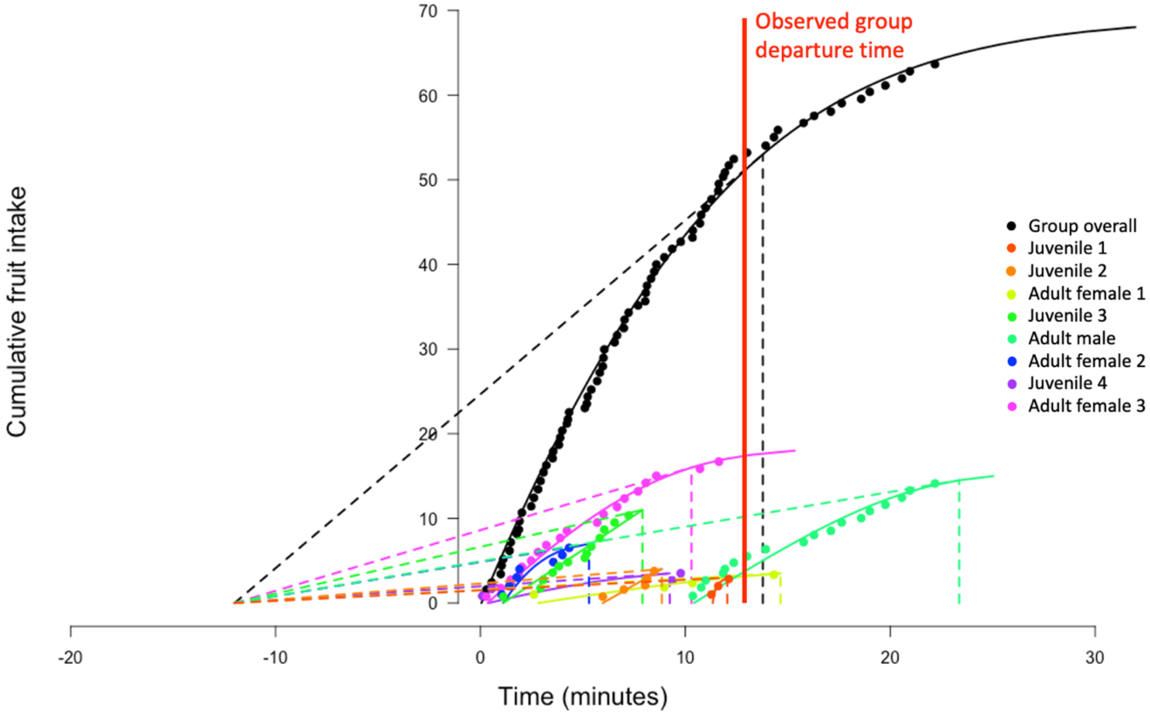

Figure 16. Results from a representative focal tree of a capuchin group feeding in an *A. butyracea* palm. Points represent distinct feeding observations, colored by individual (the group overall is in black). Negatively accelerating gain curves were fitted to each individual's cumulative food gain over time using equation 2, which predicted the optimal patch departure time per individual (represented by vertical dashed lines) based on the travel time between patches. The vertical red solid line represents when the group collectively left this particular feeding tree (the observed group departure time).

Conflicts of interest between group members over when to leave

Consistent with my hypothesis that conflicts of interest occur over when to go, I found conflicts of interest over when to leave feeding trees in every focal tree and between all individuals, age classes, and dominance ranks in both monkey groups (see Figure 16 for an example of how conflicts of interest exist in one focal tree).

When examining the relative timing of optimal departure times across individuals in a focal tree, I found no effect of dominance rank on the ordering of optimal departure times (see Table S1 for results of my ordinal logistic regression models, while I report my raw data in Figures 17a, b). I also found that adults tended to have later optimal departure times in a focal tree when compared to juveniles, contrary to my prediction (see Table S1 for results of my ordinal logistic regression models, while I report my raw data in Figure 17c, P_2).

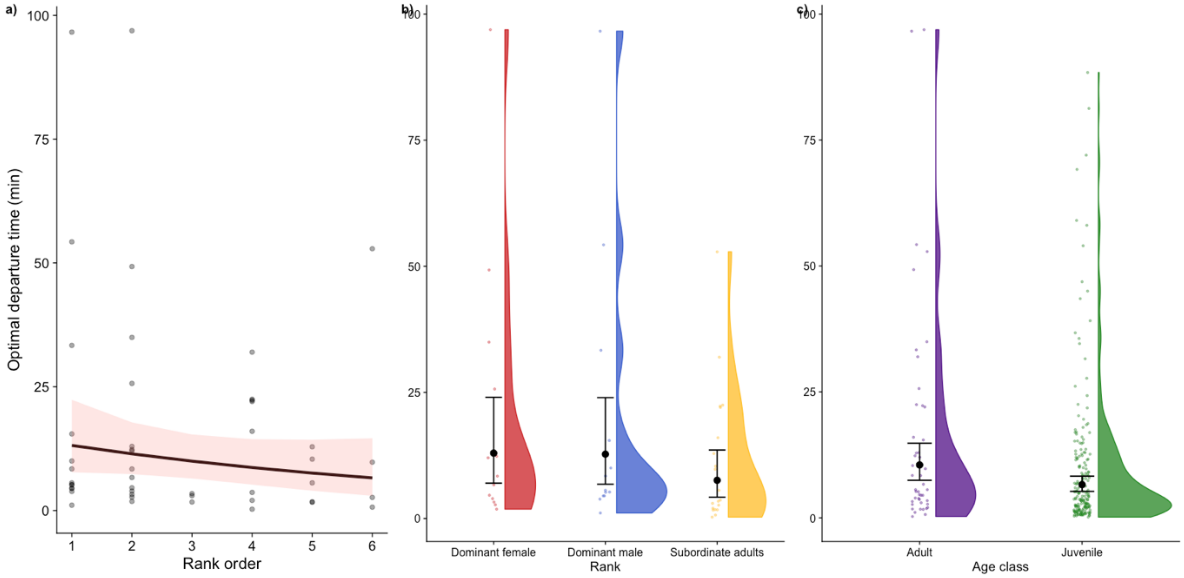

Figure 17. While dominance rank did not predict the ordering of optimal departure times in a focal tree, adults tended to have later optimal departure times than juveniles. These panels represent the comparison of optimal departure times by a) dominance rank order, b) dominance rank category (dominant female, dominant male, and subordinate adults), and c) age class (adult and juvenile). In panel a, the black line represents a basic model prediction, with 95% confidence intervals in shaded red. The shaded points represent the raw data values. In

panels b and c, solid black dots represent the predicted mean optimal departure time, with error bars showing 95% confidence intervals. Colored points represent the raw data values. Colored half-violin distributions denote the density distributions of the raw data values. I note that here I report my raw data results, while my results from my ordinal logistic regression models are presented in table S1.

The process(es) of group decision-making

To examine the process of group decision-making, I compared the *observed* group departure times with the *predicted* optimal departure times based on foraging gain curves for each individual, the average individual (represented as the median of all individual optimal departure times), and the cumulative group overall. Across observed group departures for both monkey groups, groups tended to leave closest to the optimal departure time predicted by the group-level gain curve (GLM: $\chi^2 = 25.75$, $p = 0.05$, Figures 18 and 19). In fact, in 34% of all departures from focal trees, the group left within one minute of the predicted optimal group-level departure time, 50% of departures within 2 minutes of this predicted optimal, and 69% of departures within 5 minutes of this predicted optimal. While both monkey groups left closest to the optimal group-level departure time in the majority of focal trees (56% of all focal trees I observed for both capuchin monkey groups), I still observed some variation over which group members may have influence over when to go. For 16% of all focal trees, the group left closest to the dominant male’s preferred optimal departure time, 11% of trees the dominant female’s, and 10% of trees the median individual. Groups occasionally departed trees closest to a juvenile’s preferred leave time (6% of the time). I only observed one focal tree across both groups where the group left closest in time to the optimal of a subordinate adult female (1% of the time). Observed group departure times tended to be after the optimal departure time predictions across individual group members.

I further tested whether dominance rank or age class predicted the *time consensus cost* individual's paid by compromising their preferred behavior and leaving a tree at a sub-optimal time. While time consensus cost was not predicted significantly by continuous rank order (GLMM: $\chi^2 = 0.23$, $p = 0.6305$), dominant adult males paid the lowest time consensus costs when compared to all other adults (GLMM: $\chi^2 = 3.563$, $p = 0.075$, dominant male: $\bar{x} = 6.75$ minutes, 95% CI [3.52, 12.93], dominant female: $\bar{x} = 13.13$ minutes, 95% CI [6.93, 24.86], subordinate adults: $\bar{x} = 11.51$ minutes, 95% CI [6.48, 20.44]; Figure 20a and b). I additionally found that age class had a significant effect on the time consensus costs individuals pay, with juvenile individuals having higher time consensus costs than adults (GLMM: $\chi^2 = 8.170$, $p = 0.004$, adults: $\bar{x} = 5.06$ minutes, 95% CI [3.52, 7.27], juveniles: $\bar{x} = 6.56$ minutes, 95% CI [4.69, 9.19]; Figure 20c).

Observations of group departures away from focal trees suggested that higher ranking individuals were more successful at initiating group movements (GLM: $\chi^2 = 12.763$, $p < 0.001$, Figure 21a and b). In particular, dominant adult females were the most successful members of the group at initiating group movements. I also found that adult individuals were more successful at initiating group movements when compared to juveniles (GLM: $\chi^2 = 10.546$, $p = 0.001$, Figure 21c). While all individuals in the group made initiation attempts, the dominant adult female was the most successful leader in both groups, with approximately two-thirds of their movement initiation attempts being successful (Figure 22). The beta adult females for both groups were also relatively successful at initiating movement away from patches, with between 50 and 60% of their movement initiation attempts being successful.

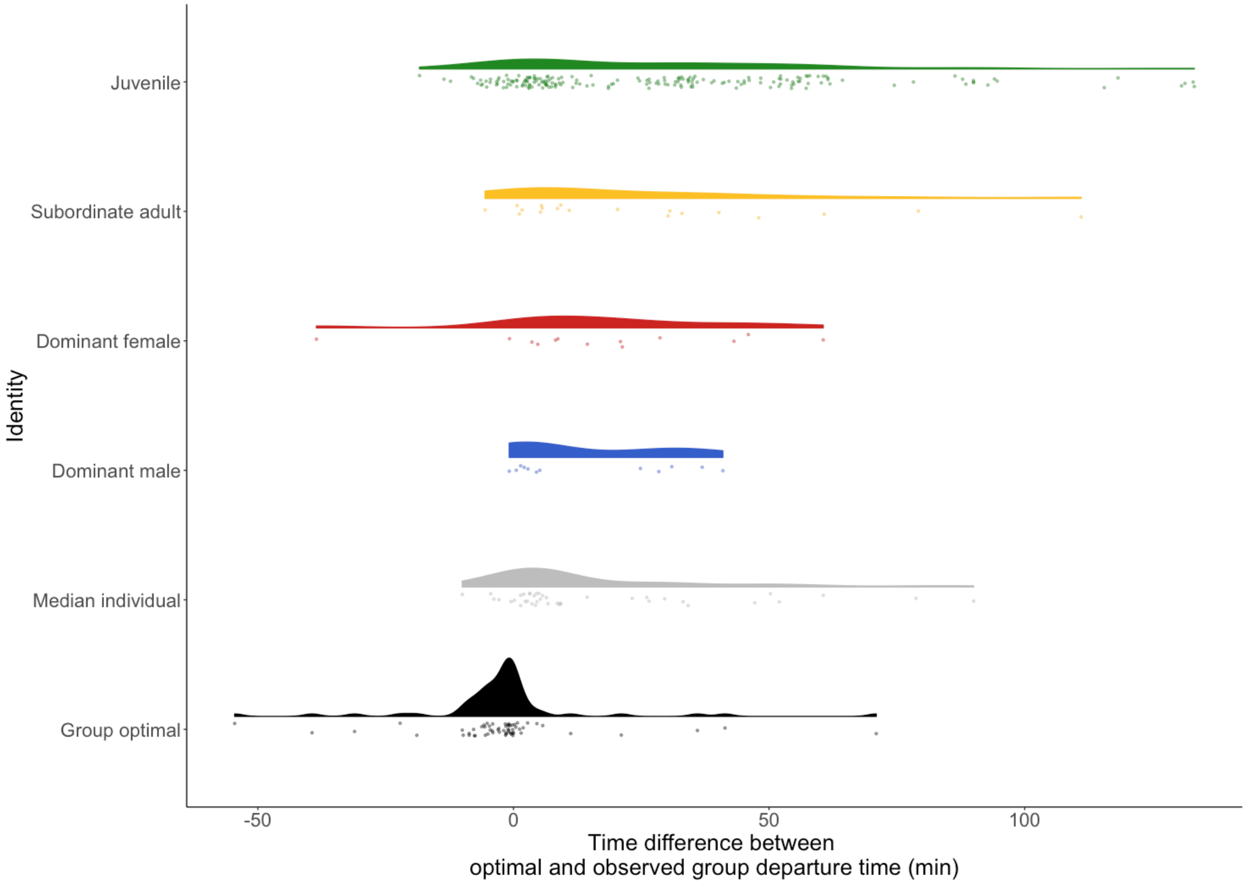

Figure 18. Groups departed focal trees closest to the predicted optimal departure time for the group-level gain curve. This graph shows the distribution of time consensus costs for both monkey groups on the x axis (the time difference between optimal and observed group departure time) for the group-level gain curve (in black), the median individual gain curve (in gray), the dominant male (in blue), the dominant female (in red), subordinate adults (in yellow), and juveniles (in green). Colored points represent the raw data values. Colored half-violin distributions denote the density distributions of the raw data values.

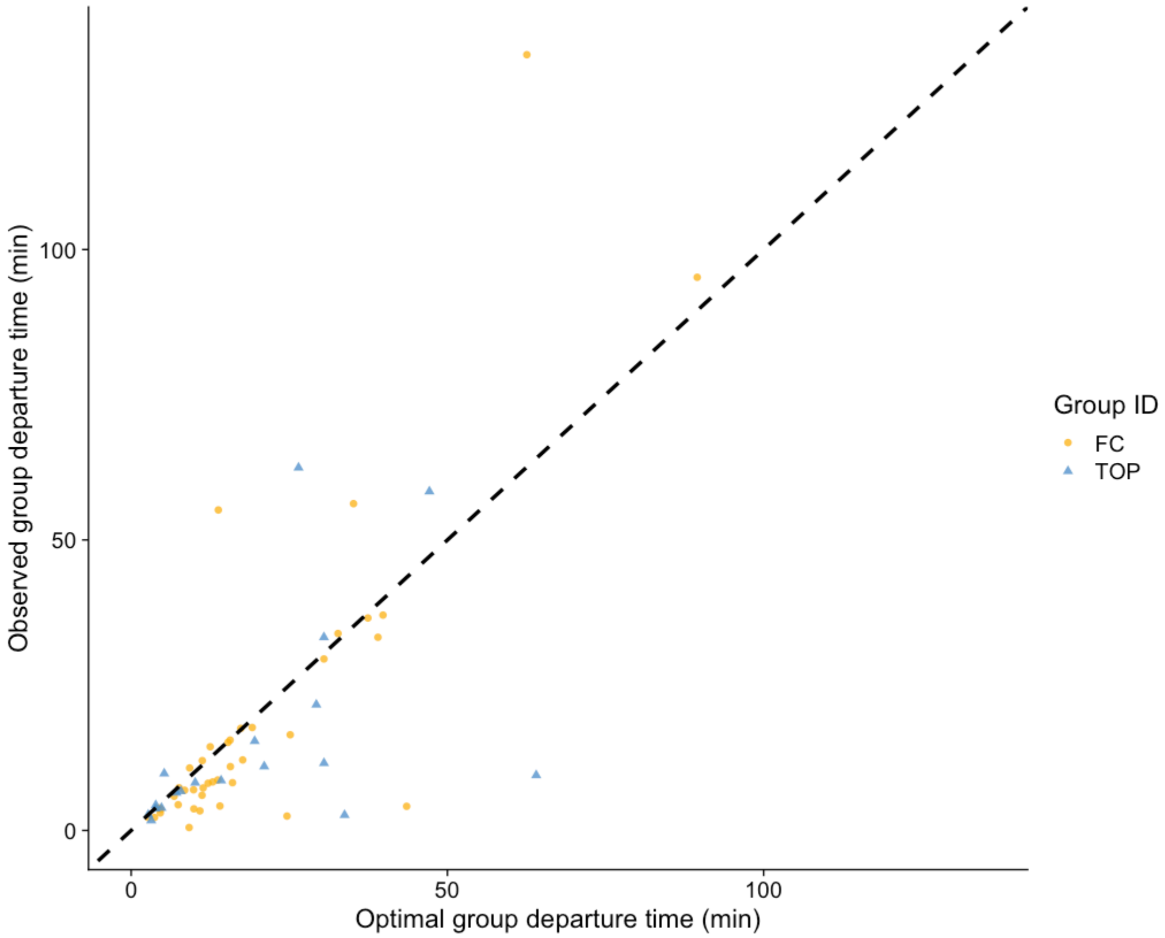

Figure 19. Group decisions of when to leave focal trees aligned closely to the predicted optimal group departure time as calculated from the group-level gain curve. In this graph, I plot a 1:1 axis for the optimal group-level departure time and the observed group departure time. Data points represent raw data values for focal trees, colored and shaped by monkey group identity (yellow circles for FC, blue triangles for TOP). The dashed black line denotes a slope = 1, whereby data points closer to this line indicate equivalent values of optimal versus observed departure times.

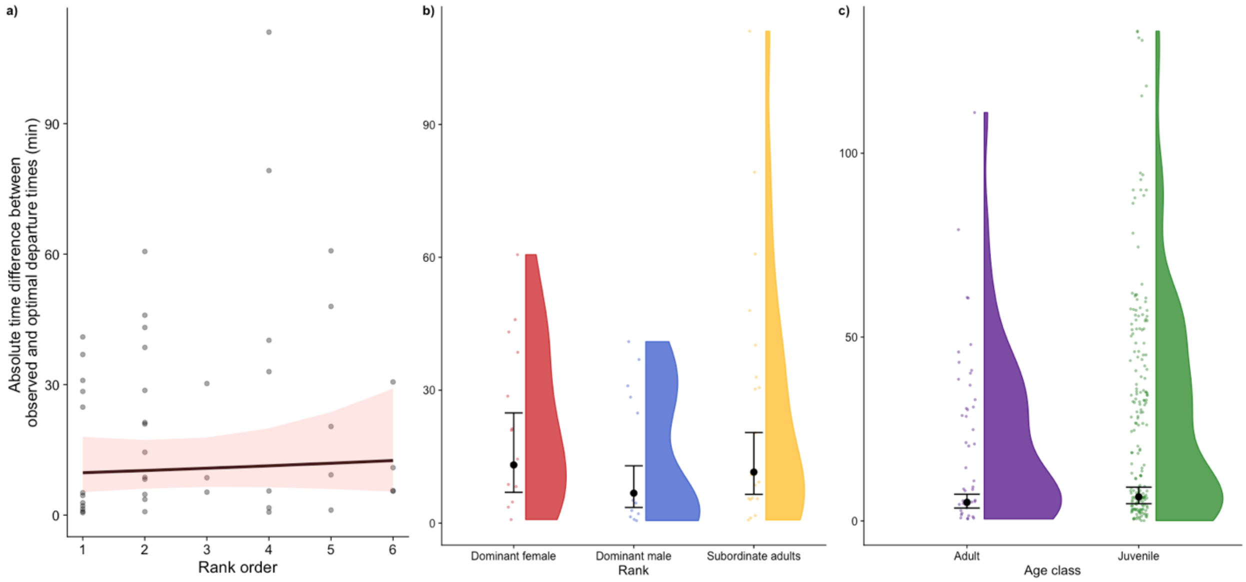

Figure 20. Dominant adult males paid the lowest time consensus costs, while juvenile individuals paid the highest time consensus costs. These panels represent the comparison of time consensus costs by a) dominance rank order, b) dominance rank category (dominant female, dominant male, and subordinate adults), and c) age class (adult and juvenile). Time consensus costs were calculated as the absolute time difference between optimal departure times and the observed group departure time. In panel a, the black line represents my model prediction, with 95% confidence intervals in shaded red. The shaded points represent the raw data values. In panels b and c, solid black dots represent the predicted mean optimal departure time, with error bars showing 95% confidence intervals. Colored points represent the raw data values. Colored half-violin distributions denote the density distributions of the raw data values.

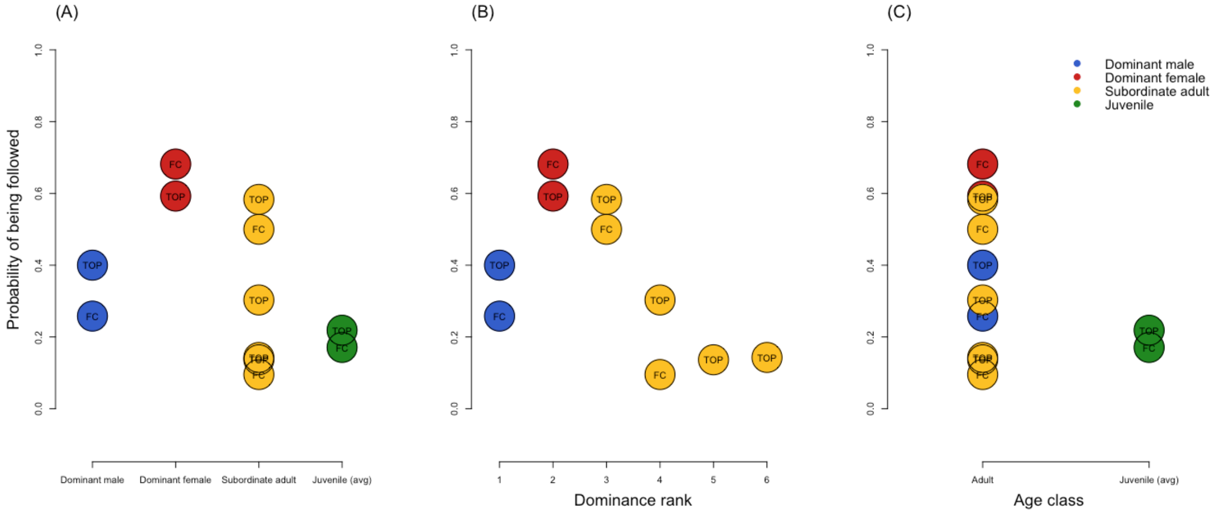

Figure 21. Individuals with high social ranks (especially dominant adult females) and adults were more likely to be followed during group movements away from focal trees. These panels show the probability of being followed by the rest of the group as represented by A) dominance rank category (dominant female, dominant male, subordinate adults, and juveniles), B) dominance rank order, and C) age class (adult and juvenile). In all panels, dominant adult males are represented in blue, dominant adult females in red, subordinate adults in yellow, and juveniles in green. The monkey group (FC or TOP) for each value is overlayed on top of the point.

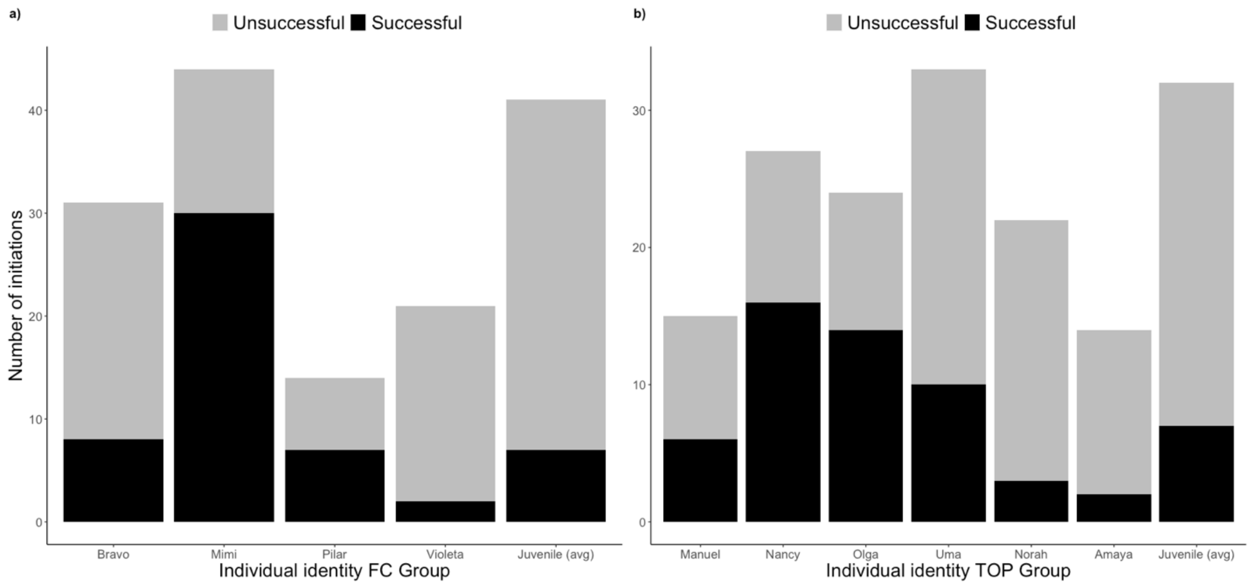

Figure 22. While all individuals in both monkey groups were successful at initiating group movements away from focal trees, dominant adult females were the most successful leaders. These stacked barplots show the results of 318 recorded initiation attempts away from focal trees across all the individuals in a) FC group and b) TOP group. Each bar represents the number of initiations one individual made and individuals are ordered by dominance rank (high to low) on the x axis. The black portion of the bar are the successful initiations where the group followed that individual, while the gray portion of the bar represent unsuccessful initiations.

Consensus costs

I found that individuals who paid higher time consensus costs (i.e., those whose optimal patch departure times deviated farther from the observed group departure time) received less food overall in focal trees (GLMM: $\chi^2 = 5.898$, $p = 0.015$, Figure 23).

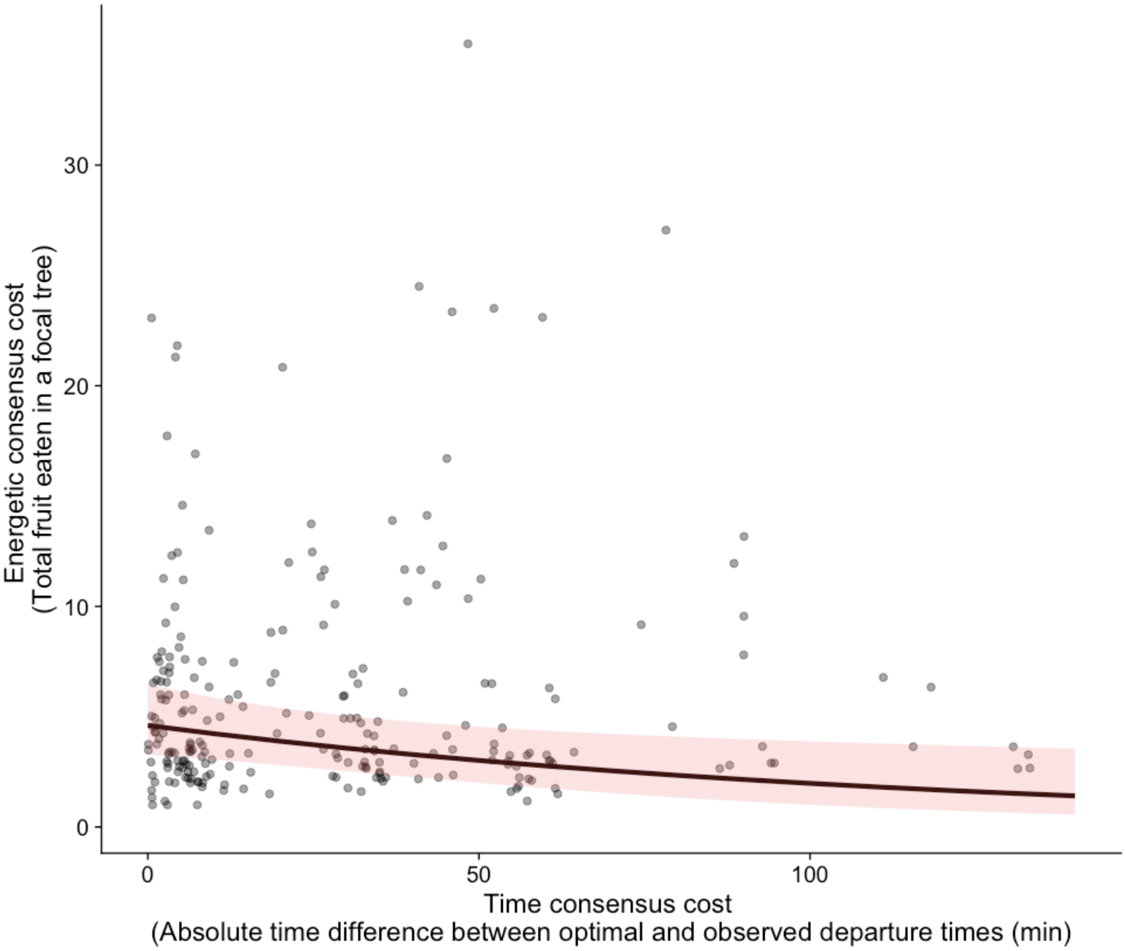

Figure 23. Individuals who paid a higher time consensus cost received less food overall in focal trees. Time consensus costs were calculated as the absolute time difference between optimal departure times and the observed group departure time. My model prediction is represented by the solid back line, with the shaded area showing the 95% confidence interval. Points represent raw data values for individuals.

DISCUSSION

In this chapter, I integrated theoretical predictions from optimal foraging theory into an empirical study of social foraging behavior in cohesive groups of wild capuchin monkeys. Importantly, my study demonstrates the straightforwardness of applying classical theories to help us tackle novel research questions. Despite many studies and theoretical models of collective decision-making in animals (Papageorgiou et al. 2020, Bettinger & Grote 2016, Conradt et al. 2013, Sueur et al. 2012, Conradt & Roper 2009, Conradt & Roper 2007, Couzin et al. 2005), few empirical studies move beyond asking “who leads” to explicitly testing how groups make decisions. Furthermore, quantifying the underlying preferences of what group members want to do and when has remained remarkably challenging, especially in wild systems. By integrating optimal foraging theory with observations of collective decision-making, I illustrate a readily achievable approach to not only predict individual preferences, but also quantify conflicts of interest, determine the group decision-making processes, and calculate consensus costs. My study followed five simple steps: obtain foraging data over time for group members in a patch, fit individual- and group-level gain curves, estimate individual- and group-level optimal departure times, compare optimal departure times with the observed group decision over when to leave, and calculate the consensus costs individuals paid to leaving at a suboptimal time. While in this study I applied the marginal value theorem to cohesive social groups with stable membership, I maintain that optimal foraging theory models can similarly be used in other species that nevertheless benefit from collective behaviors. For example, studies could apply the MVT to fission-fusion social groups where individuals must balance the need to remain with close social affiliates versus pursue their own preferences and depart trees at divergent times. My study illustrates a powerful way to apply theoretical predictions in empirical research, and overcome some of the challenges of studying leadership and group decision-making in the wild.

My results suggest that conflicts of interest over when to leave a foraging patch are ubiquitous, existing across all group members, all age classes, all social ranks, and throughout all foraging trees I observed (supporting my hypothesis 1). The widespread prevalence of inter-individual differences in predicted optimal patch departure times contrasts previous social foraging theory that assumes group members should optimally want to leave at the same time (Giraldeau & Caraco 2000). As I outline in Chapters 1 and 2 of this dissertation (Davis et al. 2022), even simple measures of heterogeneity within a group can lead to significant differences in foraging behavior and efficiency, ultimately leading to variation in the gain curves of group members and their predicted optimal departure times (their preferences over when to leave). My results highlight the value of applying formal models to understand individual preferences and how variation in preferences produces conflicts of interest between group mates.

I further predicted that dominant, adult individuals would want to leave patches earlier, as they likely obtain preferential access to the patch and thus have higher foraging rates and reach their optimal point of leaving faster than other group members (as in Chapter 1, Figure 2). While dominance rank had no effect on the specific ordering of optimal departure times in a tree, I found that adult individuals tended to have later optimal predicted departure times when compared to juveniles, contrary to my predictions. As group members in my study entered foraging patches asynchronously, it is possible that juveniles entered into trees first while adult individuals entered later, such that the foraging gain curves of adults are shifted later in time and have later predicted optimal departure times. If so, juveniles may act as finder individuals (or producers) by entering into trees first to achieve a boost in foraging payoff before competition for the patch ensues (see Chapter 2 of this dissertation).

Interestingly, I found that groups largely left focal trees closest in time to the predicted optimal departure time based on the group-level gain curve (supporting my hypothesis 2C, in comparison to individual gain curves and the median of all individuals' optimal departure times). Indeed, in 56% of all focal trees observed, groups left trees around the predicted optimal departure time for the group-level gain curve (versus optimal departure times for individuals and the median individual). These results suggest that for the majority of cases, capuchin groups tended to follow a group-level optimal decision-making process as opposed to a shared or unshared (despotic) decision-making process. Leaving at the group-level optimal departure time could indicate a mechanism of collective sensing, whereby pooling information across individuals results in a better estimate of the environment (i.e., the patch and the optimal time to leave it). Prior research suggests that information pooling results in more accurate decisions in social groups, benefiting all group members (Franks et al. 2003, Couzin & Krause 2003, Seeley & Buhrman 1999). As I illustrate in Chapter 1 of this dissertation, leaving at the group-level optimal departure time can potentially optimize individual-level energy gains across patches. For instance, if individuals unpredictably vary in their foraging behaviors and efficiency from one patch to the next, then their individual-level energy gain across multiple patches can be maximized by departing at the group-level optimal departure time. I emphasize that my novel result that groups often follow a type of group-level optimal decision process reveals an alternative mechanism for reaching consensus decisions that has not been previously considered, further corroborating using well-established theories to understand the mechanisms driving collective behaviors.

While the capuchin monkey groups left the majority of focal trees around the predicted optimal departure time for the group-level gain curve, I nevertheless found instances where groups tended to leave closest to the optimal departure times of certain individuals, in particular dominant adult males (16% of the time) and dominant adult females (11% of the time). In contrast, I rarely observed groups leaving patches closest to the optimal departure times of juveniles or subordinate adults (in 6% and 1% of cases, respectively). These results indicate that unshared decision-making also occurs (hypothesis 2A), where the highest-ranking adult of both sexes occasionally influence group departure decisions while subordinates and younger individuals rarely do. I note that I defined social rank in my study in the conventional sense used in many studies of animal behavior, whereby higher-ranking individuals are those who most often win aggressive interactions, and vice versa. An alternative way to assess higher rank could be simply by classifying individuals who have greater influence on group departure decisions as "dominants" (i.e., individuals whose optimal departure times most often align with real observed group departure times). I also found that in 10% of focal trees, groups left at the time predicted by the median individual's optimal departure time. These results suggest that occasionally shared decisions occur over when to go, where once half of the group had reached their optimal departure time (a majority rule), the group departed. The variation I observed in who had influence over the timing of group departures suggests that decisions do not always follow a singular process, and that group-level optimal, unshared decision-making, and shared decision-making all play a role. A promising direction of future research could evaluate factors driving instances of these different types of decision processes.

To compare my foraging theory results with common methods to infer influence over group decisions (e.g., Papageorgiou et al. 2020), I observed movement initiation attempts away from feeding trees and which individuals (‘leaders’) were most successful at recruiting the group to move on to the next resource. My results suggested that higher ranking individuals and adults were more successful at initiating group movements when compared to subordinates and juveniles. While all individuals in the group made initiation attempts and were successful at times, suggesting some element of shared decision-making, the dominant adult female was the most successful leader in both groups, with approximately two-thirds of her movement initiation attempts being successful (Figures 21 and 22). The beta adult females for both groups were also relatively successful at initiating movement away from patches, with around half of their movement initiation attempts being successful. I highlight that these results from observations of group movement departures somewhat contrast my results of group departure decisions using optimal foraging theory. Using foraging theory, dominant and adult individuals (and the alpha and beta females) had limited influence over group departure decisions and were not consistently as “heavy influencers” (like my movement initiation results suggested). Instead, I found that group departure decisions were most often predicted by a group-level optimal process. I emphasize that optimal foraging theory in this case provides clear predictions of animal departure preferences versus observations of the decision outcome (such as who successfully initiates, who moves first, or who is in front). This further supports why theoretical backing from foraging theory is helpful to understand the process of collective decision-making and who contributes.

I predicted that the magnitude of individual time consensus costs (the time difference between predicted optimal and observed group departure times) would be related to social rank and age under unshared decision-making processes, while evenly distributed under shared decisions. My results indicated that juveniles paid the highest time consensus costs by leaving the farthest from their optimal preferred leave times. Subordinate adults also paid high time consensus costs, with the dominant male in both monkey groups paying the lowest time consensus cost overall. Measuring consensus costs based on time (i.e., leaving at a suboptimal time) reflects missed opportunity costs when an individual could have allocated their time to other behaviors (Brown 1988). In foraging, an individual leaving with the group at a time before they have reached their optimal departure time means they missed out on more time to forage in the patch, while leaving after their optimal departure time suggests they are forgoing opportunities to move along and search for new patches to exploit that have yet to be depleted. Regardless, individuals can pay consensus costs by forgoing their preferred choices to compromise with other group members, and I found that juveniles and subordinate adults most often paid the highest time consensus costs.

I also hypothesized that individuals who compromise their optimal foraging timing would pay a foraging consensus cost, by obtaining less food overall in patches. In support of my prediction, I indeed found that individuals who paid higher time consensus costs also received less total fruit in focal trees. This indicates that leaving at a suboptimal time is not only temporally costly, but also energetically costly. While I used the total amount of fruit consumed as a proxy of energetic consensus costs (i.e., what amount of food/energy an individual forgoes by complying with the group decision), I maintain that energetic consensus costs are likely asymmetrical depending on whether an individual leaves before versus after their optimal departure time. If a group member leaves before their optimal time, they are still in the part of their gain curve with the highest slope, and so they may miss out on obtaining more food in that particular patch. If a group member instead leaves after their optimal time, they may still obtain the optimal level of food in that patch, but they miss out on moving on to the next patch where their energy gain is greatest at the start. A promising future direction is to assess consensus costs not just based on the total amount of food received in a patch, but based on the exact energetic (foraging) loss of leaving early versus late, as outlined in chapter 1 of this dissertation (Figure 3A of this dissertation, Davis et al. 2022).

While focusing on one fruit tree species in my study allowed for repeated measures of foraging gain curves, optimal departure times, group departure decisions, and consensus costs, expanding data collection to include different foraging tree species would further advance our understanding of collective foraging decisions. For instance, obtaining data on a range of patch richness and distributions (travel times) could explore whether resource quality and distribution influences group decision-making processes and which group member(s) have influence. As I discuss in chapter 1 (Davis et al. 2022), group-level consensus costs can be minimized in resource-rich (short travel times) environments, and maximized in environments with intermediate resource availability. One way to collect data in environments of varying resource availability is to record collective foraging behaviors in a season of plenty (where patches are abundant) versus a season of scarcity (where patches are few and far between). More replicates of capuchin monkey groups would offer more statistical power for my analyses, and allow assessments of collective foraging across groups. Comparing groups of different sizes would also be interesting to examine if predictions from the MVT hold true, like if larger groups leave patches sooner and deplete resources to a greater extent than smaller groups (Davis et al. 2022, Giraldeau & Caraco 2000, Livoreil & Giraldeau 1997). Future studies could also investigate how variables such as satiation, physiological state, or even genetic ties (e.g., does a mother wait for her offspring to reach their optimal needs before moving on?) play a role in the preferences individuals have over when to leave. In addition to individual differences influencing the degree of conflict between group members, environmental factors could also influence whether conflicts between group members are higher versus lower in a patch. For instance, the size of the patch, quality of the food, ease of access to the patch, and/or the location of the patch in an animal group's home range could all be factors influencing the extent of conflict between group members. Ultimately, by applying concepts from foraging theory we can open the door to a wide range of interesting study avenues in the field of collective behavior.

This study applies classic theories from optimal foraging to observations of collective behavior, exemplifying ways to generate discrete, tractable predictions of animal preferences and then link these to collective outcomes. Further, the great strength of making such clear quantitative predictions is that the observational methods employed in this study are relatively straightforward and achievable, without requiring expensive technology. I emphasize that while I used one facet of foraging theory here (the marginal value theorem), additional models that have been well-established and studied for years can continue to provide us with key insights into social foraging behavior, a promising direction for future research. By combining theory and models from social foraging theory and collective decision-making, my work contributes to understanding how group-living individuals with conflicting interests achieve consensus and exploit resources in their habitat. Together, this captures important elements of group decision-making in social animals: when to leave food patches, how such decisions are made, and which group members pay the costs of compromise.

REFERENCES

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, *49*(3), 227-266.

Amornbunchornvej, C., Brugere, I., Strandburg-Peshkin, A., Farine, D. R., Crofoot, M. C., & Berger-Wolf, T. Y. (2018). Coordination event detection and initiator identification in time series data. *ACM Transactions on Knowledge Discovery from Data (TKDD)*, *12*(5), 1-33.

Boinski, S., & Campbell, A. F. (1995). Use of trill vocalizations to coordinate troop movement among white-faced capuchins: a second field test. *Behaviour*, *132*(11), 875-901.

Brown, J. S. (1988). Patch use as an indicator of habitat preference, predation risk, and competition. *Behavioral Ecology and Sociobiology* **22**(1): 37-47.

Chancellor, R. L., & Isbell, L. A. (2009). Food site residence time and female competitive relationships in wild gray-cheeked mangabeys (Lophocebus albigena). *Behavioral Ecology and Sociobiology*, *63*(10), 1447-1458.

Charnov, E. L. (1976). Optimal foraging: the marginal value theorem. *Theoretical Population Biology* **9**, 129-136.

Clark, C. W., & Mangel, M. (1986). The evolutionary advantages of group foraging. *Theoretical population biology*, *30*(1), 45-75.

Clutton-Brock, T. H., Guinness, F. E., & Albon, S. D. (1982). *Red deer: behavior and ecology of two sexes*. University of Chicago press.

Clutton-Brock, T. H., & Harvey, P. H. (1977). Primate ecology and social organization. *Journal of Zoology*, *183*(1), 1-39.

Conradt, L. (1998). Could asynchrony in activity between the sexes cause intersexual social segregation in ruminants?. *Proceedings of the Royal Society of London B: Biological Sciences*, *265*(1403), 1359-1368.

Conradt, L. & Roper, T. J. (2009). Conflicts of interest and the evolution of decision sharing. *Royal Society Philosophical Transactions Biological Sciences* **364**, 807-819.

Conradt, L., & Roper, T. J. (2003). Group decision-making in animals. *Nature*, *421*(6919), 155-158.

Conradt, L., & Roper, T. J. (2005). Consensus decision making in animals. *Trends in ecology & evolution*, *20*(8), 449-456.

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

Crofoot, M. C., Gilby, I. C., Wikelski, M. C. & Kays, R. W. 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 (2008).

Dahl, J. F. (1986). The status of howler, spider and Capuchin monkey populations in Belize, Central America. *Primate Rep*, *14*, 161.

Davis, G. H., Crofoot, M. C., & Farine, D. R. (2022). Using optimal foraging theory to infer how groups make collective decisions. *Trends in Ecology & Evolution*, 37(11): 942-952.

Di Bitetti, M. S., & Janson, C. H. (2001). Social foraging and the finder's share in capuchin monkeys, Cebus apella. *Animal Behaviour*, *62*(1), 47-56.

Dostálková, I., & Špinka, M. (2007). Synchronization of behaviour in pairs: the role of communication and consequences in timing. *Animal Behaviour*, *74*(6), 1735-1742.

Farine, D. R., & Sánchez-Tójar, A. (2017). aniDom: inferring dominance hierarchies and estimating uncertainty. *R package version 0.1*, *2*.

Fragaszy, D., Visalberghi, E. & Fedigan, L. (2004). "Life History and Demography". *The Complete Capuchin*. Cambridge University Press. pp. 74–79.

Freese, C. H., & Oppenheimer, J. R. (1981). The capuchin monkeys, genus Cebus. *Ecology and behavior of neotropical primates*, *1*, 331-390.

Giraldeau, L. A. & Caraco, T. (2000). *Social Foraging Theory*. Princeton University Press.

Gompper, M. E. (1996). Sociality and asociality in white-nosed coatis (Nasua narica): foraging costs and benefits. *Behavioral ecology*, *7*(3), 254-263.

Holekamp, K. E., & Strauss, E. D. (2016). Aggression and dominance: an interdisciplinary overview. *Current Opinion in Behavioral Sciences*, *12*, 44-51.

Isbell, L. A. (1991). Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behavioral ecology*, *2*(2), 143-155.

Isbell, L. A., Pruetz, J. D., Lewis, M., & Young, T. P. (1999). Rank differences in ecological behavior: a comparative study of patas monkeys (Erythrocebus patas) and vervets (Cercopithecus aethiops). *International Journal of Primatology*, *20*(2), 257-272.

Janson, C. (1985). Aggresive competition and individual food consumption in wild brown capuchin monkeys (Cebus apella). *Behavioral Ecology and Sociobiology*, *18*(2), 125-138.

Janson, C. H. (1988). Food competition in brown capuchin monkeys (Cebus apella): quantitative effects of group size and tree productivity. *Behaviour*, *105*(1), 53-76.

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

Janson, C. H. & van Schaik, C. P. (1988). Recognizing the many faces of food competition: Methods. *Behaviour* **105**, 165-186.

Janson, C. H., & Goldsmith, M. L. (1995). Predicting group size in primates: foraging costs and predation risks. *Behavioral Ecology*, *6*(3), 326-336.

Kappeler, P. M., & van Schaik, C. P. (2002). Evolution of primate social systems. *International Journal of Primatology*, *23*(4), 707-740.

King, A. J. & Cowlishaw, G. (2009). All together now: behavioural synchrony in baboons. *Animal Behaviour* **78**, 1381-1387.

King, A. J., & Cowlishaw, G. (2009). Leaders, followers, and group decision-making. *Communicative & integrative biology*, *2*(2), 147-150.

King, A. J., Sueur, C., Huchard, E., & Cowlishaw, G. (2011). A rule-of-thumb based on social affiliation explains collective movements in desert baboons. *Animal Behaviour*, *82*(6), 1337-1345.

Koenig, A. (2002). Competition for resources and its behavioral consequences among female primates. *International Journal of Primatology*, *23*(4), 759-783.

Koenig, A. (2002). Competition for resources and its behavioral consequences among female primates. *International Journal of Primatology*, *23*(4), 759-783.

Krause, J., Bumann, D., & Todt, D. (1992). Relationship between the position preference and nutritional state of individuals in schools of juvenile roach (Rutilus rutilus). *Behavioral Ecology and Sociobiology*, *30*(3-4), 177-180.

Leca, J. B., Gunst, N., Thierry, B., & Petit, O. (2003). Distributed leadership in semifree ranging white-faced capuchin monkeys. *Animal Behaviour*, *66*(6), 1045-1052.

Leigh, E. G. (1999). *Tropical forest ecology: a view from Barro Colorado Island*. Oxford

University Press.

Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., ... & Engelhardt, A. (2011). Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. *Animal Behaviour, 82*(4), 911-921.

Olsson, O., Brown, J. S. & Smith, H. (2001). Gain curves in depletable food patches: a test of five models with European starlings. *Evolutionary Ecology Research* **3**, 285-310.

Papageorgiou, D., & Farine, D. R. (2020). Shared decision-making allows subordinates to lead when dominants monopolize resources. *Science advances*, *6*(48), eaba5881.

Perry, S.; Manson, J. (2008). *Manipulative Monkeys: The Capuchins of Lomas Barbudal*. Cambridge, MA: Harvard University Press. pp. 118, 145–154, 169–214, 229–241.

Petit, O., & Bon, R. (2010). Decision-making processes: the case of collective movements. *Behavioural Processes*, *84*(3), 635-647.

Petit, O., Gautrais, J., Leca, J. B., Theraulaz, G., & Deneubourg, J. L. (2009). Collective decision-making in white-faced capuchin monkeys. *Proceedings of the Royal Society of London B: Biological Sciences*, *276*(1672), 3495-3503.

Prins, H. (1996). *Ecology and behaviour of the African buffalo: social inequality and decision making* (Vol. 1). Springer Science & Business Media.

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rands, D. G., & Nowak, M. A. (2013). Human cooperation. *Trends in cognitive sciences*, *17*(8), 413-425.

Ripley, B., Venables, B., Bates, D. M., Hornik, K., Gebhardt, A., Firth, D., & Ripley, M. B. (2013). Package 'mass'. *Cran r*, *538*, 113-120.

Rowe, N. (1996). *Pictorial guide to the living primates*. Pogonias Press.

Ruckstuhl, K. E. (1999). To synchronise or not to synchronise: a dilemma for young bighorn males?. *Behaviour*, *136*(6), 805-818.

Ruckstuhl, K. E., & Neuhaus, P. (2002). Sexual segregation in ungulates: a comparative test of three hypotheses. *Biological Reviews*, *77*(1), 77-96.

Silk, J. B. (2007). The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1480), 539-559.

Snaith, T. V., & Chapman, C. A. (2007). Primate group size and interpreting socioecological models: do folivores really play by different rules?. *Evolutionary Anthropology: Issues, News, and Reviews*, *16*(3), 94-106.

Stephens, D. W. & Krebs, J. R. (1986) *Foraging Theory*. Princeton University Press.

Sterck, E. H., & Steenbeek, R. (1997). Female dominance relationships and food competition in the sympatric Thomas langur and long-tailed macaque. *Behaviour*, *134*(9), 749-774.

Sterck, E. H., Watts, D. P., & van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, *41*(5), 291-309.

Stewart, K. J., & Harcourt, A. H. (1994). Gorillas' vocalizations during rest periods: signals of impending departure?. *Behaviour*, *130*(1), 29-40.

Strier, K. B. (2015). *Primate behavioral ecology*. Routledge.

Stueckle, S., & Zinner, D. (2008). To follow or not to follow: decision making and leadership during the morning departure in chacma baboons. *Animal Behaviour*, *75*(6), 1995-2004.

Sueur, C., Deneubourg, J. L., Petit, O., & Couzin, I. D. (2010). Differences in nutrient requirements imply a non-linear emergence of leaders in animal groups. *PLoS Comput*

Biol, *6*(9), e1000917.

Sueur, C., King, A. J., Conradt, L., Kerth, G., Lusseau, D., Mettke-Hofmann, C., Schaffner, C. M., Williams, L., Zinner, D. & Aureli, F. (2011). Collective decision-making and fission-fusion dynamics: a conceptual framework. *Oikos* **120**, 1608-1617.

Terborgh, J. (1986). Community aspects of frugivory in tropical forests. In *Frugivores and seed dispersal* (pp. 371-384). Springer Netherlands.

Terborgh, J., & Janson, C. H. (1986). The socioecology of primate groups. *Annual Review of Ecology and Systematics*, *17*(1), 111-136.

Vogel, E. R. (2005). Rank differences in energy intake rates in white-faced capuchin monkeys, Cebus capucinus: the effects of contest competition. *Behavioral ecology and sociobiology*, *58*(4), 333-344.

Vogel, E. R. & Janson, C. H. (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.

Ward, A., & Webster, M. (2016). Sociality: the behaviour of group-living animals.

Watts, D. P. (1985). Relations between group size and composition and feeding competition in mountain gorilla groups. *Animal Behaviour*, *33*(1), 72-85.

White, F. J., & Wrangham, R. W. (1988). Feeding competition and patch size in the chimpanzee species Pan paniscus and Pan troglodytes. *Behaviour*, *105*(1), 148-164.

Windsor, D. M. (1990). Climate and moisture variability in a tropical forest: long-term records from Barro Colorado Island, Panama. *Food and Agriculture Organization of the United Nations*.

Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour*

75(3), 262-300.

SUPPLEMENTARY MATERIALS

Behavior	**Description**
Enter palm	An individual initially enters the focal palm tree. We noted the direction the individual enters from following 45 degrees: N, NW, NE, S, SW, SE, E, W.
Enter Fruit	An individual begins to descend from the top of the fruiting clump stem.
Touch	An individual uses its hands to test fruits on the fruiting clump, without pulling them off the clump. We also recorded how many fruits the monkey touched.
Drop	An individual removes a fruit from the fruiting clump and discards it without eating. We also recorded how many fruits the monkey dropped.
Bite	An individual uses their teeth to bite into a fruit, without eating it.
Start Eat	An individual begins to chew, swallow, and eat a fruit. This behavior implies that the individual removed a fruit from the clump.
Stop Eat	An individual discards a fruit that it was consuming to the forest floor. The observer recorded the percentage of the fruit eaten in the following categories: 0-25%, 25-50%, 50-75%, 100%, or Unknown if unable to observe the proportion of fruit pulp consumed.
Exit fruit	An individual leaves the fruiting clump, but remains in the palm tree.
Exit palm	An individual leaves the palm tree completely. Note the direction of departure following the 45-degree system above.
Contact calls	An individual makes a small staccato “ooo” call. Each syllable was noted as one contact call.
Displace	Individual A (the actor) moves toward individual B (the recipient) and takes the position in which B was previously while B moves away (there may or may not be bodily contact during this shift; a.k.a. supplant). We noted the identity of the actor and the recipient (as for all social interactions listed below).
Visual threat	Individual A threatens individual B via a facial expression (raises eyebrows or opens mouth in threat grin while looking at B), a head

	bob (A, while looking at B, quickly moves its head down and then back up again), or a sharp look or stare threat (A sharply turns its head so that it is facing B and/or looks at B intensely).
Vocal threat	Individual A vocalizes a threat call at individual B.
Chase	Individual A runs behind individual B, following B, while B is running away from A.
Aggressive contact	Individual A uses hand(s) to touch individual B in an aggressive context - includes grabbing or pulling B's skin or hair, swiping or hitting B, holding B down on the ground, or pulling or pushing B.
Chomp	Individual A uses mouth to grab a piece of skin or body part of B in an aggressive context.
Fight	A complex series between two individuals of back-and-forth grabs, lunges, and/or bites that happen too quickly to record individually.

Table S1. The ethogram for focal tree follows of the capuchin monkeys in *A. butyracea* palm trees. The focal tree follow began the moment the first individual in a group entered a palm tree and terminated when the last individual exited the tree. I recorded these behaviors for all monkeys in trees using all-occurrence sampling (Altmann 1974). I inputted these behaviors into the Animal Behaviour Pro iPhone application (Newton-Fischer, 2016), which recorded a time to the second of the behavior, the monkey identity of who performed the behavior, and the recipient of the behavior (if applicable).

(a)	**Value**	**Std. Error**	**t value**	**p value**
Rank Dominant male	-0.281982048983011	0.803052450873941	-0.35113777272722	0.725484991360156

Rank Subordinates	-0.50427744220992	0.749785405845751	-0.672562360214387	0.501225754577333
1|2	0.57431629528684	0.550934605376455	1.04244004584611	0.297207708263463
2|3	1.85386966371757	0.642267522924853	2.88644466292667	0.00389621255906334

(b)	**Value**	**Std. Error**	**t value**	**p value**
Rank order	-0.0994192084076574	0.19568414621275	-0.508059596711363	0.611411548832084
1|2	0.588811429386584	0.607664547272285	0.968974464660922	0.332557929906748
2|3	1.86434853845462	0.693150492488795	2.68967353937898	0.00715219488685934

(c)	**Value**	**Std. Error**	**t value**	**p value**
Age_classJuvenile	-0.337120559820646	0.29228804249516	-1.15338471236376	0.248752513494328
1|2	-1.35571695737772	0.283975959160035	-4.77405538619451	1.80552691370755e-06
2|3	-0.591869911893059	0.273942607072419	-2.16056172575508	0.0307292106647511

3|4	-0.0965789242400457	0.272587766856293	-0.35430395631423	0.723111103106135
4|5	0.24285594819269	0.27351990108808	0.887891327931144	0.374599209963543
5|6	0.576509024488226	0.275289006928013	2.09419559074141	0.0362425604014372
6|7	0.893205480026353	0.278560696813047	3.20650217437465	0.00134359289543444
7|8	1.24387228908352	0.285974450245971	4.34959237796821	1.36390819700894e-05
8|9	1.55064578343822	0.296760699962101	5.22523967505216	1.73929667199759e-07
9|10	1.81373944845391	0.309152836077446	5.86680514229393	4.44272267919345e-09
10|11	2.041127581429	0.322376220020771	6.33150789254086	2.42776749199519e-10
11|12	2.32140870764259	0.342232883673569	6.78312581399049	1.17603133903422e-11
12|13	2.60789088161609	0.367043542075048	7.10512672930466	1.20212180993162e-12
13|14	2.99424816591617	0.409807088382668	7.30648212487776	2.74226962800544e-13
14|15	3.60180439086227	0.505511867943495	7.12506395846848	1.04032368358333e-12
15|16	5.23037494289133	1.02681366678588	5.09379170932094	3.50972351463031e-07

Table S2. Age class, but not rank or rank order, predicted the ordering of optimal patch departure times in a focal tree. (a) The summary of the ordinal logistic regression model for rank category in adults. (b) The summary of the ordinal logistic regression model for rank order in adults. (c) The summary of the ordinal logistic regression model for age class. The logical way of testing the hypothesis is to make exclusion of the predictor variable and the probability of occupying the response variable, as done here. However, because the data are difficult to interpret this way, I present the raw data in Figure 17 of my results.