Cracking Capuchins:
Investigating stone tool use by white-faced capuchin monkeys using camera traps

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MAX PLANCK INSTITUTE
OF ANIMAL BEHAVIOR

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“If we look straight and deep into a chimpanzee’s eyes, an intelligent self-assured personality looks back at us. If they are animals, what must we be?”

Frans de Waal

Summary

The use of tools enables human and non-human animals alike to achieve goals that would otherwise be unattainable. Whether it is a human using a needle to sew clothing, bees placing feces on hive entrances to deter predators, or a chimpanzee fishing for termites with a thin stick — tool use in the animal kingdom manifests in diverse ways, reflecting the ecological challenges and cognitive adaptations of each species. Yet, despite occurring in many different taxa — from insects to primates — tool-using animals make up only a small fraction of all known animal species, suggesting that tool use has evolved several times independently. Understanding the factors that drive the emergence, persistence, and spread of tool use is of great interest, not only to better grasp the role tool use played in hominin evolution but also because of the remarkable variation observed both within and between species. The evolution of tool use has been linked to various ecological, social, and cognitive factors, which often overlap and can be difficult to distinguish.

In this thesis, I use a unique study system to investigate what drives tool use to arise, persist, and spread in groups of animals. Since 2017, motion-triggered camera traps have been used to study the white-faced capuchin monkeys (*Cebus capucinus imitator*) living on the islands of Coiba and Jicarón in Panama, which have a tradition of stone tool use unique to the *Cebus* genus. These capuchins are uniquely suited to study the drivers of tool-use evolution, because tool-using and non-tool-using groups coexist in the same habitat, allowing for comparisons that exclude many ecological factors.

To better understand the variation in tool use *between* groups, it is necessary to examine how it varies *within* groups, as behavior spreads through individual dispersal. In chapter 1, I consider the striking male bias in tool use on Jicarón island. I show that females have the physical ability and opportunity to use tools, but do not engage in this behavior. This absence is not due to sampling bias, and has important implications for the cultural transmission of tool use. In chapter 2, I examine the development of tool use by comparing tool use proficiency between age classes. Using detailed frame-by-frame coding of one year of tool use events at two different experimental anvil sites, I show that the development of tool use proficiency is a slow process in which social attention and social tolerance play important roles. In chapter 3, I explore a potential ecological driver of the tool use behavior on Jicarón, namely the tidal cycles. Using a novel statistical approach, I compare the timing of coastal activity in relation to the tidal cycles between tool-using and non-tool-using capuchins. I find that tool-using capuchins show a

stronger correlation of coastal activity with tidal cycles, suggesting that tool use facilitates more efficient exploitation of intertidal resources.

In chapter 4, I describe a previously undocumented social tradition of interspecies abduction. On Jicarón, the same capuchins that use tools have also begun to abduct and carry infant howler monkeys. This behavior suggests that the environmental and social conditions that favor innovation of tool use might also favor innovation more generally. Importantly, this chapter highlights that innovations can emerge and spread via social learning even in the absence of a clear functional advantage. In chapter 5, I examine one possible consequence of tool use by comparing social cohesion between a tool-using group and a non-tool-using group. Because stone tool use relies on hammerstones and anvils, which can be monopolized by individuals, it is likely to increase within-group competition. I found that, in order to overcome this competition, the tool-using group may have become less socially cohesive. Notably, this shift in social structure affects not only tool-using males but the entire group, with cascading effects on within- and between-group dynamics.

Taken together, these chapters highlight that tool use is likely to require a combination of many factors to develop. My findings suggest that conditions conducive to innovation of tool use may also facilitate innovation more broadly and that islands may provide unique environments in which these factors co-occur. Furthermore, I propose that once localized tool-use traditions emerge, they may drive secondary behavioral differences, such as changes in social cohesion, that further differentiate tool-using and non-tool-using individuals. Finally, I demonstrate the power of camera traps as a non-invasive method for studying the behavior of unhabituated, wild primates in great detail, providing insights into everything from spatial and temporal activity patterns to the emergence and spread of a novel cultural tradition.

Zusammenfassung

Der Gebrauch von Werkzeugen ermöglicht es sowohl menschlichen als auch nichtmenschlichen Tieren, Ziele zu erreichen, die sonst unerreichbar wären. Ob es sich um einen Menschen handelt, der eine Nadel benutzt, um Kleidung zu nähen, Bienen, die Kot am Eingang ihres Bienenstocks deponieren, um Raubtiere abzuschrecken, oder ein Schimpanse, der einen dünnen Stock benutzt, um Termiten zu angeln — Werkzeuggebrauch zeigt sich im Tierreich auf vielfältige Weise und spiegelt die ökologischen Herausforderungen und kognitiven Anpassungen der einzelnen Arten wider. Doch obwohl Werkzeuggebrauch in vielen verschiedenen Taxa vorkommt — von Insekten bis zu Primaten — machen werkzeugnutzende Tiere nur einen kleinen Teil aller bekannten Tierarten aus, was darauf hindeutet, dass Werkzeuggebrauch mehrfach unabhängig voneinander entstanden ist. Es ist von großem Interesse, die Faktoren zu verstehen, die die Entstehung, das Fortbestehen und die Verbreitung des Werkzeuggebrauchs vorantreiben, nicht nur um die Rolle des Werkzeuggebrauchs in der Evolution der Hominini besser zu verstehen, sondern auch wegen der bemerkenswerten Unterschiede, die sowohl innerhalb als auch zwischen den Arten beobachtet werden. Die Evolution des Werkzeuggebrauchs wurde mit verschiedenen ökologischen, sozialen und kognitiven Faktoren in Verbindung gebracht, die sich oft überschneiden und schwer voneinander zu trennen sind.

In dieser Arbeit verwende ich ein einzigartiges Studiensystem, um zu erforschen, was die Entstehung, Ausdauer und Verbreitung von Werkzeuggebrauch bei Tieren antreibt. Seit 2017 werden bewegungsausgelöste Kamerafallen eingesetzt, um Weißgesichtskapuziner (*Cebus capucinus imitator*) auf den Inseln Coiba und Jicarón in Panama zu untersuchen, die eine für die Gattung *Cebus* einzigartige Tradition der Nutzung von Steinwerkzeugen haben. Diese Kapuzineraffen eignen sich hervorragend, um die treibenden Kräfte hinter der Evolution des Werkzeuggebrauchs zu untersuchen, da werkzeugbenutzende und nicht werkzeugbenutzende Gruppen im selben Lebensraum koexistieren und somit Vergleiche möglich sind, die viele ökologische Faktoren ausschließen.

Um die Unterschiede im Werkzeuggebrauch *zwischen* den Gruppen besser zu verstehen, ist es wichtig zu untersuchen, wie er *innerhalb* der Gruppen variiert, da sich das Verhalten durch die Abwanderung einzelner Individuen verbreiten kann. In Kapitel 1 untersuche ich das auffällige geschlechtsspezifische Muster im Werkzeuggebrauch auf Jicarón. Obwohl Weibchen die physischen Voraussetzungen und Gelegenheiten zum Werkzeuggebrauch haben, wurde dieses Verhalten bisher ausschließlich bei Männchen beobachtet Das Fehlen dieses Verhaltens ist nicht auf

Stichprobenfehler zurückzuführen und hat wichtige Auswirkungen auf die kulturelle Weitergabe des Werkzeuggebrauchs. In Kapitel 2 untersuche ich die Entwicklung des Werkzeuggebrauchs indem ich die Werkzeuggebrauchskompetenz zwischen den Altersklassen vergleiche. Anhand einer detaillierten Bild-für-Bild-Kodierung von Werkzeuggebrauchsereignissen eines Jahres an zwei verschiedenen experimentellen Ambossstandorten zeige ich, dass die Entwicklung der Werkzeuggebrauchskompetenz ein langsamer Prozess ist, bei dem soziale Aufmerksamkeit und soziale Toleranz eine wichtige Rolle spielen. In Kapitel 3 untersuche ich einen möglichen ökologischen Einflussfaktor auf das Werkzeuggebrauchsverhalten in Jicarón, nämlich die Gezeitenzyklen. Mithilfe eines neuen statistischen Ansatzes vergleiche ich das Timing der Küstenaktivitäten in Bezug auf die Gezeitenzyklen zwischen werkzeugbenutzenden und nicht werkzeugbenutzenden Kapuzinern. Ich stelle fest, dass Werkzeugbenutzer eine stärkere Korrelation zwischen ihrer Küstenaktivität und den Gezeitenzyklen aufweisen, was darauf hindeutet, dass der Werkzeuggebrauch eine effizientere Nutzung der Gezeitenressourcen ermöglicht.

In Kapitel 4 beschreibe ich eine bislang nicht dokumentierte soziale Tradition der artübergreifenden Tierentführung. Auf Jicarón haben dieselben Kapuzineraffen, die Werkzeuge benutzen, damit angefangen, junge Brüllaffen zu entführen und herum zu tragen. Dieses Verhalten deutet darauf hin, dass ökologische und soziale Bedingungen, die Innovationen im Werkzeuggebrauch begünstigen, auch Innovationen im Allgemeinen begünstigen können. Wichtig ist, dass dieses Kapitel zeigt, dass Innovationen durch soziales Lernen entstehen und sich verbreiten können, auch wenn es keinen eindeutigen funktionalen Vorteil gibt. In Kapitel 5 untersuche ich eine mögliche Folge des Werkzeuggebrauchs, indem ich die soziale Kohäsion innerhalb einer Gruppe, die Werkzeuge benutzt, und einer Gruppe, die keine Werkzeuge benutzt, vergleiche. Da die Verwendung von Steinwerkzeugen von Hammersteinen und Ambosse erfordert, die von einzelnen Individuen monopolisiert werden können, ist es wahrscheinlich, dass sie den Wettbewerb innerhalb der Gruppe verstärkt. Ich habe herausgefunden, dass die werkzeugnutzende Gruppe möglicherweise eine geringere soziale Kohäsion entwickelt hat, um diesen Wettbewerb zu überwinden. Diese Verschiebung in der Sozialstruktur betrifft nicht nur die männlichen Werkzeugnutzer, sondern die gesamte Gruppe, mit kaskadenartigen Auswirkungen auf die Dynamik innerhalb und zwischen den Gruppen.

Insgesamt zeigen diese Kapitel, dass die Entwicklung des Werkzeuggebrauchs vermutlich eine Kombination vieler Faktoren erfordert. Meine Ergebnisse deuten darauf hin, dass Bedingungen, die Innovationen im Werkzeuggebrauch begünstigen, auch Innovationen im weiteren Sinne erleichtern können, und dass Inseln ein einzigartiges Umfeld bieten können, in dem diese Faktoren zusammenwirken. Darüber hinaus schlage ich vor, dass, sobald lokale Traditionen von Werkzeuggebrauchs entstanden sind, diese zu sekundären Verhaltensunterschieden führen können, wie etwa Veränderungen in der Gruppenkohäsion, die Individuen, die Werkzeuge benutzen, weiter von denen unterscheiden, die keine Werkzeuge benutzen. Abschließend zeige ich das Potenzial von Kamerafallen als nicht-invasive Methode zur detaillierten Untersuchung des Verhaltens nicht habituierter, wildlebender Primaten, und biete Einblicke von räumlichen und zeitlichen Aktivitätsmustern bis hin zur Entstehung und Verbreitung einer neuen kulturellen Tradition.

Acknowledgments

Working on this project felt like a twist of fate to me. I applied to study baboons, until I was asked what I thought of investigating unusual tool-using capuchin monkeys on an uninhabited island in the middle of nowhere instead. The mystery was too tempting to resist — and I'm so glad I didn't. While the journey had its share of twists, frustrations, and data limitations, it also offered endless opportunities to satisfy my curiosity and grow as a scientist.

From the beginning, my advisor Brendan Barrett has been an integral part of this experience. Much of this project was his brainchild, and I thank him for sharing some custody (and capuchin naming rights) with me. As a scientist, Brendan demonstrates the utmost integrity, and I've learned so much from his devotion to open science, dedication to statistical soundness, and passion for the scientific process. For me, Brendan was the ideal supervisor of my PhD, he trusted in my abilities yet provided me guidance and steering whenever I needed it. I think we were both lucky to have a shared sense of humor, and I always appreciated the levity he brought. More importantly, he always reminded me that science will take as much of you as you give it, so it is up to you to set boundaries on what you are willing to give. Over the years of my PhD, I have cultivated a work-life balance I take pride in, and Brendan has always encouraged me to protect it fiercely.

I also want to express my sincerest thanks to Meg Crofoot, for making this PhD possible and providing mentorship, supervision, and advice throughout this journey. Her gift for seeing the bigger picture — the "so what" — of research and articulating it clearly has deeply inspired me. I hope to one day communicate my science as effectively as she does. Our brainstorming sessions and feedback meetings were formative, and her encouragement to branch out more beyond primatology helped shape me into a broader biologist and ecologist. It has been great watching her department grow into a vibrant, inclusive scientific community.

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My family has been a constant source of strength. We joke that I'm living out my father's dream, since he started two PhDs and never finished one. Now that I'm here, I'm even more in awe that he tried twice — especially with three young kids at home. With all the knowledge he holds, he's earned a PhD ten times over. To my mother, Jacqueline, thank you for your unwavering support, thoughtful feedback, and for always picking up the phone on my walks to and from work. To Dylan and Luna — my brother and sister — thank you for always believing in me. My parents' cat Cleo for treating me like a beloved family member even though I only see her three times a year. And to the mice, Hazel, Maple and Coco, who shared a much bigger part of this journey than originally expected.

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Ethics statement

This entire dissertation would not exist without the animals whose behavior I am describing. Ensuring that animal research is conducted ethically is not only a personal priority for me but also essential for the well-being of the studied animals and the integrity of the science itself. Data for all the chapters of this thesis were collected in the least invasive manner possible, and we obtained ethical permission for all studies from the relevant authority, Ministerio de Ambiente, Panama (scientific permit no. SE/A-37-17, SC/A-23-17, SE/A-98-19, SE/A-6-2020, ARB-158-2022, and corresponding renewals and addenda).

We used motion-triggered camera traps, which, while not entirely free from disturbance, are far less disruptive to animals than alternatives such as habituation or trapping and collaring. We took further steps to minimize the impact of the camera traps on the animals' well-being. All camera traps were programmed to use infrared rather than white flash, which is less visually disruptive. We conducted only brief trips to deploy and retrieve camera traps, and ensured we left no trace of our presence aside from the camera traps themselves.

When other data collection methods were employed, such as collecting hair samples for DNA analysis, these too were designed to minimize disturbance and avoid pollution. We used hair traps consisting of plastic tubes containing quail eggs, with double-sided tape placed at the entrance. When a capuchin reached in for the egg, a few hairs would adhere to the tape, from which DNA can be extracted. All materials from these traps were always collected and removed afterward.

Our responsibility to the animals extends beyond the duration of fieldwork. It also includes ensuring that our results are widely disseminated, accessible, and reproducible, and that we engage with the ethical and conservation implications of our research. Accordingly, all chapters of this thesis are (or will be) published open access, freely available to all. We also engaged in outreach whenever possible, in English, German, and Spanish, to further disseminate our findings. In addition, for every chapter, I have shared the data and code necessary to replicate the analyses.

Contents

General Introduction

When primatologist Jane Goodall first reported on chimpanzee tool use in 1960, her supervisor, paleoanthropologist Louis Leakey, responded “Now we must redefine tool, redefine man, or accept chimpanzees as human” [1]. Humans’ fascination with tool use in animals has always partly been due to anthropocentric sentiments: as stated by Shettleworth [2], dropping a rock on a shell is not necessarily more complex or interesting than dropping a shell on a rock. Nonetheless, we consider ourselves to be the most proficient tool users in the animal kingdom, and tool use is widespread across human cultures and societies, ranging from hammers to smartphones, creation and use of tools is a vital part of human life. Over the decades, much research has aimed to defend (or question) the position of tool use as being unique to humans [3]. As evidence of tool use was uncovered in a greater variety of animal taxa, interest grew in studying animal tool use to better understand what may have driven the evolution of human tool use [4]. Aside from human-focused interest in tool use, using tools provides an example of animals innovating to overcome an obstacle in their environment [5]. Tool use is rare in the animal kingdom, occurring in less than 1% of currently identified animal genera [6], yet at the same time there is great diversity in both the species that show tool use, and the type of tool use present [7]. Ranging from chimpanzees using sticks to fish for termites [8], to dolphins protecting their rostra with sponges while foraging [9], and bees using animal feces as deterrents to defend their colonies [10], this vast diversity suggests that tool use evolved independently several times [11]. Once innovated, tool use behavior may spread between individual animals via social learning [9, 12–14]. Studying tool use in animals provides evidence for the extent of their cognitive abilities, such as their understanding of causal relationships [15]. Furthermore, despite tool use occurring in such a variety of species and settings, it is as of yet unclear what drives the emergence of tool use. Examining why tool use emerges in some groups of animals but not in others, how it is maintained, and how it spreads, can shed light on the evolutionary origins of both human and non-human animal tool use.

0.1 Defining tool use

The definition of tool has shifted over the years, along with the debate about the difference between human and non-human animal tool use. The variety of definitions used for tool use over the decades makes it more difficult to compare tool use behavior between species as well as contrast studies done at different points in time. While Charles Darwin already described various examples of tool use by primates [16], tool use by non-human animals was not considered comparable to human tool use until Jane Goodall's description of termite fishing in chimpanzees [8]. Goodall defined tool use as an animal using an external object as an extension of the mouth or hand to achieve an immediate goal [1]. This definition was adapted to become more specific, and one of the definitions of tool use still most widely used today is by Beck [17], where a behavior is considered tool use when it meets three criteria: 1) the animal uses a tool that is not part of their own body 2) the tool is not attached to the surrounding environment, and 3) the animal manipulates the tool to reach a useful outcome. While there have been later adaptations to this definition, such as including objects that are attached yet manipulatable [6], and specifying that tools must be used in specific contexts rather than perpetually [18], it remains the most common definition of tool use and therefore is what I adhere to in this thesis.

0.1.1 Types of tool use

Researchers also make distinctions in the type of tool use animals show, and these categories are also often linked to differing levels of cognitive complexity. Hunt and colleagues [11] proposed that tool use can be stereotyped or flexible, where stereotyped tool use arises without extensive individual or social learning, with little variation within species and does not require great cognitive capacities to evolve. A classic example of stereotyped tool use is archerfish spitting water at prey, which is an inborn behavior that occurs only in specific contexts. Flexible tool use, in contrast, is acquired through long periods of individual and social learning, varies greatly between individuals and populations, and requires multiple cognitive skills. An example of flexible tool use is termite fishing in chimpanzees: it is not innate but learned over the course of an individual's life, varies across populations, and is used in multiple contexts [11]. This distinction is also sometimes framed as customary tool use (hard-wired behavioral specializations) contrasted to habitual tool use (reflecting cognitive flexibility, and requiring social learning to be acquired) [5]. Fragaszy and colleagues [19] proposed a framework distinguishing between zero-, first-, and second-order tool use, where the order refers to the number of relationships between objects involved in the tool use and only first- and second-order tool use are considered true tool use. First-order tool use, which can be dynamic or static, involves manipulation of two objects, while second-order tool use involves simultaneous or sequential manipulations involving three objects (Figure 1). Second-order tool use is often viewed as the most cognitively demanding type of tool use, as it involves monitoring relationships between several objects, and therefore it is of great interest in comparing animal to human tool use.

Percussive technology — the use of hammerstones and anvils to open inaccessible food items — is an example of second-order tool use [19] that is sometimes seen as the pinnacle of animal tool use. Hammerstone and anvil tool use is thought to reflect a high level of cognitive complexity [20], since it is a flexible behavior with various sequential steps, which can involve skills like planning (e.g., find a nut, bring a nut to a suitable anvil site, find a suitable hammerstone, hit the nut with the hammerstone in the right way to open it). Furthermore, percussive technology

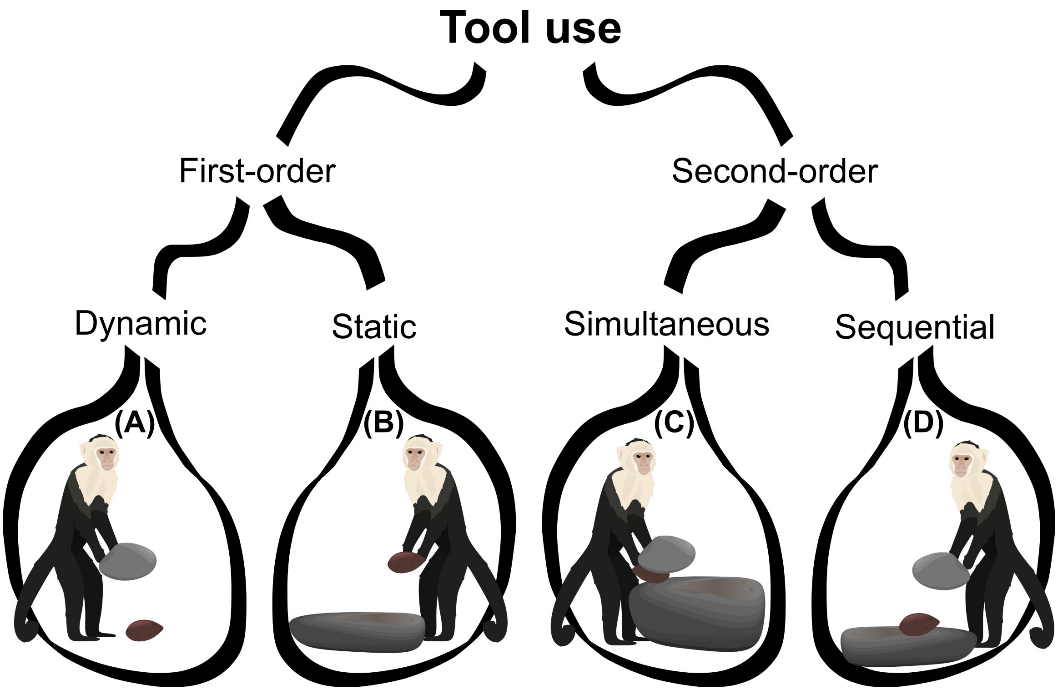

Figure 1: An overview of the distinction between first-order and second-order tool use as defined by Fragaszy and colleagues [19]. Examples of each type of tool use are A) pounding a loose nut with a stone, B) pounding a nut on a fixed stone, C) pounding a nut with a stone, while holding the nut to keep it in place, and D) placing a nut on a stone, and then pounding this nut with another stone. Illustrations credit to Imran Razik

is thought to have played a prominent role in hominin evolution [21]. Hammerstone and anvil tool use allowed hominins to access a wider variety of food items, and likely was a first step in creating stone flakes used for cutting, which further opened up creation and use of other tools. Stone tool use for extractive foraging is rare in the animal kingdom, and its occurrence appears entirely limited to the order of primates, making it an ideal candidate behavior for comparative research. Studying stone tool use in non-human primates can also contextualize interpretations of archaeological records of hominin tool use [22]. Aside from humans, the only wild primates that show percussive stone tool use are chimpanzees (*Pan troglodytes* [23]), long-tailed macaques (*Macaca fascicularis* spp. [24, 25]), robust capuchins (*Sapajus* spp. [26–29]), and gracile capuchins (*Cebus* spp. [30–32]), who all use hammerstones and anvils to crack open food items. An important distinction between stone technology in animals and in hominins is that the former appears to mostly be limited to pounding, whereas the latter included pounding, grinding, and flaking. The rarity of percussive stone tool use in the animal kingdom and its convergent emergence in various primate species makes it a prime target of research into the drivers of the evolution of tool use.

0.2 Hypotheses on the evolution of tool use

While tool use, at face value, appears to be a behavior with adaptive benefit — after all, it usually offers access to novel resources which can improve diet quality [33] — there is limited evidence that tool use is adaptive [5]. Additionally, tool use can be a costly behavior, both in terms of time and effort invested in acquisition and fine-tuning of tool use behaviors, as well as there likely being a cognitive expenditure for using tools flexibly. In New Caledonian crows (*Corvus moneduloides*), who make and use stick tools to probe for insects, young individuals spend much time using tools with little pay-off, but these energetic costs may be offset by the benefits received as a competent tool-using adult [34]. The broad phylogenetic spread of tool use behaviors means that it is harder to pinpoint any specific ecological or social factor as driving its development.

0.2.1 Ecological factors

Several, not mutually exclusive, hypotheses have been proposed by Fox and colleagues [35] for how ecological factors can drive tool use to evolve. Firstly, the "*necessity hypothesis*", which states tool use emerges as a way to access novel food sources when easily accessible resources are scarce. Necessity appears to be able to account for probe tool use in woodpecker finches, where during the dry season when food is scarce, finches in arid zones show much higher rates of tool use than those in zones with abundant food [36]. An important caveat of the necessity hypothesis is that the environmental conditions a tool-using animal currently lives in may have changed significantly from the conditions that drove tool use to arise in that population. Secondly, the "*opportunity hypothesis*" [35] states that tool use develops in environments where animals are repeatedly exposed to the appropriate conditions for tool use (e.g., tool materials, resources that are inaccessible without tools). In contrast to the necessity hypothesis, the opportunity hypothesis predicts that tool use would be more likely when inaccessible resources are more abundant, rather than accessible resources being scarcer. Termite fishing by chimpanzees in Gombe follows a pattern of opportunity rather than necessity: fruit is more abundant during the rainy season, however this is when chimpanzees show the highest rates of termite fishing, as it is when termites are most accessible [37]. As neither necessity nor opportunity can account for all cases of animal tool use, later research proposed a combination of the two in the "*relative profitability hypothesis*" [38]. This hypothesis states that tool use will develop when it is more profitable than non-tool-assisted strategies for foraging, and was proposed to account for the emergence of tool use by New Caledonian crows.

0.2.2 Social factors

In the article that originally proposed the necessity and opportunity hypotheses [35], a third hypothesis, the "*limited invention hypothesis*", was proposed to account for variation in the emergence of tool use in the absence of any ecological explanations. This poses tool use might be so rare because it is only rarely innovated, and relies on social learning to spread between individuals. The rare occurrence of tool use in the animal kingdom would then be a result of neutral rather than selective evolutionary processes, and it would be more likely to arise in areas where dispersal is limited. Later research has given more attention to the importance of social learning in the spread of novel innovations, and social tolerance is purported to be an important driver allowing individuals to closely observe the behavior of others [39]. Social learning appears to play an especially important role in the acquisition and development of complex tool use behaviors, like percussive technology. In both chimpanzees and robust capuchins, who crack nuts using stone tools, immature individuals acquire the behavior through social learning processes [12, 40–42], and in chimpanzees, insufficient exposure to nut-cracking at an early age is thought to impede acquisition of the behavior [40, 43, 44]. While social learning can aid the spread of a tool use behavior like stone tool use, behavior can only spread after it has been innovated at least once, and thus we also always need to consider individual animal's cognitive and innovative abilities.

0.2.3 Cognitive limitations

The evolution of flexible tool use is thought to be constrained by cognitive demands. The frequency of tool use emerging in different taxonomic groups suggests there are cognitive constraints: tool use is rarest in invertebrates and fish, and most commonly found in the taxa of birds and primates [11]. In birds, occurrence of tool use correlates both with overall brain size as well as the size of the neostriatum [45], a part of the avian brain involved in learning, analogous to the neocortex in mammals. In primates, tool use also correlates with brain size [46]. Taxa that are considered to be better at tool use, innovation, and social learning, are also usually the taxa that perform well in cognitive experiments [20]. Flexible tool use in the animal kingdom may then be rare because it relies on complex cognitive processes that are similarly rare. However, even within species where complex tool use occurs, its occurrence is not ubiquitous. Taking percussive stone technology as an example — being the 'pinnacle' of animal tool use — its occurrence is limited to specific populations within each species. Only 15% of all studied wild chimpanzee communities crack nuts with stone tools [47], nut-cracking by robust capuchins is customary in a handful of populations [48], cracking of shellfish by macaques is limited to several islands [49, 50], and stone tool use by white-faced capuchins only occurs on two islands within one archipelago [30, 31]. As such, it is very likely that a combination of ecological factors, social factors, and individual characteristics is required for an animal to develop tool use.

0.2.4 Tool use and islands

Although the taxa in which tool use occurs are so varied, there is one striking similarity between several tool-using populations of animals: island-living. Habitual tool use is observed in many endemic island-living species (i.e., Woodpecker finches [*Cactospiza pallida* [51]]; New-Caledonian crows [*Corvus moneduloides* [38]]; Hawaiian crows [*Corvus hawaiiensis* [52]]; and Keas [*Nestor notabilis*, [53]]), or restricted to populations that live on islands (i.e. Burmese long-tailed macaques [*Macaca fascicularis* [25, 54]] and white-faced capuchin monkeys [*Cebus capucinus* *imitator* [30]]) or in urban populations (i.e., white-fronted capuchin monkeys [*Cebus albifrons* [32]]). The term 'island' can refer to any ecological system that is an isolated area of suitable habitat surrounded by an unfavorable environment that limits individual dispersal [55], which includes urban islands like parks in cities or other habitats fragmented by human presence. Marine islands in particular are often called "natural laboratories" as their characteristic features of genetic isolation and limited cultural transmission can drive evolution [56], as well as innovation of novel behaviors [57]. Compared to the mainland, ecological stressors might be heightened on islands due to decreased dietary richness [58], reduced resource abundance, or harsher seasonal fluctuations. Additionally, islands tend to have fewer predators, allowing animals to expand their niches, and affording free time and opportunity for tool use to develop. In robust capuchins (*Sapajus* spp.), the degree of terrestriality, which is closely linked to predation, was found to be the strongest predictor for tool use [59]. Islands are also subject to founder effects [56], and the following community assemblages mean animals might have fewer competitors, driving niche expansion (such as in New Caledonian crows [38]). The high incidence of tool use on islands could reflect that certain ecological features of islands favor innovation of tool use specifically, or innovation more generally [30], but further research is required to identify these driving forces.

0.3 The tool-using capuchins of Coiba National Park

The white-faced capuchin monkeys (*Cebus capucinus imitator*) in Coiba National Park, Panama are an ideal study system to disentangle the many different possible drivers of tool use, because they are a population of tool-using animals of a well-studied species that does not show tool use in other sites. Several groups of capuchins on the islands of Coiba and Jicarón in Coiba National Park use stone tools to open a variety of resources [30, 31] (Figure 2). By closely examining what differentiates this specific population from other non-tool-using populations, we can shed light on the specific ecological factors supporting the development of tool use.

The genus *Cebus* — the gracile capuchins — diverged from the genus *Sapajus* — the robust capuchins — ~ 6.5 mya [60]. *Sapajus*' habitual reliance on tools for foraging [26, 61] was long considered a distinguishing characteristic between this genus and *Cebus* [60]. Nonetheless, *Cebus* is known to be innovative and capable of overcoming the defenses of a variety of prey [62], appearing to meet the cognitive requirements for tool use. White-faced capuchins rely heavily on extractive foraging to access resources that are structurally protected and are exploratory dietary generalists [63, 64]. They are long-lived primates with a large brain-to-body size ratio, show high rates of innovation across several behavioral domains [65], and social learning of social and foraging traditions between and across generations [66–69]. The discovery of stone tool use by *Cebus* capuchins is thus not surprising in itself, and recently, an urban population of *Cebus albifrons* in Ecuador was also found to use stone tools [32]. However, white-faced capuchins specifically have been studied for decades at several field sites [70, 71], where stone tool use was never observed.

Island-living can change animals both physically [72] and behaviorally [57], and not much is known about how the Coiban capuchins differ from mainland populations in these regards [30]. Typically, white-faced capuchins live in cohesive multi-male, multi-female groups, with extensive home range overlap with neighboring groups, and hostile intergroup encounters [73, 74]. On Coiba and Jicarón, group composition appears to be similar to mainland populations, however, the density of capuchins on Coiba and Jicarón seems high [30, 75]. White-faced capuchins in mainland sites are largely arboreal, but, likely due to the absence of predators, capuchins on Coiba and Jicarón are more terrestrial than their mainland counterparts [76].

0.3.1 Localized stone tool use

Capuchins in Coiba National Park use hammerstone and anvils to open a variety of resources, including fruits like sea almonds (*Terminalia catappa*), coconuts (*Cocos nucifera*) and palm fruits (*Bactris major*, *Astrocaryum standleyanum*) as well as sessile and mobile invertebrates like Halloween crabs (*Gecarcinus quadratus*), hermit crabs (*Coenobita compressus*), nerite snails (*Nerita sp.*) and other freshwater mollusks [30, 31]. The first observation of stone tool use by white-faced capuchins on Jicaron island dates from 2004, and the tool use tradition appears to have continued uninterrupted at the location of this sighting [30]. Stone tool use by white-faced capuchins in Coiba National Park is incredibly localized — it was reported to occur only in males in a single group on Jicarón [30], and in both sexes in one group of capuchins on Coiba [31] — allowing for comparisons within and between tool-using groups as well as of tool-using and non-tool-using groups of capuchins sharing the same habitat. Many of the resources which are consumed by the capuchins using tools are also consumed by non-tool-using capuchins, who eat different parts of the food item or overcome the defenses without tools [30].

Figure 2: Photograph of a deployed camera trap on Jicarón Island attached to a tree in a metal case (left) and an image taken by a camera trap of a juvenile capuchin using stone tools to crack open a sea almond (right). Credit for the photo of the camera trap belongs to Christian Ziegler.

Tool use occurs at three kinds of sites, which can be differentiated from one another by the intensity of tool use activity and amount of debris accumulation (Figure 3) [30]. First, tool use can be ephemeral, occurring in areas where physical evidence does not linger, such as the intertidal zone or inside a stream. Second, tool use occurs in sites with intermediate accumulation, such as a streambed, where tool use debris eventually gets washed away by the stream. Third, the kind of tool use that appears to be most rare is habitual, high activity tool use at sites (hereafter: 'anvils') with great amounts of accumulation. These anvils are away from streambeds, and due to their repeated use over long periods of time can see accumulation of a lot of debris. The archaeological signature of these sites is distinct, and unlike tool use in the intertidal and streambed, its physical evidence accumulates. Based on surveys, it is clear that on Jicarón high-accumulation tool use at fixed sites is entirely limited to a single capuchin group, despite comparable availability of resources and tool use materials along the island's coast [30]

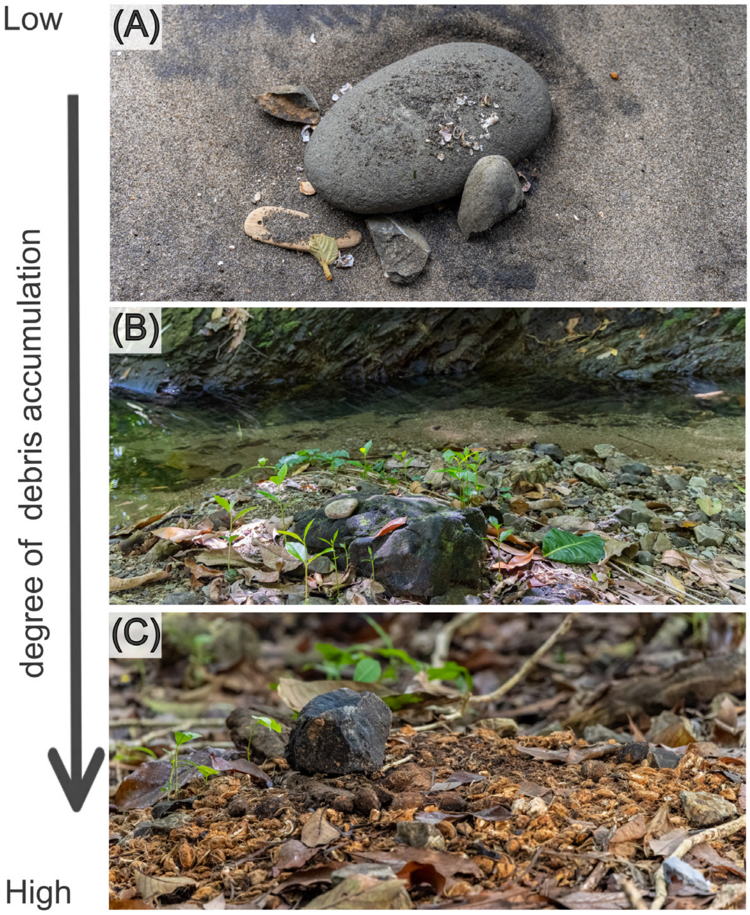

Figure 3: Photographs of the types of tool use sites on Jicarón, ordered from low to high debris accumulation. A) an example of a low accumulation site in the intertidal zone, B) an intermediate accumulation site in a streambed, and C) a high accumulation (or 'anvil') site. Photo credits belong to Christian Ziegler.

0.4 Objectives

Jicarón Island offers a unique opportunity to study the drivers of tool use. Stone tool use emerged and has persisted in a single group of capuchins, yet does not seem to spread to other capuchin groups on the island. There are no physical boundaries between tool-using and non-tool-using groups, nor is there great variation in the availability of materials for tool use. Thus, many of the proposed hypotheses for the development of tool use, such as opportunity and necessity, cannot explain why tool use would remain so localized. In this thesis, I investigate the conditions that led to the emergence and persistence of a stone tool use tradition in this population of white-faced capuchin monkeys. The chapters presented here primarily focus on the tool-using group on Jicarón Island, which has been studied using camera traps since 2017.

0.4.1 Coiba National Park

Coiba National Park consists of nine islands and over 100 islets approximately 30 km off the Pacific coast of the Veraguas Province, Panama. Coiba, the largest island, is estimated to have been geographically isolated for 14 000-18 000 years [77]. Coiba and Jicarón were used as a penal colony from 1919 until 2004 [75]. Before this, the islands were inhabited by indigenous people from 250 CE until the 16th century [78]. In recent years, only the island of Coiba and Rancheriá see frequent human occupation in the form of a police station and two research stations; the other islands (including Jicarón) are largely undisturbed [30]. Coiba National Park contains one of the largest preserved areas of mature forest in Pacific Central America, with a distinct wet and dry season, with 3000 mm of precipitation in the wet season (mid-April to mid-December) and less than 60 mm of precipitation in the dry season. The archipelago is a UNESCO world heritage site, containing many endemic marine and terrestrial animal and plant species [79, 80]. Species richness varies between the islands as a function from distance to the mainland, with Coiba having higher plant richness than the more distant island of Jicarón [81, 82]. White-faced capuchins live on the islands of Coiba (50 314 ha), Jicarón (2 002 ha), and Rancheriá (222 ha). Few other mammal species inhabit the islands aside from capuchins, including four endemic (sub)species of mammals. On Coiba and Jicarón, there are small unidentified rodents (one of which is likely *Rattus rattus*) and the endemic Coiban agoutis (*Dasyprocta coibae*) and Coiba Island howler monkeys (*Alouatta pailliata coibensis*). On Coiba there are also black-eared and Robinson's mouse opossums (*Didelphis marsupialis battyi* and *Marmosa robinson*), and the endemic Coiba Island white-tail deer (*Odocoileus virgninianus*). There are no terrestrial mammalian predators, and the only predators which could hypothetically prey on capuchin monkeys are the Central American Boa (*Boa imperator*) and American crocodiles (*Crocodylus acutus*), whose occurrence is localized on the islands.

0.4.2 Data collection using camera traps

Due to the remoteness and rugged terrain of Coiba and Jicarón, a long-term research presence is not possible and the white-faced capuchins are unhabituated to humans. Thus, all the data presented in this thesis was collected using motion-triggered, unbaited, photo and video camera traps. Camera traps are much less disruptive than direct observation, though they do cause disturbance to animals through production of visual and auditory signals, as well as the human presence during deployment and pick-up, and lingering olfactory cues [83]. However, these disturbances can be minimized by using infrared instead of white flash, maximizing deployment lengths, and being careful to not leave human smells on the camera traps. I built on existing data collected at Coiba and Jicarón since March 2017, with the main focus on the tool-using group on Jicarón Island, who have been monitored most extensively. Since 2017, camera traps have been placed at 10 locations on Jicarón to collect continuous data on the tool-using group. Additionally, camera traps collected data at around 45 other locations on the islands during shorter periods often across several seasons. The camera traps consisted of a combination of video and still-image camera traps, and sampled both tool-using and non-tool-using groups of capuchins on the two islands. Most camera traps in the tool-using areas were placed at anvil sites, but some were placed at non-anvil sites. In this thesis, I report on data collected between 2017 and 2023, totaling over 160 camera traps placed in more than 120 different locations on Coiba and Jicarón (Figure 4).

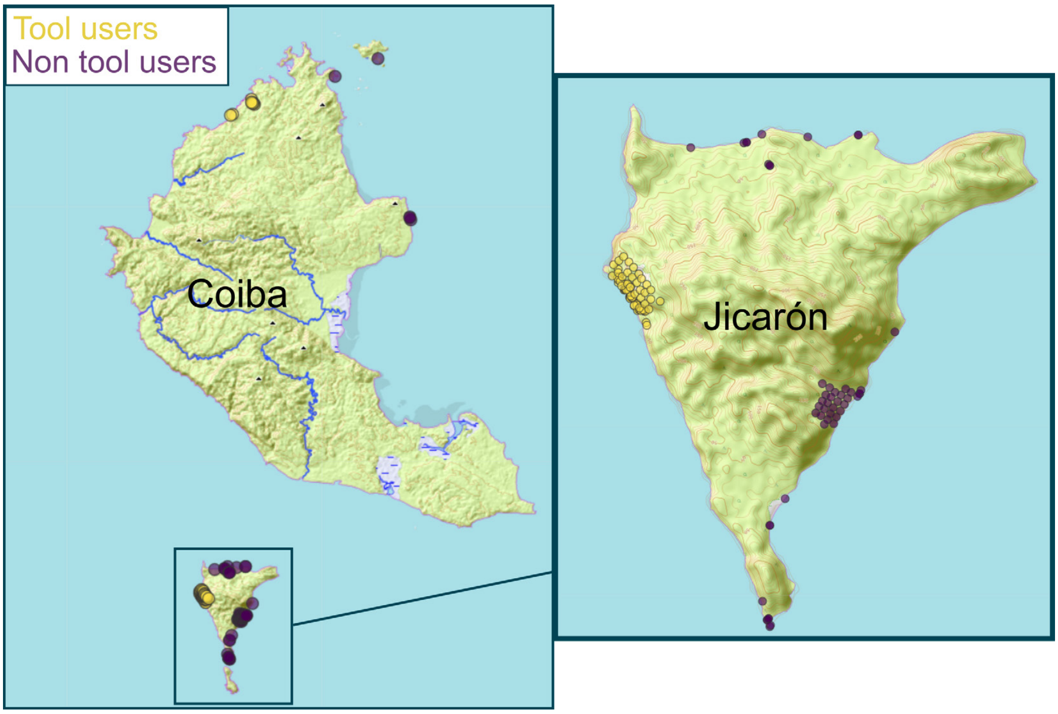

Figure 4: Overview of all locations on Coiba and Jicarón where camera traps were placed. Each circle reflects a camera location, with yellow representing cameras placed in the range of a group of tool-using capuchins, and purple in the range of a group of non-tool-using capuchins.

0.5 Thesis outline

In this thesis, I explore the ecological drivers, within-group variation, and consequences of the stone tool use tradition of white-faced capuchins on Jicarón Island, in order to better understand the conditions that might have driven its emergence and persistence. First, I assess who uses tools, focusing on variation *within* groups. Understanding differences in the tendency to use tools between age and sex classes is crucial to understanding why tool use may differ *between* groups, as only some individuals disperse and potentially spread local behaviors.

In chapter 1, I examine several hypotheses that might explain why tool use on Jicarón Island is restricted to males, while both sexes use tools on Coiba. Through placement of camera traps in streambeds as well as 'random' locations in the forest interior, I evaluate whether females on Jicarón do not use tools, or whether female tool use has been overlooked due to sampling bias. In the absence of a sampling bias, I further assess whether an absence of female tool use is likely to have arisen through a lack of physical ability, opportunity, or differences in risk perception or diet between males and females.

I expand on intragroup differences in tool use in chapter 2, where I compare tool use proficiency between adults and juvenile capuchins. I do this through frame-by-frame coding of videos of tool-using events at two experimental anvils placed within the range of the tool-using group. Additionally, I consider the development of tool use proficiency by using one year of data, and by analyzing social attention to tool use events.

To understand why tool use arose on Jicarón and not in other populations of white-faced capuchins, I first consider an ecological factor in chapter 3. In this chapter, I study the coupling of tool-using and non-tool-using capuchins' coastal activity with the tidal cycles. Foraging in the intertidal zone can be greatly enhanced by the use of tools, and these valuable resources are only available for a limited, shifting window of time each day. I contrast the coastal activity of the tool-using group to that of the non-tool-using group, further differentiating between the wet and the dry season, to get at the importance of intertidal foraging in their daily activity.

The ecological conditions on Jicarón which favored the development of tool use may also underlie the origin and spread of other innovations, which I explore in chapter 4. I describe the rise and spread of an entirely unique social tradition of interspecies abduction. In the tool-using group on Jicarón, using only camera traps, we captured capuchins abducting and carrying howler infants. I analyze the features of this tradition in order to better understand the conditions on this island that favor innovation, and how these may also have favored innovation of tool use.

Lastly, what is much less frequently explored is how habitual tool use may affect social behavior. In chapter 5, I explore this novel angle by comparing social cohesion between the tool-using group and one non-tool-using group on Jicarón. These two groups share the same habitat, yet have this different tool-using tradition, which may have cascading effects on their social dynamics as anvils are monopolizable and can increase within-group competition. Previous camera trapping on Jicarón was biased towards anvils in the tool-using group's range, and brief surveys in areas occupied by non-tool-using capuchins, making comparison between them difficult. By placing two comparable grids of camera traps at the tool-using group and a non-tool-using group, I contrast the temporal variation in party size, party composition and spatial cohesion between tool-using and non-tool-using capuchins.

Taken altogether, this thesis leverages data from minimally invasive camera traps to examine the stone tool use tradition of white-faced capuchins on Jicarón and Coiba Islands, shedding light on the possible drivers involved in the origin, maintenance, and spread of tool use.

Chapter 1

Male-biased stone tool use by wild white-faced capuchins

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1.1 Abstract

Tool-using primates often show sex differences in both the frequency and efficiency of tool use. In species with sex-biased dispersal, such within-group variation likely shapes patterns of cultural transmission of tool use traditions between groups. On the Panamanian islands of Jicarón and Coiba, a population of white-faced capuchins (*Cebus capucinus imitator*) —some of which engage in habitual stone tool use — provide an opportunity to test hypotheses about why such sex-biases arise. On Jicarón, we have only observed males engaging in stone tool use, whereas on Coiba, both sexes are known to use tools. Using 5 years of camera trap data, we provide evidence that this variation likely reflects a sex difference in tool use rather than a sampling artifact, and then test hypotheses about the factors driving this pattern. Differences in physical ability or risk-aversion, and competition over access to anvils do not account for the sex-differences in tool use we observe. Our data show that adult females are physically capable of stone tool use: adult females on Coiba and juveniles on Jicarón smaller than adult females regularly engage in tool use. Females also have ample opportunity to use tools: the sexes are equally terrestrial, and competition over anvils is low. Finally, females rarely scrounge on left-over food items either during or after tool-using events, suggesting they are not being provisioned by males. Although it remains unclear why adult white-faced capuchin females on Jicarón do not use stone-tools, our results illustrate that such sex biases in socially learned behaviors can arise even in the absence of obvious physical, environmental, and social constraints. This suggests that a much more nuanced understanding of the differences in social structure, diet, and dispersal

patterns are needed to explain why sex-biases in tool use arise in some populations but not in others.

1.2 Introduction

A small but taxonomically diverse set of primate species are known to use tools for extractive foraging (e.g., Burmese long-tailed macaques [*Macaca fascicularis*], [54]; tufted capuchins [*Sapajus spp.*], [26]; chimpanzees [*Pan troglodytes*], [85]; white-faced capuchins [*Cebus capucinus imitator*], [30, 66]). Despite providing access to high-quality food items that are often otherwise unavailable, tool use behavior tends to be highly variable, meaning that only some members of a tool-using group or population actually use tools. Sex-differences in extractive foraging behavior are often observed in tool-using primates [86–88]. In the majority of instances, such biases are a matter of degree not kind: one sex might use tools more frequently or with more proficiency than the other, but both sexes show the tool use behavior. Identifying the factors that drive sex differences in tool use is key to understanding how and why tool use traditions first arose, as well as the mechanisms responsible for their maintenance and patterns of transmission. Because tool use spreads between individuals via social learning [9, 12–14], and many species of primates show sex-biased dispersal [89], differences in tool use frequency and proficiency between sexes has important implications for the cultural transmission of tool use behavior between groups of primates.

Considerable attention has been paid to sex differences in tool use in primates, in part because of the hypothesized connection between such behavioral differentiation and the emergence of a sexual division of labor that is so prominent in human societies [90]. However, sex-differences in tool use are not universal. Among the apes, orangutans (*Pongo pygmaeus*) and gorillas (*Gorilla gorilla*), show no reported sex differences in tool use [91, 92], although gorillas rarely show tool use in the wild. Tool-using bird species, for example, New Caledonian crows (*Corvus moneduloides*; [93]) and woodpecker finches (*Cactospiza pallida*; [36]) show little evidence of sex-biased tool use. Where sex differences in tool use by animals do exist, neither males or females consistently emerge as the more frequent or proficient tool users. For example, while sponging behavior in bottle-nosed dolphins (*Tursiops sp.*) is female biased [94], tool use proficiency in captive Goffin cockatoos (*Cacatua goffini*) appears to potentially be higher in males [95]. This variability suggests that different social and/or ecological pressures underlie the patterns of sex-biased tool use we observe across the animal kingdom, raising the question: when and why do sex-biases in tool use emerge?

Energetic requirements — and specifically the high costs of pregnancy and lactation — are hypothesized to play a key role in driving sex-differences in tool use among primates, although they have been invoked to explain both male- and female-biased patterns of tool use. To explain female-biased tool use in primates, researchers have invoked the high nutritional demands of pregnancy and lactation which, they argue, lead to females investing more heavily in learning to use tools that increase their foraging efficiency [88, 96]. Direct evidence supporting this hypothesis, however, is lacking. Female-biased tool use is known to exist in chimpanzees (*P. troglodytes*) and bonobos (*Pan paniscus*), where females acquire skills faster [97, 98], and use tools more frequently and, in some cases, more efficiently than males [97, 99, 100], but these differences have not been explicitly tied to the energetic needs of females. Incongruously, it has also been speculated that the increased energetic demands of pregnancy and lactation might also give rise to male-biased tool use, since males can better sustain the energetic costs of high risk/high reward foraging strategies than females [101]. Among primates, male-biased tool use is found in the *Sapajus* and *Cebus* capuchin monkeys. In bearded capuchins (*Sapajus libidinosus*) and tufted capuchins (*Sapajus* spp.) males use stone tools [26, 27, 102] more frequently than females and only males use probing stick tools [101, 103]. In blonde capuchins (*Cebus flavius*), termite fishing appears male-biased [104]. However, there is currently no direct evidence linking the male-bias in *Sapajus* tool use to the energetic costs of failure. Rather, the male bias in *Sapajus* stone tool use is thought to be due to physical limitations of females, as males open more high resistance nuts than females [27]. Further, sex differences in the male-biased probe tool use behavior of bearded capuchins arise only later in life: while juveniles of both sexes engage in manipulation of sticks, only males develop the probing tool use. This is hypothesized to be the result of a 'sex motivational bias' [86], that is, a stronger motivation in one sex to observe (and by extension acquire) a specific behavior. In the case of probing tool use, male juveniles and adults were more often seen observing the behavior than female juveniles and adults [86].

In addition to differences in nutritional needs, morphological differences can also drive variation in behavior between sexes. In species with marked sexual dimorphism, which includes many primate species [105], the larger sex tends to be more efficient at behaviors that require significant strength. Male-biased nut-cracking by bearded capuchins likely arises as a result of this dynamic. Bearded capuchins show strong sexual dimorphism; female capuchins weigh only 60% as much as males and handle the large stones used for nut-cracking less efficiently [27, 106]. Burmese long-tailed macaques (*M. fascicularis aurea*), which use stone tools to open coastal resources, provide additional evidence that differences in morphology can underlie sex-differences in tool use behavior. Although similar to bearded capuchins in their degree of sexual dimorphism, male and female Burmese long-tailed macaques did not differ in tool use proficiency, but females used smaller hammerstones and targeted more sessile prey than males [87]. Marked sexual dimorphism may thus give rise to sex-based differences in tool use behavior because the smaller sex is physically incapable of using tools, is inefficient enough that the costs of tool use outweigh the benefits, or adopt alternate behavioral strategies, preferentially selecting different tools or focusing on alternate food resources.

Sex differences in behavior do not necessarily arise from differences in morphology; significant evidence suggests that male and female primates also differ in fundamental behavioral tendencies [88]. A meta-analysis found that male primates show higher innovation rates than females [107], although no difference between sexes was found in a long-term study of a large population of white-faced capuchin monkeys (*C. capucinus*; [65]). Higher innovativeness of one sex can be driven by inherent cognitive differences, but may also be a result of sexes facing different constraints and needs in their environment. One sex may be at greater risk of predation, be more risk-averse or engage in more anti-predatory behaviors. For example, female chimpanzees spent more time building nests than males [108] and female and juvenile chimpanzees built their nests at higher, more peripheral locations, potentially to decrease risk of predation [109]. In contrast, in woolly monkeys (*Lagothrix lagotricha poeppigii*), males engage in more vigilance behavior than females [110]. Sex differences in predation risk and risk perception can also lead to variation in tool use behavior. In the case of bearded and tufted capuchins, for example, females are thought to be more vulnerable on the ground where nut-cracking takes place, which may lead them to use tools less frequently than males [111]. Additionally, increased terrestriality correlates with the diversity of tool use repertoires in bearded capuchins [112], suggesting sex differences in time spent on the ground could be a driver in variation between sexes in tool use behavior. While a study that explicitly tested key assumptions of the risk hypothesis found that female and male bearded capuchins did not differ in the amount of time they spent on the ground [101], predation risk may still differ between the sexes and between sites.

Dominance and competition also affect the opportunities of males and females to access resources, perhaps including the sites and materials for tool use. In white-faced capuchins, high ranking group members often displace lower ranking individuals at important food sites and, as a result, energy intake rates vary depending on rank [113]. Competition may be particularly strong when tool use relies on fixed, monopolizable resources, such as anvils, where high-ranking individuals can displace lower ranking individuals for access (e.g., in bearded capuchins, [27, 114]). When one sex is dominant over the other sex, the lower-ranking sex may have limited opportunities to use tools and thus engage in this behavior less often.

Sex-differences in tool use behavior can also arise as a result of sexual selection if, for instance, females favor inventive males or if males display their quality and strength through tool use [101]. For example, female bearded capuchins, who use stone and stick tools during foraging, were found to throw these stones and sticks at males as a part of sexual displays [115, 116]. Further, while tool use for extractive foraging allows access to otherwise inaccessible resources, these benefits are not necessarily limited to the tool user themselves. Other individuals can scrounge during tool-using events if the tool user allows it, or on resulting debris afterwards. Bearded capuchins scrounge on food remains in 24%–35% of nut-cracking events [41, 101], and if females routinely get access to resources in this manner such male provisioning could explain sex differences in tool use frequency. If one sex is already a less frequent tool user, for instance because of physical limitations due to size or strength, easy access to resources opened by tool use might be further incentive to use tools less frequently — thus widening the gap between sexes.

Studies of tool-using primates have, to date, rarely focused on multiple groups within the same population that differ in their patterns of tool use, making it challenging to disentangle the morphological, social, and environmental factors that may contribute to sex differences in behavior. The white-faced capuchin (*C.*

capucinus imitator) population that inhabits the Coiba Archipelago thus provides a rare opportunity to test hypotheses about why such sex-biases arise. Despite decades of studies on white-faced capuchins across multiple field sites [70, 71], stone tool use has only been documented on Coiba and Jicarón, two islands off the Pacific coast of Panama. Here, capuchins habitually use stone tools to open sea almonds, palm fruits, hermit crabs, snails, coconuts, and other resources [30, 31]). White-faced capuchins are generalist foragers that, across their geographic range, show a diverse repertoire of extractive foraging behaviors that are transmitted via social learning [67, 68]. They are sexually dimorphic ($♂_{\text{weight}} = 3.7$ kg, $♀_{\text{weight}} = 2.5$ kg; [117]), and live in multimale, multifemale groups with male dominance and female philopatry. Females exhibit linear dominance hierarchies, while males have no clear hierarchy beyond the alpha male [19, 118, 119]. In some populations, slight sex differences exist in extractive foraging behavior, with males more frequently consuming foods that require such processing [120] and using different techniques than females [69].

Hammerstone and anvil tool use by white-faced capuchins on the island of Jicarón appears to be male-biased similar to probing tool use in bearded capuchins: no instances of female tool use have been reported [30]. This is in sharp contrast to the neighboring island of Coiba, where females routinely use tools [31]. On Jicarón, stone tool use occurs at three types of sites, classified based on debris accumulation due to activity intensity and site erasure (see [30]): (i) elusive sites with no to low accumulation, for example, rocks in the intertidal zone where debris is washed away regularly, (ii) small- and medium-sized accumulation sites in dry streambeds where some debris accumulates before washing away, and (iii) high accumulation sites (from here on referred to as 'anvils'), which are on higher ground away from streambeds and the shore. Anvils are used by tool-using capuchins on a near-daily basis, and are easily identifiable due to the large accumulation of tools and processed food debris. Even with extensive coastal surveys and observations going back over a decade [121], the presence of high accumulation anvil sites appears to be limited to a small stretch of coast on Jicarón (∼1 km; [30]). On Coiba, we have not found any evidence of high accumulation sites, but only of small- and medium-sized accumulation sites in streambeds.

In this study, we examine factors that could account for the apparent male bias in stone tool use in the white-faced capuchin population living on Jicarón island. We first investigate whether the observed sex bias reflects a true difference in the behavior of tool-using capuchins on Jicarón or if it is, instead, a result of biases in our sampling. Data collection on these tool-using capuchins relies heavily on camera traps placed at targeted anvil sites. This biased, targeted sampling collection might not capture female tool use for a variety of reasons, for instance, if females are outcompeted at these sites. To obtain more unbiased data in a variety of environmental conditions, we analyzed data from camera traps deployed along streambeds, where tool use occurs largely on invertebrates (e.g., snails) at ephemeral, small- to medium-sized accumulation sites, as well as in the forest interior where tool use is unlikely to occur.

Using all of our camera trap data from both Jicarón and Coiba, we then test five main hypotheses to explain the male-bias in stone tool use observed in capuchins on Jicarón (Table 1.1). While females are likely physically capable of tool use — juvenile capuchins are prolific tool users [30] and females on the neighboring island of Coiba do use tools [31] — physical differences, including smaller body size, may reduce tool use efficiency [**H1**] leading females to avoid this foraging strategy. Furthermore, if females, especially those carrying offspring, spend less time on the ground due to risk aversion, female tool use might occur but go undetected, either because it happens in the trees (and all camera traps are on the ground [30]) or because it occurs infrequently [**H2**]. Additionally, as anvils and hammerstones can be monopolized [114], it is also possible that females rarely use tools because of within-group competition [**H3**], which would be expected to be particularly high at the high accumulation anvil sites which see intensive daily use by the capuchins. Alternatively, similar to the potential male provisioning described by de A. Moura and Lee [101] female capuchins might not frequently use tools because they instead scrounge on food opened by others [**H4**]. Lastly, female white-faced capuchins might use tools on different food items than males [**H5**], which could go undetected in our initial sampling regime focused largely on one food item (sea almonds, which are the primary food item accessed by males using stone tools). Based on preliminary observations, females on Coiba appear to largely use tools to access freshwater and marine snails and palm fruits (*Bactris major* and *Astrocaryum standleyanum*), whereas sea almond processing appears more opportunistic (B. Barrett, pers. comm.).

1.3 Methods

Data used in this study come from a long-term study of the tool-using groups of white-faced capuchins living on the islands of Jicarón and Coiba, and include camera trap images collected between March 2017 and January 2023.

1.3.1 Study site

Jicarón (2002 ha) and Coiba (50 314 ha) are two of the nine islands and 100 islets that make up Coiba National Park, a designated UNESCO World Heritage site off the Pacific coast of Veraguas Province, Panama. Both have depauperate mammalian communities compared to the mainland and lack mammalian predators [80]. In comparison to mainland populations, white-faced capuchins on Jicarón and Coiba live at unusually high densities [30, 75], and are markedly more terrestrial [76]). Both Jicarón and Coiba were inhabited from 250 CE until the 16th century by indigenous communities, and used as a penal colony from 1919 until 2004 [78]. Currently, there is a small but constant human presence on Coiba in the form of a National Park station and police station, as well as occasional tourism. Jicarón is largely undisturbed without postcolonial human occupation.

1.3.2 Study subjects

White-faced capuchins living on Jicarón and Coiba island are unhabituated, and thus all data presented here originates from indirect means of data collection,

Hypotheses	*Predictions*
H1 – Morphology: Females are physically limited in their ability to use tools	**P1a** – Female and juvenile tool use does not occur **P1b** – Female and juvenile tool use is less efficient than male tool use **P1c** – Females and juveniles use smaller tools than males
H2 - Risk: Females are more risk averse and spend less time on the ground than males, or do not use stone tools on the ground	**P2a** – Adult females are less frequently detected on the ground on camera traps than adult males **P2b** – Adult females are less likely than males to be seen on camera traps in open spaces (i.e., streambeds and close to the coast) **P2c** – Adult females carrying infants will be less likely to be seen in open spaces (e.g. streambeds and close to the coast) than females without infants
H3 – Competition: Females are not observed using tools because they are competitively excluded from (especially high accumulation) anvil sites	**P3a** – Displacements at high accumulation anvil sites are common **P3b** – Females are displaced at high accumulation anvil sites **P3c** – Female tool use occurs at elusive, small- and medium-sized accumulation anvils sites such as in streambeds
H4 – Scrounging: Females do not frequently use tools because they scrounge on food opened by others	**P4a** – Females scrounge on items opened by tool users during the tool-using event **P4b** – Females often forage on anvil debris left over after tool use by group mates
H5 – Diet: Females are not observed using tools because they use tools on different food items than males.	**P5a** – If we observe female tool use on Jicarón, it will (like on Coiba) be on snails in streambeds and palm fruits and not on sea almonds

Table 1.1: Overview of hypotheses and predictions

primarily via the deployment of camera traps. The group size of the Jicarón tool-using group appears to be between 20 and 25 individuals, with at least 5 adult males and 5 or 6 adult females (fluctuating throughout the data collection) (for details on group identification, see [122]). Less is known about the tool-using group on Coiba island, so we cannot make estimates of group size or composition. Sex of adults and subadults can reliably be determined from camera trap footage, but estimating sex of juveniles is not reliable. Juveniles can only be sexed using clear photos of the genitalia, and this has an inherent male-bias. We identified several subadult male capuchins and juvenile male capuchins, but only one subadult female and no juvenile females, so we make no distinction between male and female subadult and juvenile capuchins in our analyses.

1.3.3 Data collection

Camera trapping protocol

On Jicarón, camera traps have been placed in the tool-using group's range continuously since March 2017 (with a gap in data collection in 2020 due to the COVID pandemic, see Table A.1 for details on camera deployments). Initially, most camera traps were placed on targeted locations at tool-using anvils and in sea almond groves. However, in 2021, we placed additional cameras along streambeds and at randomly selected locations, to reduce the bias in our sampling by capturing areas where tool use was either more ephemeral (streambeds) or entirely absent (random locations). Furthermore, in 2022, we placed a grid of 24 cameras spaced at 100 m in the tool-using group's range. On Coiba, we have placed camera traps in the tool-using group's range intermittently since March 2019. We use still (Reconyx Hyperfire HC600 & HF2X) and video (Reconyx Ultrafire XR6 & XP9) camera traps, with infrared rather than white flash to minimize animal disturbance. Per trigger event, still camera traps recorded 10 images on Rapidfire mode with ~1 s between images and no between-trigger delays. Video cameras recorded over a 24-h period, and per trigger recorded one image and either a dynamic or a static video. During a dynamic video recording, the camera trap stops after 3 s of inactivity, and is retriggered by additional movement within 27 s from stopping. Dynamic videos can be of varying lengths, with a maximum length of 30 s, while static videos record one video of a set length of 30 s per trigger. Of our 15 deployed video traps, 2 were static.

On Jicarón, we surveyed 61 camera locations (11 anvil, 13 streambed, 37 random). Anvil cameras were directed at anvils (high accumulation anvil sites). Streambed cameras were placed both at suspected small- and medium-sized accumulation sites in streambeds and at other streambed locations within the tool-using group's range without clear evidence of previous tool use. Random cameras were placed in three ways: (a) paired with a stream camera, placed by walking approximately 15 m away from the streambed camera perpendicular to the stream on whichever side of the stream the terrain was accessible, (b) at random locations in the landscape within (what we estimated to be) the tool-using group's range, or (c) as part of a 24 camera grid placed in the tool-using group's range at 100 m spacing. All random cameras were deployed on an available tree facing a random direction. A total of 94 cameras (79 stills and 15 videos) were deployed during the sampling period. 46 of these camera deployments had a single sampling period, the other 15 were sampled repeatedly (between 2 and 6 deployments in the same location). Cameras were collected and deployed twice a year around March and December, and not all cameras ran until pick-up so sampling was not fully continuous. Per camera, the average duration of sampling nights was 135.6 (range 10–256), totaling 12 748 sampling nights (anvil = 3129, streambed = 3120, random = 6499).

On Coiba, we surveyed nine camera locations, all of which were streambed sites where we placed still cameras for a single sampling period. In contrast to our sampling on Jicarón, streambed cameras on Coiba were placed at locations where we saw physical evidence of tool use in the streambed. Further, we never observed any high accumulation anvil sites on Coiba, so placed no anvil cameras, and the logistical challenges posed by the terrain made it impossible to place random cameras. Altogether, this led to less sampling effort on Coiba than on Jicarón, with per camera, the average duration of sampling nights being 145.4 (range 28–190), totaling 1309 sampling nights.

Data processing and behavioral annotation

All images and videos were compiled into sequences, where one video is a single sequence, and all bursts of images triggered within 30 s of one another are combined into one sequence. Sequences were coded in Agouti, an online platform for archiving and annotating camera trap data [123].

Per sequence, we identified which animal species were visible and recorded the number of individuals per species. For white-faced capuchins, we coded the age class (adult, subadult, juvenile, infant) and sex of each individual, and assigned an individual ID whenever this was possible. We were able to successfully sex 90% of observed adult capuchins (compared to 63% of subadults and 13% of juveniles). For 25% of all observed capuchins ($n_{\text{total}} = 33\ 465$), we were unable to reliably assign sex or age, largely because these individuals were only partially in view (e.g., only a tail) or inspecting the camera so closely that they were unidentifiable. For every individual capuchin in a sequence, we coded which behavior(s) best described their activity in the majority of the sequence (for ethogram see Table A.2). More active behaviors took precedent over passive behaviors, i.e., we only coded 'resting' if this was truly the only thing the capuchin did in the sequence. If they foraged, even briefly, this was coded instead. We calculated the distance of each camera site on Jicarón to the coast by taking the distance from a camera's GPS point to the nearest coastal vegetation boundary (for more details see [122]).

For analyses, we only considered sequences containing capuchins ($n_{\text{Jicarón}} = 18\ 353$, $n_{\text{Coiba}} = 395$). Since camera traps only capture snapshots in a limited spatial area of the environment, an absence of triggers does not necessarily mean that no capuchin was present in this area (and camera traps also do not always trigger fast enough to capture a traveling animal). We also excluded days on which cameras were deployed and collected from analyses, as the human presence on these days could affect capuchin behavior. All statistical analyses were done in R v. 4.2.2 [124].

Statistical analyses

To evaluate whether females are physically incapable of tool use or whether females and juveniles are less efficient than males (**H1**), we examined tool use events on Jicarón in detail through frame-by-frame coding of video observations in `BORIS` v. 8.14 [125]. For each tool-using sequence (the opening of a single item), we assessed (a) the number of pounds, and (b) the time in seconds required to open the item, as well as (c) the number of misstrikes. Additionally, we examined the frequency of female tool use on Coiba (where we only recorded the number of sequences containing tool use and were unable to do detailed frame-by-frame coding due to the distance of tool use events from the camera).

To assess whether females (with and without infants) are less likely to be detected on the ground, particularly in "riskier" open areas such as streambeds or closer to the coast (**H2**), we employed two hierarchical logistic regressions per island, (i) comparing the ratio of females to males and (ii) comparing the ratio of females with infants to females without infants. Females with infants are categorized as such if they are observed providing infant care such as nursing or carrying an infant dorsally or ventrally (Table A.2).

All logistic regressions were fit using Bayesian regression modeling with `Stan` [126] via the `brm` function in the `brms` package v. 2.16.1 [127], and included only sequences with adults present where at least one of the adults was successfully sexed ($n_{\text{Jicarón}} = 6603$, $n_{\text{Coiba}} = 252$). First, we compared the ratio of adult females to adult males at the three location types (anvil, streambed, and random cameras) on Jicarón. In this logistic regression, the number of 'successes' was the number of females observed in a sequence and the total number of adults observed in a sequence was the number of trials. This allows us to obtain the ratio of adult females to adult males. For predictors, we estimated the effect of the type of location (random, anvil or streambed, with random as reference level) and the distance of each specific location site to the coast. We also included the specific site of the camera deployment as a random effect, and compared our findings to the ratio of adult females to adult males on Coiba (where all cameras are streambed cameras).

To compare adult females with infants to those without, we fit another logistic regression with the same structure, but where the number of successes was the number of adult females with infants, and the trials the total amount of adult females in the sequence. Here, only sequences were included where at least one adult female was present ($n_{\text{Jicarón}} = 2329$, $n_{\text{Coiba}} = 209$). We again included the specific site of the camera deployment as a random effect, as well as the month of the year to account for seasonality in births. We compared the results of this model to the ratio of adult females with infants to adult females without infants on Coiba, month was not included in the Coiba model due to limited data collection throughout the year.

To test whether females are being outcompeted at anvils (**H3**), we quantified competition at anvils on Jicarón through the number of displacements observed, where a displacement means that one individual supplants another from the tool anvil and/or hammerstone (see Table A.2). We considered the actual number of displacements in relation to the opportunity for displacement, quantified as the number of sequences when individuals of the age-sex class were at an anvil with at least one other individual present. We further considered the opportunity for adult females to use tools by examining how frequently adult females were observed at anvil sites without adult males present (under the assumption that this would be a situation of low competition).

To examine whether females do not frequently use tools because they scrounge on food opened by others (**H4**), we compared the likelihood of different age-sex classes to scrounge during tool-using events or on anvil debris by comparing the frequency of observed scrounging to the opportunity to scrounge. For scrounging during tool-using events, the number of opportunities to scrounge is reflected by the number of sequences a capuchin was present at an anvil together with a tool user. Opportunity to forage on anvil debris were all sequences where a specific age-sex class was present at the anvil, regardless of how many other capuchins were present.

In a first investigation of whether females use tools on different food items than males (**H5**), we used data from Coiba as a comparator. We deployed camera traps in the streambeds on both Jicarón and Coiba to quantify tool use away from anvils (i.e., in small- to medium-deposition sites. Due to the limitations of camera traps in inferring diet (e.g., not capturing all items consumed, bias toward observing consumption of larger food items), our examination of sex differences in diet is necessarily limited.

All models were fit with regularizing Normal (0,1) priors for intercepts and predictors, and exponential (1) priors for standard deviations of varying effects. We performed a prior predictive simulation to visualize the predictive implications of the priors and evaluate identifiability of parameters. We ran the final models with three chains, each having 3000 iterations, including a warm-up period of 1500 iterations per chain. Our models were stable with large effective sample sizes (Bulk_ESS and Tail_ESS over 1000 for all estimates; [127]) and Rhat values <1.01 [128]. For all models, Pareto k estimates were below 0.5. We used the posterior predictive check function to visually assess model fit and confirm our choice of priors.

1.4 Results

1.4.1 H1: Females are physically limited to use tools

We observed no instances of female tool use on Jicarón in the 5 years of camera trap data we have collected (12 748 sampling days, 18 353 sequences with capuchins), compared to 1453 tool use events by adult males, 694 by subadults and 2594 by juveniles. On Coiba, we observed adult females use tools 11 times (1309 sampling days, 395 sequences with capuchins), which is more than we observed for adult males (3 times), subadults (4 times), or juveniles (3 times).

Based on a preliminary comparison of the time and number of pounds required to successfully open an item in 339 tool use sequences on Jicarón, juveniles are less efficient (mean from raw data 5.9 pounds [range 1–34], 24.8 s [range 3.1–180.8]) than adult males (mean 3.8 pounds [1–14], 10.2 s [2.6–44.8]). Nonetheless, juveniles used the same hammerstones as adult males (mean weight of all measured hammerstones on Jicarón is 660 g [n = 174]), and longer processing times by juveniles can also be a result of less experience using tools.

1.4.2 H2: Female tool use is limited due to increased risk aversion

Ratio of adult females to adult males

Our model comparing the ratio of adult females to adult males estimated considerable differences between all three location types (Figure 1.1, see Table A.3 for estimates). Based on our estimates of the true ratio of adult females to adult males in the group (five adult males and five or six adult females; 0.50–0.55), both sexes were equally as likely to be seen on the ground at random cameras (Mean = 0.56 [95% CI: 0.50–0.62]). The ratio of adult females to adult males at streambed cameras (Mean = 0.38 [95% CI: 0.30–0.47]) was considerably lower than at random cameras (posterior probability exceeding 95%). At anvils we observed the lowest ratio of adult females to adult males (Mean = 0.33 [95% CI: 0.21–0.47]), considerably lower than at random cameras, but comparable to streambed cameras. On Coiba, where all cameras were placed on streambeds, the ratio of adult females to adult males was higher than at any of the location types on Jicarón (Mean = 0.76 [95% CI: 0.61–0.85], Table A.4 and Figure A.2).

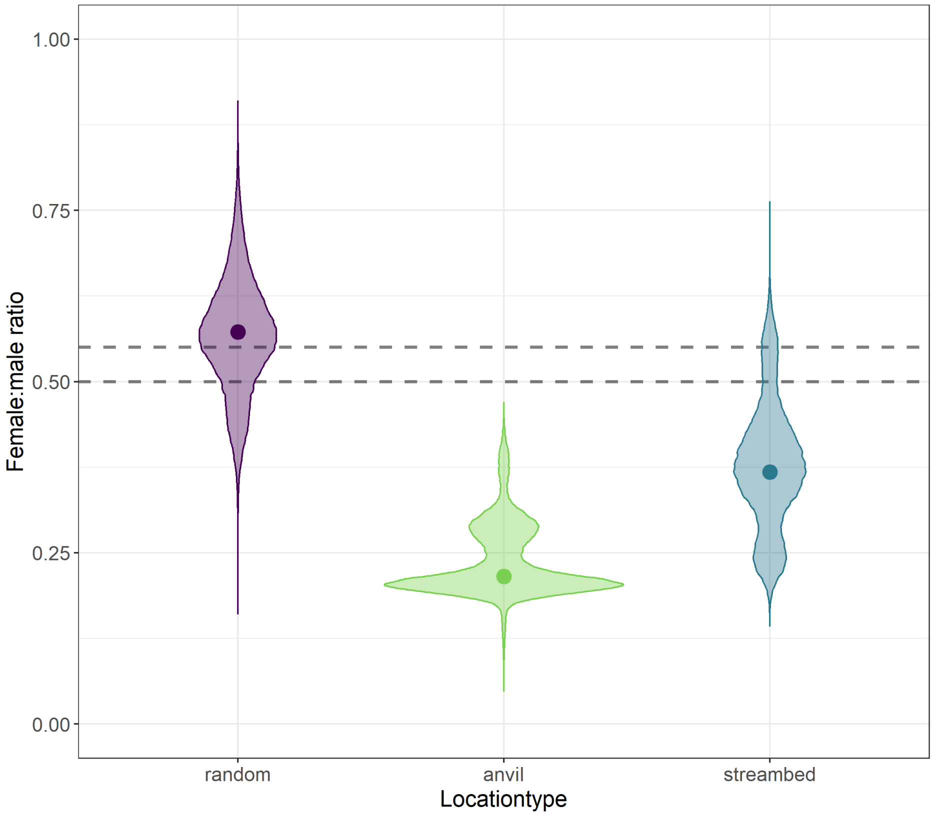

Figure 1.1: Model estimates and mean values of the ratio of adult females to adult males at each location type (random, anvil, streambed). Model estimates are reflected by violin plots, and observed means from data are represented as points. Dashed horizontal lines represent range of the estimated true ratio of adult females to adult males based on how many distinct individuals are present in the group (5 or 6 adult females and 5 adult males).

The interaction effect of distance to coast and anvil sites (Mean = 1.00 [95% CI: 0.17–2.12]) has a 96% probability of being positive (>0) and is a moderate effect, indicating that adult females were slightly less likely to be seen at anvil sites closer to the coast compared to those further inland (Figure 1.2). At both random (Mean = 0.05 [95% CI: -0.07–0.16]) and streambed cameras (Mean = 0.23 [95% CI: -0.22–0.67]), the interaction with distance to coast was also estimated to be positive (77% posterior mass for random cameras, 84% for streambed cameras), but these positive relationships were weaker and less reliable. Note that anvil sites are limited to the coast, and the range of camera distances varied between the location types (random = 8.1–328.3 m, anvil = 0.8–30.8 m, streambed = 25.2–140.4 m).

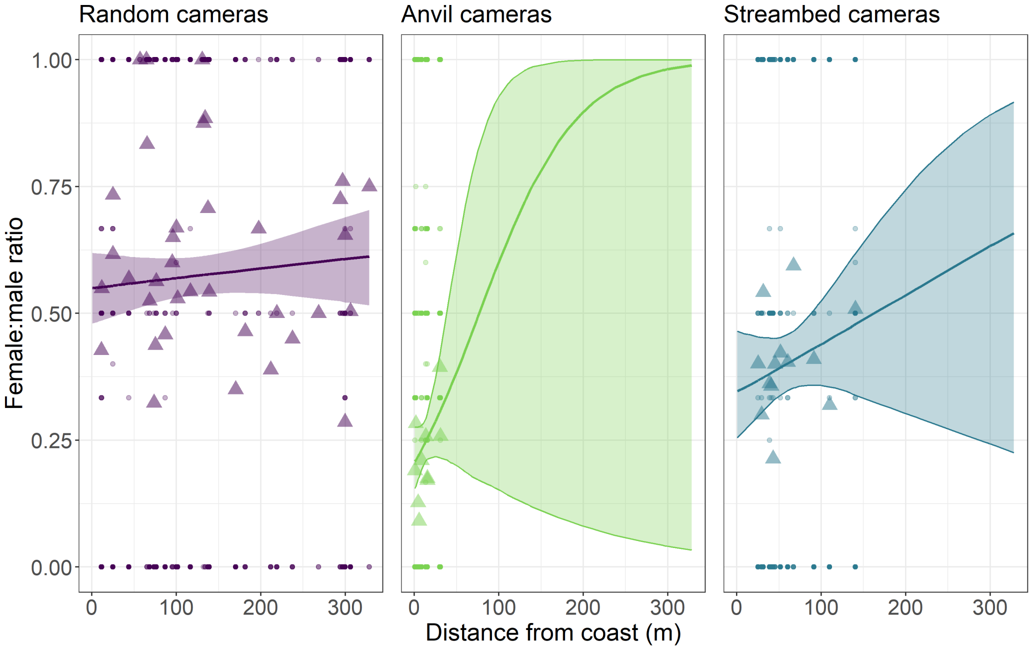

Figure 1.2: Marginal effects of the type of camera location (random, anvil, or streambed) and the distance to coast on the female to male ratio. Lines indicate the marginalized median sex ratio from model predictions, with the ribbon reflecting the 95% CI. Triangles represent the empirical means per camera trap. Circles are raw datapoints.

Ratio of adult females with infants to adult females without infants

There were no strong differences in the ratio of adult females with infants to the ratio of adult females without infants between any of the three location types (Figure 1.3, see Table A.5 for model estimates). Adult females with infants were less likely to be seen than adult females without infants at random cameras (Mean = 0.21 [95% CI: 0.15–0.28]), streambed cameras (Mean = 0.27 [95% CI: 0.18–0.38]) and anvils (Mean = 0.16 [95% CI: 0.08–0.29]). We do not know the true ratio of adult females with infants to adult females without infants, so can only compare between locations. At the streambed cameras on Coiba, the ratio of adult females with infants to adult females without infants was lower than at any of the location types on Jicarón (Mean = 0.08 [95% CI: 0.01–0.37], Table A.6 and Figure A.5).

We find that adult females with infants were more likely to be seen at anvil sites

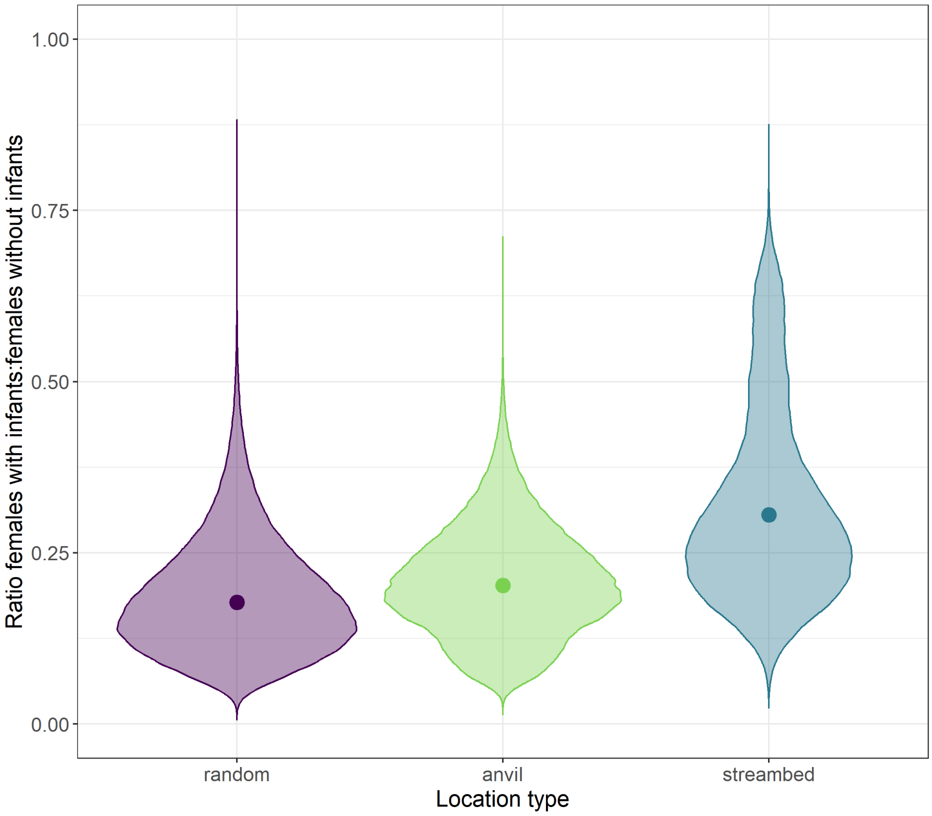

Figure 1.3: Model estimates and mean values of the ratio of adult females with infants to adult females without infants at each location type. Model estimates are reflected by violin plots, and observed means from the data are represented as points.

closer to the coast than at those further inland (Figure 1.4). The interaction effect of distance to coast and anvil sites (Mean = -0.52 [95% CI: -1.89–0.97], 75% of posterior <0) is a moderate negative effect. At random cameras, the negative effect is smaller and less reliable (Mean = -0.08 [95% CI: -0.25–0.09], 80% of posterior <0). At streambed cameras, the positive relationship is reliable and of moderate size (Mean = 0.75 [95% CI: 0.12–1.36], 99% of posterior >0). Thus, adult females with infants were considerably less likely to be seen at streambed cameras closer to the coast than at streambed cameras further inland.

Both models indicated considerable variation between camera locations and the second model indicated monthly variation in the ratio of females with infants to females without females (see Figure A.1 and Figure A.3 for model estimates per camera location, Figure A.4 for model estimates per month).

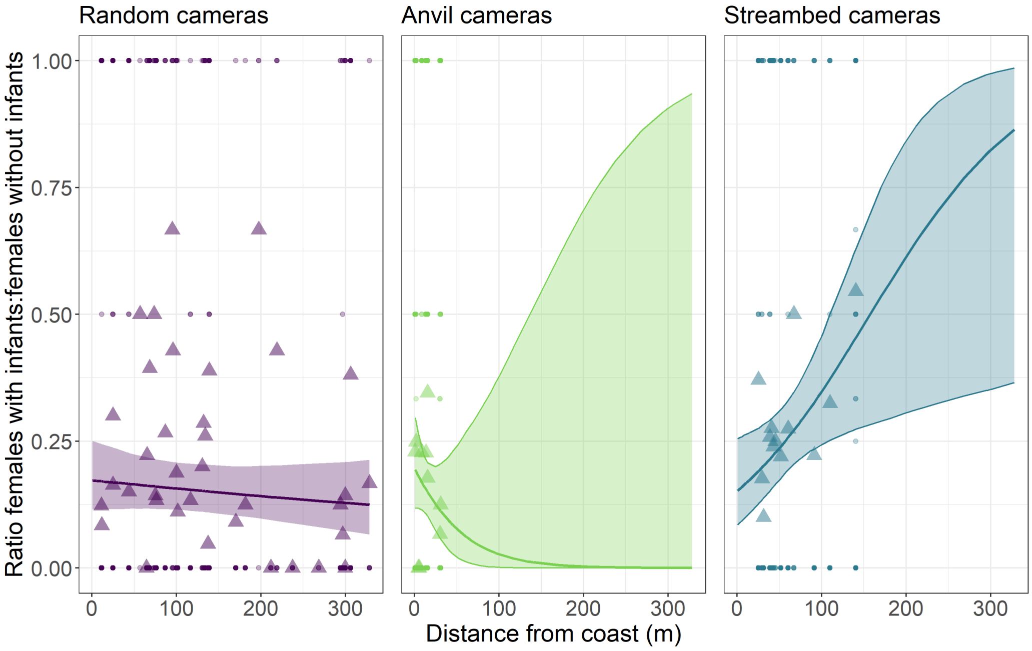

Figure 1.4: Marginal effects of the type of camera location (random, anvil, or streambed) and the distance to coast on the ratio of adult females with infants to females without infants. Lines indicate the marginalized median sex ratio from model predictions, with the ribbon reflecting the 95% CI. Triangle points represent empirical means per camera trap, and round points are raw datapoints.

1.4.3 H3: Females are outcompeted at tool use anvils

Direct competition at anvils on Jicarón appears to be extremely low. We observed capuchins at anvil sites in 12 274 sequences, and in less than half of those (5184 sequences) more than one individual was present, meaning there was an opportunity for displacements to occur. Despite these opportunities, displacements were rare, occurring only 92 times (1.77% of all displacement opportunities).

Direct competitive dynamics over anvils likely cannot explain why adult females do not engage in stone-tool use. They were rarely displaced themselves (Figure 1.5), and were also observed to displace other (primarily juvenile) members of the group. Further, adult females were observed at anvil cameras in 736 sequences without any adult males present who could outcompete them (under the assumption that females would mostly be outcompeted by adult males and not by juveniles). In 638 of these sequences, there were also no juveniles using tools, so the female(s) could easily access the anvil. On Coiba, we observed no displacements, despite 141 opportunities for displacement (i.e., more than one capuchin present in a sequence).

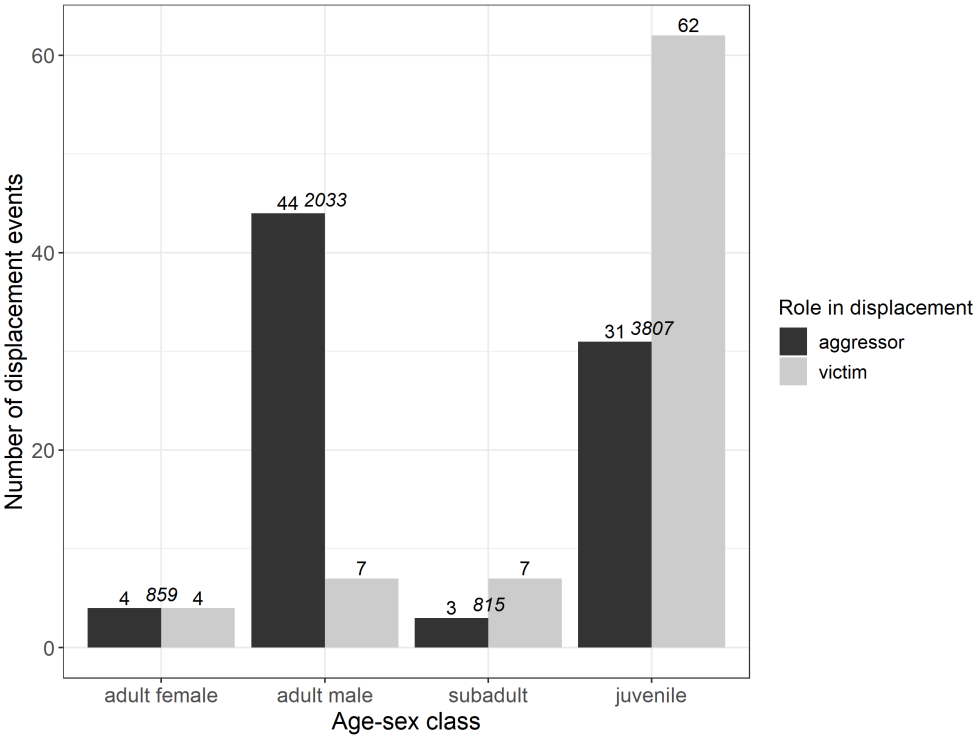

Figure 1.5: Number of times each age-sex class was observed being the aggressor (black bar) or victim (gray bar) in a displacement event. Events when we could not identify the age-sex class of the aggressor (n = 10) or victim (n = 12) are excluded. Italicized numbers reflect the number of events where at least two individuals were present in a sequence, representing opportunities for displacement events to have occurred.

1.4.4 H4: Females frequently scrounge on food opened by others

Resource scrounging during tool-using events was rarely observed, occurring in 3.5% of all opportunities (Table 1.2), and adult females were only observed scrounging on two occasions (1% of their opportunities). The lack of scrounging does not appear to be related to tool users refusing to tolerate scrounging. Foraging on anvil debris left over after tool use was similarly rare (occurring in 5.1% of opportunities). In both situations, juveniles, subadults, and adult males were more likely to scrounge during tool use or forage on anvil debris than adult females.

Age-sex class	Observed events	Opportunities	Percentage
Scrounging during tool use events			
Adult female	2	205	1%
Adult male	17	801	2.1%
Subadult	4	348	1.1%
Juvenile	83	1396	5.9%
Unknown	5	391	1.3%
Scrounging on anvil debris			
Adult female	43	1224	3.5%
Adult male	211	3900	5.4%
Subadult	71	1658	4.3%
Juvenile	761	9954	7.6%
Unknown	74	6001	1.2%

Table 1.2: Proportion of times each age-sex class was observed scrounging during a tool-using event or on anvil debris afterwards

1.4.5 H5: Females use tools on different resources than males

Despite a total of 3120 sampling nights at 13 streambed camera locations, we did not observe any tool use on snails or other bivalves by adult females on Jicarón. In contrast, all observed female tool use events (n = 11) by females on Coiba were on snails or other invertebrates in the streambed. Males on Jicarón were mostly observed using tools at high accumulation anvil sites, which are away from streambeds and close to sea almond groves (1439 instances of tool use across 3129 trapping days). At streambeds, adult males also used tools to process invertebrates, but this was less frequently observed (12 instances of tool use across 3120 trapping days).

1.5 Discussion

Stone tool use by white-faced capuchins on Jicarón island is strongly male-biased. We observed no instances of female tool use on Jicarón in more than 5 years of data collection with camera traps at different locations in the tool-using group's range (totaling 12 748 camera trapping days), and despite the fact that females regularly use stone tools on the neighboring island of Coiba. Differences in physical capacity, risk-aversion, competition, or scrounging behavior cannot account for the observed differences in tool use among males and females in the Jicarón population.

Sampling biases are unlikely to explain the observed differences in female versus male tool use behavior, given the temporal and spatial depth of our data. Female capuchins are less frequently seen at anvil sites than male capuchins, but at the 13 cameras placed at streambeds and 37 cameras placed on random locations we saw comparable female and male activity. On the neighboring island of Coiba, capuchins — including adult females — use tools at small- to medium-sized accumulation sites in streambeds. Although we only monitored a subset of the streambeds on Jicarón, we would have captured evidence of female tool use if female capuchins on Jicarón use tools at comparable rates to males or females living on Coiba. Our findings indicate that the sex bias in tool use we observe in our data almost certainly reflects a real behavioral difference, and that adult female capuchins in the tool-using group on Jicarón rarely use stone tools (if at all).

1.5.1 Adult females are physically capable of tool use

Adult female capuchins are almost certainly physically capable of stone tool use, as evidenced by the frequent tool use of juveniles who, although smaller than adult females, regularly use the same hammerstones as adult males, and tool use by adult females on the neighboring island Coiba. Comparable to macaques [87] and *Sapajus* capuchins [27], adult female tool users might employ different size hammerstones and/or be less efficient than adult males due to differences in size or strength. In other populations of white-faced capuchins, adult males engage in more extractive foraging of *Luehea* and *Sloana* fruits than adult females, perhaps because of the strength required to break fruits off their stems [69]. However, as we observed juveniles successfully using the same size hammerstones as adult males, physical strength is unlikely to be a limitation for tool use by adult females in this population.

1.5.2 Adult females have opportunity to use tools

Adult females, both with and without dependent offspring, were just as likely to be seen on the ground as adult males at random cameras in the vegetation, similar to findings by A. de Moura and Lee [101]. The lower likelihood to observe adult females at anvil sites and streambeds is likely not due to risk, but rather a consequence of the lack of tool use by females and/or less interest in consuming sea almonds than males. Both sexes of capuchins on Jicarón appear to have low risk aversion, given their generally high degree of terrestriality and investigation of camera traps [76], which could be related to the absence of mammalian predators on the island [80]. However, even though males and females are similarly terrestrial, females could still show different behavior while on the ground (e.g., be more vigilant and less likely to engage in conspicuous behavior like tool use) due to a higher perceived risk than males. Our finding that adult females are less likely to be seen at cameras closer to the coast compared to further inland, particularly at anvil sites, also appears unrelated to risk: sea almonds, the main food type stone tools are used to access on Jicarón, are a coastal species that is abundant along the coast and absent inland. Furthermore, the ratio of adult females with infants to adult females without infants was comparable between location types. Adult females with infants being more common at anvils closer to the coast could be due to the social dynamics in the group: adult males spend more time using tools at coastal anvils than further inland, since sea almonds are a coastal species, consequently the whole group might spend more time in this area than at less suitable anvils. The opposite relationship we observe for streambed cameras, females with infants being more likely to be seen inland, could be capturing that some feature of the streambeds is mitigated by distance to the coast (for instance, freshwater shrimp are more common upstream than at the entrance of streams where water is more brackish).

Adult females were less likely to be seen at anvil sites than at streambeds and random cameras, which would suggest that potentially they are being outcompeted at anvil sites. However, displacements at anvils were strikingly uncommon. In nearly half of all tool-using events, only one tool-using individual was seen in the camera trap photos. This suggest that either competition at anvils is not particularly high (in contrast to [114]), or competition is resolved via behavioral mechanisms other than displacement such as increasing interindividual foraging distances. The apparently solitary nature of stone tool use makes it unlikely that it serves a display function driven by sexual selection as suggested in bearded capuchins [101]. Additionally, adult females evidently have access to anvil sites, which is reflected by the large number of sequences with adult females being the only capuchin in frame at an anvil site.

1.5.3 Adult females might have different diets than adult males

The near absence of scrounging and consumption of anvil debris suggests that adult females in the Jicarón tool-using group may spend less time at anvils because they are not interested in consuming the resources available there (unlike findings in *Sapajus* capuchins [41, 101]). At high accumulation anvil sites on Jicarón, sea almonds are the primary resource consumed. On Coiba, female tool use is largely focused on snails, palm fruits and other invertebrates in streambeds — sea almond consumption is opportunistic and, unlike on Jicarón, does not involve active transport of food items, but instead focuses on washed up fruits. Further research, for instance by using DNA barcoding, is required to test whether female and male capuchins on Jicarón truly have different diets, as the data we currently have available do not allow us to conduct detailed dietary comparisons. Previous research on other populations of white-faced capuchins did find sex differences in diet and foraging, with females spending more time foraging than males, females consuming more embedded invertebrates than males, and pregnant and lactating females focusing on foods that required little handling [129]. Later research indicated that apparent sex differences in foraging, specifically differences in invertebrate foraging, might be a consequence of sex related variation in color vision: male capuchins all have dichromatic color vision, while females can have di- or trichromatic vision [130]. Trichromatic females spent more time foraging on insects because they can spot them less well than males and dichromatic females, who showed similar foraging times but were more efficient foragers. However, this difference may be mediated by energetic requirements of reproduction, as a later study found that nursing females foraged less overall than cycling females and di- and trichromats did not differ in time spent foraging on different food types [131].

1.5.4 Development of male-biased stone tool use

Our results indicate that adult female capuchins on Jicarón are physically capable of tool use, frequently use terrestrial substrates where tool use would be possible, and have access to anvils where such hammerstone tool use occurs. Nonetheless, we find no evidence that females in this population use tools. Differences in diet between sexes might lead to female tool use being undetected, but even if females use tools on snails instead of sea almonds female tool use would likely have been detected by our camera traps in streambeds. However, the intertidal zone is also an area where tool use occurs on Jicarón (pers. obs.) where we are unable to record behavior with camera traps, so if female tool use would occur exclusively on marine resources in the intertidal we would miss it with our current sampling regime. Yet, we would expect tool use to not be limited to one area, but used flexibly on comparable resources in different locations like streambeds or at high accumulation anvil sites, given the propensity of white-faced capuchins in other sites to apply similar food processing behavior to several resources with comparable structural defenses [65, 66].

Given 5 years of sampling, it appears most likely that adult females on Jicarón do not use tools at all, or only very rarely, comparable to the sex bias in bearded capuchin' probe tool use [86]. Similar to the probing tool use, female capuchins on Jicarón might engage with tools as juveniles yet stop or reduce the frequency of this behavior once they mature. As we cannot reliably identify female juveniles, this hypothesis is as of yet untestable in this study system, but seems likely given the large number of juveniles we observe using tools. The mechanism triggering a cessation in tool use by mature female capuchins could be, as shown in the bearded capuchins, a stronger motivation of one sex to observe or acquire specific behavior [86], potentially driven by a higher tendency of male capuchins to engage in pounding behavior [69]. Alternatively, the onset of the sex difference in tool use may be linked to females caring for dependent offspring. Carrying an infant might interfere with an individual's ability to use stone tools due to limitations to movement and increased risk of the infant of falling off or being injured. However, in bearded capuchins, females are seen nut-cracking while carrying offspring [132], and we have some observations of male capuchins using tools while carrying a juvenile dorsally or even ventrally (pers. obs.), suggesting infant carrying and stone tool use are not wholly incompatible.

1.5.5 Possible explanations for strong differences in sex-biased tool use between islands

Why female capuchins on Jicarón do not use tools and both sexes on Coiba use tools is as of yet unknown. Whether this stark behavioral difference is a flexible behavioral adaptation to different ecological conditions (i.e. dietary richness, interspecific competition, population density) between islands, or a side effect of some other difference is social behavior or genetic difference remains unclear. One possible explanation lies in a reversal or change of dispersal tendency, as suggested by Barrett et al. [30]. Changes from a species' 'common' dispersal tendency — male-biased dispersal in white-faced capuchins [133] — to something else, has been observed in other populations of white-faced capuchins [134] and can occur under high density conditions [89] — conditions which appear met on Jicarón island where capuchins occur at unusually high densities compared to mainland populations [30, 75]. However, it is challenging to make predictions as to exactly when dispersal patterns can switch as there remains a gap linking quantitative theory of dispersal and empirical study of sex-biased dispersal [135]. Important factors likely affecting sex-biased dispersal include population density, competition for limited resources, timing of breeding, dispersal mortality, and resource-sharing/territorial overlap, and inbreeding avoidance or attraction: all things that might differ in island, compared to well-studied mainland, populations. If females learn how to use tools and do so rarely, but subsequently disperse from their natal tool-using group, then tool use might be less likely to spread. Alternatively, differential sex-linked mortality could explain the observed pattern on Jicarón. Rare, deleterious traits are common on islands, including Coiba, where albinism has been reported in white-faced capuchins [136].

1.6 Conclusion

Tool use by adult female capuchins in the group of stone-tool-using capuchins on Jicarón appears to be entirely absent, rather than undetected. None of the conventional hypotheses can explain the lack of female tool use: females are physically capable of tool use, present at tool-using sites, and have access to tool-using materials and resources. Despite having ample opportunity, females show also little interest in scrounging on leftovers of stone tool use. Although we are limited in our understanding of the development of this sex bias since we cannot yet reliably sex juveniles, our findings suggest that adult female white-faced capuchins on Jicarón might have a different diet than male capuchins, or learn how to use tools as juveniles but are limited by infant-care as adults, migrate out of the tool-using group, or experience differential sex-linked mortality. Further evidence, particularly DNA analyses of diet and relatedness, is required to illuminate which of these hypotheses might hold true. Causal mechanisms for these sex differences likely have different implications for the origin and maintenance of tool use within the tool-using group, and its potential transmission between groups. Our findings show that there is great intragroup variation in the tool use behavior on Jicarón island, which might explain why there is also such stark intergroup variation.

1.7 Data availability

For full model specifications and details, see section A.2 and associated reproducible `R` code [137].

1.8 Acknowledgments

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Chapter 2

Development and social dynamics of stone tool use in white-faced capuchins

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2.1 Abstract

Percussive tool use for extractive foraging allows animals to access otherwise inaccessible resources and forage more efficiently, with potentially important implications for their fitness. The development of tool use proficiency has been well-documented in nut-cracking chimpanzees and robust capuchins, and in shellfish-cracking long-tailed macaques, where mothers and proficient tool users are the most important models. However, little is known about how tool use develops in populations where opportunities for social learning are scarce. White-faced capuchins (*Cebus capucinus imitator*) on Jicarón Island, Panama, provide a unique case to consider this question: stone tool use is entirely male-biased, meaning juveniles cannot learn from their mothers, and reduced group cohesion further limits social learning opportunities. Here, we investigate the acquisition and development of stone tool proficiency in this population using a year-long dataset from camera traps placed at two experimental anvils. We assess differences in proficiency between age classes, examine the development of tool use proficiency over time, and explore patterns of social attention during tool use. We show that juvenile capuchins are less proficient than subadults and adults, but their proficiency remains stable over the course of one year, suggesting that skill development may require prolonged practice or physical maturation. In contrast to other primates, social learning opportunities on Jicarón appear limited and scrounging is rare, yet we do find robust patterns in

social attention when it occurs. Social attention to tool use mostly comes from juveniles too young to use tools themselves, who observe proficient subadults that tolerate scrounging. Our results contribute to the understanding of how complex tool use behaviors are acquired and maintained in primates, highlighting the role of social tolerance in the development of proficiency.

2.2 Introduction

Tool use is a striking example of behavioral flexibility in animals, and the use of tools for extractive foraging can increase fitness by allowing faster access to a greater variety of resources [5]. However, depending on the complexity of the tool use behavior, reaching proficiency is a process which can take years [139]. A behavior is considered tool use when an animal i) uses an object which is not part of their own body, ii) which is unattached to the surrounding environment (or attached and manipulatable [6]), and iii) the animal manipulates the object to reach a useful outcome [17]. To describe complexity of tool use behavior, a distinction can be made between first-order tool use (involving a single object, e.g., pounding a nut on a fixed surface) and second-order tool use (involving two objects, e.g., pounding a nut on a fixed surface using a hammerstone) [19]. Second-order tool use is thought to reflect greater cognitive complexity, as it requires more planning and physical coordination to correctly bring together all separate objects to obtain the desired outcome. Percussive stone technology — particularly extractive foraging using hammerstone and anvil tool use — is the focus of much research, given its high level of complexity, but also its relative rarity in the animal kingdom despite its prominent role in human evolution [21]. The only non-human wild primates that regularly use stone tools for extractive foraging are chimpanzees (*Pan troglodytes* [23]), long-tailed macaques (*Macaca fascicularis* spp. [24, 25]), robust capuchins (*Sapajus* spp. [26–29]), and gracile capuchins (*Cebus* spp. [30–32]). Examining how stone tool use is acquired and how proficiency develops is key to understanding how a tool use tradition is maintained within a group, as well as how it spreads between groups.

For particularly complex techniques like percussive stone technology, acquisition of the skill may require sufficient exposure at a young age. In chimpanzees, insufficient exposure to nut-cracking during a critical learning period (between 3-10 years) may hinder or completely impede learning of the behavior in adulthood [40, 43, 44]. In robust capuchins [140] and macaques [49], acquisition of tool use also mostly occurs early in life. Exposure to tool use has an important social component: in both chimpanzees and robust capuchins, immature individuals are thought to acquire nut-cracking via social learning processes such as local enhancement, emulation, and social facilitation [12, 40–42]. Though social learning has been argued not to be critical to the acquisition of nut-cracking in captive chimpanzees [141], evidence from wild chimpanzees continues to support its important role [142].

In chimpanzees, most transmission of tool use behaviors occurs from mothers to their offspring [143, 144]. Juveniles spend a great deal of time with their mothers during the sensitive learning period, and mothers are highly tolerant of their offspring observing their tool use events and scrounging on opened nuts. There is also some evidence of female chimpanzees providing learning opportunities for their offspring through 'scaffolding' (sharing nut-cracking materials such as hammers with their offspring) [145]. In contrast, robust capuchins mothers were not common models to their offspring. Rather, juveniles preferably observed tool use events by proficient tool users [41], who were older and also more dominant than themselves [12]. Social closeness or physical proximity did not affect who juveniles chose to observe. However, they did prefer individuals who were more tolerant of observers, and scrounging occurred in 75% of tool use events [12].

High inter-individual social tolerance is thought to be an important pre-condition for tool use acquisition [39], as observational learning of a complex skill involves close visual attention to the tool use activities. Being in such close proximity to an intolerant tool-user is risky for an observer, who risks being chased off or attacked. With high social tolerance the opportunity to scrounge often arises, which not only gives naïve individuals the chance to observe the end-result of tool use, but also allows them to share in the payoff — thus increasing their motivation to acquire tool use themselves [146]. After acquisition, honing of tool use skill can be a lengthy process. Younger, active learners spend more time on acquiring tool use and are less proficient than experienced adults [49]. However, in bearded capuchins (*Sapajus libidinosus*), juveniles were not found to make more mistakes than adults during tool use. Rather, juveniles' lower proficiency mainly resulted from less expertise in how to grip the hammerstone [147]. Due to differences in skill and/or strength, younger individuals may also be limited in what resources they can open [27]. Furthermore, percussive stone tool use might have an upper age limit. In chimpanzees, progressive old age led to a reduction in both nut-cracking frequency and efficiency [148].

While the ontogeny of stone tool use for nut-cracking is well-studied in chimpanzees and robust capuchins, little is known about gracile capuchins, who have only recently been added to the list of non-human primate species which habitually using stone tools. In particular, the white-faced capuchins (*Cebus capucinus imitator*) living in Coiba National Park, Panama, are an important study system for studying tool use acquisition and proficiency development, as their social learning opportunities seem to differ from other tool-using primates. White-faced capuchins on the islands of Coiba and Jicarón habitually use stone tools to crack open a variety of food items, including fruits like sea almonds (*Terminalia catappa*), coconuts (*Cocos nucifera*) and palm fruits (*Bactris major*, *Astrocaryum standleyanum*) as well as invertebrates like Halloween crabs (*Gecarcinus quadratus*), hermit crabs (*Coenobita compressus*), nerite snails (*Nerita sp.*) and other freshwater mollusks [30, 31]. However, on Jicarón, despite this tradition persisting for at least 20 years, it seems entirely localized to a 1.5 km stretch of coast, occupied by 2-3 neighboring capuchin groups [122]. Only one group of capuchins appears to use tools habitually on the full variety of resources, the other two neighboring groups have only been observed to sporadically use tools in the intertidal zone. In the most frequent tool-using group, stone tool use is fully male-biased: only males have ever been observed to use stone tools, despite females regularly using tools on the neighboring island of Coiba [84]. The absence of tool use by females means that juvenile capuchins on Jicarón cannot learn tool use from their mothers, as is common in chimpanzees. Furthermore, this group of tool-using capuchins appear to have reduced group cohesion (chapter 5), further limiting social learning opportunities. Taken together, the tool-using capuchins on Jicarón present a unique situation where tool use is incredibly localized, yet persistent, and naive individuals only have limited opportunity to observe tool use due to both less social cohesion as well as the male-exclusive nature of the behavior — which makes mothers unavailable as a model. Given these constraints, understanding how tool use is acquired and develops in this group provides insights into the flexibility of social and individual learning mechanisms in primates.

Herein, we provide a first exploration of the acquisition and development of stone tool use proficiency by one group of white-faced capuchins on Jicarón island. Using a year of data from camera traps on two experimental anvils, we compare features of tool use proficiency — efficiency and mistakes — between juvenile, subadult, and adult capuchins. Furthermore, we present a longitudinal investigation of the improvement in tool use skills by juveniles over a 1-year period, as well as an initial exploration of tool use skill in old age. Lastly, we consider potential mechanisms driving acquisition of stone tool use on Jicarón through examining social attention to tool use sequences. We explore who pays attention to tool use events, which tool users are most likely to receive social attention, and how social attention relates to scrounging and tool user proficiency. In doing so, we provide a first reference of stone tool use proficiency development in white-faced capuchins, which will allow for comparison to other stone-tool-using primate species and lays the groundwork for future studies into the maintenance and spread of tool use behavior in this population.

2.3 Methods

2.3.1 Site and subjects

Jicarón island (2002 ha) is part of Coiba National Park, a UNESCO World Heritage site consisting of nine islands and 100 islets off the Pacific coast of the Veraguas Province, Panama. Jicarón island lies approximately 60 kilometers from the mainland, and is estimated to have been separated from the mainland for 14 000-18 000 years [77]. Jicarón island was inhabited by indigenous communities from 250 CE until the 16th century, served as a penal colony from 1919 until 2004 [78], but currently is entirely uninhabited with no human presence aside from occasional scientific and touristic expeditions. White-faced capuchins occur on Jicarón island, as well as on the largest island of Coiba and the small island of Rancheriá. Jicarón has depauperate mammalian communities and a total absence of mammalian predators [80] and white-faced capuchins show increased terrestriality [76] and live at high densities [30, 75] compared to mainland populations. Two to three groups of capuchins on Jicarón — occupying a 1.5 km stretch of coast — use stone tools for extractive foraging [30], as well as at least one group on Coiba [31]. All known tool-using groups on Jicarón use tools for foraging in the intertidal zone, but only a single social group uses stone tools inland on a wider variety of resources. This group is the focus of this study, and their stone tool use appears to be entirely restricted to males, with no observations of females using tools [84].

The most active tool-using group on Jicarón has been monitored using unbaited camera traps since 2017, but based on previous reports likely has been using tools since 2004 [30]. Stone tool use for extractive foraging has been documented to occur at three types of sites in this group, distinguishable through tool use activity and intensity, site erasure and debris accumulation (see [122] for more details). For the current study, we focus on tool use at high accumulation sites, from here on out referred to as ‘anvils’, where capuchins habitually use tools and large amounts of debris accumulate over time. In 2022, the capuchin group was estimated to be comprised of around 20-25 individuals (5-6 adult males, 5-6 adult females, 4-5 subadults, 7-10 juveniles). These estimates are based on identifiable individuals (Table 2.1) as well as the maximum number of capuchins of a specific age-sex class observed together in one sequence. We are unable to obtain precise estimates of group size due to the nature of data collection via camera trapping, where the visual field is always limited, and juveniles are difficult to identify reliably from images alone.

Name	**Code**	**Sex**	**Age (years in 2022)**	**Age class (2022)**	**Tool-using sequences**	**Notes**
Known tool users						
Abraham	ABE	Male	30	Adult	0	Presumed alpha male, known tool user from previous data
Cystopher	CYS	Male	30	Adult	0	Presumed deceased
Snaggletooth McGee	SMG	Male	10-20	Adult	477	
Tom	TOM	Male	10-15	Adult	287	
Ink	INK	Male	10	Adult	6	
Larry	LAR	Male	7-8	Subadult	785	Border of old subadult/ young adult
Mick	MIC	Male	6-9	Subadult	401	Border of old subadult/ young adult
Spot	SPT	Male	7	Subadult	665	
Terry	TER	Male	5-6	Juvenile	227	Border of old juvenile/ young subadult
Balthasar	BAL	Male	4-5	Juvenile	384	
Zim	ZIM	Male	3-4	Juvenile	78	
Peaky	PEA	Male	3	Juvenile	254	
Joe	JOE	Male	<3	Juvenile	12	
Known non-tool users						
Mr. Email	MRE	Male		Adult		No tool use observed since 2017
Joker	JOK	Male		Subadult		
Olga	OLG	Female		Adult		Presumed deceased
Beatrice	BEA	Female		Adult		
Leona	LEO	Female		Adult		
Dottie	DOT	Female		Adult		
Sadie	SAD	Female		Adult		
Rosa	ROS	Female		(Sub)adult		
Blocky	BLO	Unknown		Juvenile		Very young (<2 years)
Mini	MIN	Unknown		Juvenile		Very young (<2 years)

Table 2.1: Overview of known individuals in the tool-using group, divided into known tool-users and known non-tool-users. Age estimates in years for tool users are rough approximations based on size and growth from 2017-2025. The borders for age classes are juveniles <6, subadults 6-8 years of age and adults >8 years.

2.3.2 Experimental anvil set-up

We set up two experimental anvil sites in the range of the tool-using group in January 2022: a wooden anvil at a site which has been heavily used since 2017 (location name CEBUS-02), and a stone anvil at an entirely novel location under sea almond trees (*Terminalia catappa*) where there was no evidence of prior tool use (EXP-ANV-01). To set up each experimental anvil, we first cleared the area of debris and placed a 1.8 m by 1.8 m piece of mesh on the ground, on which we placed the anvil. Anvils were selected from nearby based on the presence of a flat processing surface, as well as similarity in size to the preexisting anvil at CEBUS-02, which had washed away prior to these experiments. Additionally, at each anvil, we supplied four uniquely marked hammerstones of varying sizes and weights sourced from nearby the anvils (Figure 2.1A). While both anvils were placed under sea almond trees, no nuts were included in the experimental set-up.

Two unbaited camera traps were attached to trees and aimed at each experimental anvil: a close-up video camera (Reconyx UltraFire XP9) recording a 60 second videos per trigger, and a wider-angle still (Reconyx Hyperfire HF2X) camera trap recording 30 images per trigger event without any between-trigger delays. Camera traps were placed in two deployments lasting approximately 6 months, and ran from January 2022 until January 2023. When camera traps were replaced in July 2022, both experimental anvils were excavated (Figure 2.1B), meaning all debris was collected down to the underlying mesh. Hammerstones and fragments found within the mesh perimeter were recovered and identified on the basis of markings and refits, when necessary. The remaining intact hammerstones were provided on the anvil during the second deployment.

Figure 2.1: Photographs of the experimental anvils, showing A) placement of CEBUS-02 in January 2022, and B) EXP-ANV-01 during excavation in July 2022. Photo credits belong to Brendan J. Barrett and Meredith Carlson.

2.3.3 Frame-by-frame coding

All videos containing tool use events were coded frame-by-frame in `BORIS` v. 8.21.8 [125] by three coders (ZG, LR, and MC). We considered individual tool use sequences, where the start is defined as the moment an individual places an item on the anvil for processing and grabs the hammerstone. A sequence ends when either i) the item is opened and consumed ii) the individual relocates with the item to a place out of view of the camera or iii) the item is abandoned, which includes when the item was opened but not eaten. Per tool use sequence, we identified the age class (juvenile, subadult, or adult) of the tool user, and their identity when possible. We classified age based on visual appearance, with juveniles being individuals estimated to be <6 years old, subadults 6-8 years old, and adults >8 years old.

We subsequently coded all behaviors by the tool user following an ethogram we established (Table B.1, see also video ethogram), coding features of tool use efficiency (e.g., number of successful pounds, number of misstrikes) and technique (e.g., type of pound [crouching, standing, jumping]). We also coded asocial (e.g., type of item processed, hammerstone properties) and social factors (e.g., displacements, social attention) on the level of the sequence (Table B.2). A single video could contain one or more tool use sequences, and sequences could also span several videos if the individual was not finished processing when the video ended, and continued in the next triggered video. To obtain additional information on social attention, sequences with other capuchins present besides the tool user were coded again by one coder (ZG) following a different protocol (Table B.3). Per sequence, we coded the age-sex class of each other visible capuchin, as well as the age-sex class of capuchins paying social attention to, scrounging from, or displacing the tool user. Capuchins were identified whenever possible. Juveniles were usually not able to be sexed, as to do so requires close up images of their genitals for which the quality of the camera traps and image angle are insufficient. We also did not observe any subadult females present during tool use sequences, so only coded subadult males. Coders were all trained by ZG on a sample set of data before coding independently once inter-rater agreement on relevant measures (e.g., tool user age, outcome of sequence, number of pounds) was estimated to be good (Cohen's kappa >0.8).

2.3.4 Statistical analyses

All statistical analyses were done in `R` v. 4.3.1 [124]. All Bayesian regression models were fit via the `brm` function in the `brms` package v. 2.16.1 [127]. We calculated contrasts to evaluate the credibility of the difference between categories (e.g., comparing juveniles' time to open an item to subadults' time) using the `hypothesis` function in `brms`. To identify credible effects, we considered what proportion of the posterior probability (PP) of the contrast was greater than 0, using a cut-off of 0.89 to reflect a strong reliable effect. In the aforementioned example, a PP of 0.95 would reflect that the model estimates a 95% probability of juveniles taking more time than subadults to open an item.

Proficiency

To compare tool use proficiency between age classes, we first subsetted our data to only sequences where the item was successfully opened, as failure was too rare to study (occurring in fewer than 4% of observed tool use events). We further limited our analyses on proficiency to sequences where the tool user could clearly be identified. We also excluded sequences that were split across multiple videos, as several seconds of behavior can be missed in between triggers. Additionally, we only included sequences where sea almonds were the item being processed, since they constituted the vast majority (98%) of all tool use sequences and other items were underrepresented. In our dataset, each row represented a tool use sequence and variables were aggregated to the sequence level.

We quantified tool-using proficiency per sequence in four different ways: i) seconds needed to open an item, ii) number of pounds to open an item, iii) number of repositions of the item on the anvil in between strikes and peels of the sea almond's exocarp, iv) number of misstrikes and strikes that sent the item flying off the anvil. To compare sequence duration between age classes, we fit a generalized linear Gamma regression (*Model e1*), with sequence duration in seconds as the outcome. As predictors, we included the age class of the tool user (juvenile, subadult, or adult, with juvenile as reference level), the color of the sea almond (brown, green, red, or unknown, corresponding to its ripeness and with brown as reference level), the material of the anvil (wood or stone, with stone as reference), and a random effect of the identity of the tool user. We included the color of sea almond and the material of the anvil, as we expected both to potentially have an effect on the number of pounds required to open a sea almond. Fresh sea almond fruits are green, and turn yellow, then red, as they ripen [149]. After a while, cached fruits turn brown, and we expect these dried out fruits to be easier to crack than fresh, green ones. Stone and wood have different densities and hardness, likely also affecting how easily the sea almond cracks when smashed with a stone hammer.

To compare number of pounds to open an item between age classes, we fit another generalized linear model (*Model e2*), with the same structure as the model described above. As the predictor was the discreet number of pounds, we used a Poisson distribution. We also compared the rate of pounding (so number of pounds per second) between age classes by running a model with the same structure as *Model e2*, but with an offset of the log of sequence duration in seconds (*Model e2b*). We used the same model structure — without an offset — to consider the number of item repositions (*Model e3a* and item peels (*Model e3b*) during a sequence. Misstrikes, where a capuchin attempts to strike the item but misses it entirely, were not very common. Thus, to compare its occurrence between age classes, we fit a zero-inflated Poisson model, with the same predictors as above (*Model e4a*). Lastly, to compare the occurrence of items flying off the anvil between age classes, which was similarly rare, we fit another zero-inflated Poisson model (*Model e4b*).

Development

To examine the development of tool use proficiency over time, we looked at known individuals and how their processing of one color of sea almond (brown, which is most frequently processed) changed over the course of the full year of coding. We visually considered how the number of pounds, number of repositions, and number of misstrikes changed, with the expectation that (sub)adults would remain rather stable, while juveniles would show fewer pounds, repositions, and mistakes as their proficiency increased. For the number of pounds, we also ran a Poisson

GLM (*model dev1*) with as predictors an interaction of time (parameterized as the log of the seconds passed since January 1, 1970) with the identity of the tool user. Furthermore, we also considered a case study of one adult male, estimated to be the oldest in the capuchin group, to see if and how his tool-using behavior changed since the beginning of sampling in this project (in 2017).

Social attention

To examine social learning's role in tool use acquisition, we ran further analyses on a subset of sequences where other capuchins were present. Here, we also excluded sequences split across several videos, as well as sequences where one of the capuchins present was unable to be assigned an age-sex class, or where the ending of the tool use sequence was not captured on video (so the sequence likely continued after the video stopped recording). We also restructured our dataset to have each row reflect an individual present during a tool-using sequence, with a variable indicating whether they paid social attention yes/no.

First, to consider which age class is more likely to receive social attention, and which age-sex class is more likely to pay social attention to tool use, we fit a generalized Bernoulli logistic regression (*Model socatt1*). The outcome of this model was social attention yes/no, while the predictors included the age of the tool user (juvenile, subadult, adult, with juvenile as reference) and the age-sex class of the observer (juvenile, subadult male, adult female, and adult male, with juvenile as reference). We also included location (CEBUS-02 or EXP-ANV-01) and two social factors which may affect the probability of social attention occurring, namely the total number of capuchins present during the sequence, and the number of capuchins scrounging during the sequence. Lastly, we included an offset of the log of sequence duration, to account for longer sequences having more opportunities for social attention, and a random effect of sequence ID, to account for non-independence of observations from the same sequence.

Second, to consider whether more efficient tool users, or specific individuals, receive more social attention, we subsetted the data further to only sequences where the item was opened, and where the tool user could be identified. We ran another generalized Bernoulli logistic regression (*Model socatt1b*) with the outcome of social attention yes/no, and predictors of tool user age, age-sex of observer, the number of pounds used to open the item, and the number of mistakes during the sequence. We also included an offset of sequence duration, and also the identity of the tool user as a random effect.

All models were fit with regularizing Normal (0,1) priors for intercepts and predictors, and exponential (1) priors for standard deviations of varying effects. For each model, we did a prior predictive simulation to compare our chosen priors to default priors, and to evaluate the identifiability of parameters. The final models were ran with three chains of 3000 iterations each, with a 1500 iterations warm-up per chain. Our models were stable with large effective sample sizes (Bulk_ESS and Tail_ESS over 1000 for all estimates; [127] and Rhat values < 1.01 [128]. Additionally, Pareto k estimates for all models were below 0.7. We visually assessed model fit and confirmed our choice of priors using the posterior predictive check function.

2.4 Results

Between January 2022 and January 2023, we recorded a total of 3657 tool use sequences at the two anvil sites spread across 215 days. CEBUS-02 was the more popular site, with 2574 observed sequences compared to 1083 at EXP-ANV-01. Both locations have gaps in tool use activity over the time period (Figure B.1). At CEBUS-02, the video cameras ran out of battery prematurely due to the higher activity (cameras ran 2022-01-10 until 2022-06-29 and 2022-07-16 until 2022-09-30). At EXP-ANV-01, the capuchins only regularly started using the novel anvil in March 2022, and reduced their activity after a tree branch fell on anvil on 2022-10-10, though cameras ran the full time period (2022-01-10 until 2022-07-16 and 2022-07-17 until 2023-01-01). The average number of sequences observed on a day when tool use occurred was 17.01 (range 1-114). Sea almonds were the item being processed in the vast majority of tool use sequences (3601 sequences equal to 98%, Table 2.2).

Item		*Count*	*Percentage*
Sea almond	Brown	2381	**65.11**
	Green	553	**15.12**
	Red	78	**2.13**
	Unknown	589	**16.11**
Coconut		12	**0.33**
Fruit		1	**0.03**
Crab (halloween or hermit)		12	**0.33**
Other		16	**0.44**
Unknown		15	**0.41**

Table 2.2: Frequency of items being processed during all observed tool use sequences

Capuchins successfully opened the item in 89% of the sequences. Success rates were lower for juveniles (79%) compared to subadults and adults (93% and 90% respectively). The number of pounds needed to open a single item ranged from 1 to 34. In the remaining sequences, the tool user either abandoned the item (4%), relocated to another anvil with the item (3%), or the ending was not captured on camera (4%). In both sites, the same hammerstone was used in over 90% of the tool use sequences, and all age classes used the same hammerstones.

We were able to classify the tool user's age in all of the sequences, and reliably identify the tool user in 98% of the sequences (see Table 2.1 for the number of tool use sequences observed per individual). The tool user was the only individual visible in the video in 72% of all sequences. When other capuchins were present (1010 sequences), we observed social attention occurring in 217 sequences (21%). Both displacements and scrounging were rare, occurring in 12% and 25% of opportunities (meaning, other capuchins being present).

2.4.1 Tool-using proficiency

Efficiency (number of pounds and processing time)

The sample used for analyses consists of 2900 sequences where i) the tool user successfully opened a sea almond, ii) the tool user was identified, and iii) the sequence was not split across several videos ($n_{adult} = 662$, $n_{subadult} = 1612$, $n_{juvenile} = 626$). Our models estimated that juveniles need considerably longer to open a sea almond with stone tools than subadults and adults (Figure 2.2, for model estimates see Tables B.4 & B.5). Juveniles took an average of 19.30 seconds (95% CI [14.30, 25.53]) and 5.21 pounds (95% CI [4.39, 6.30]) to open an item, considerably longer than subadults, who took on average 9.78 seconds (95% CI [5.99, 15.33]) and 3.63 pounds (95% CI [2.75, 4.71]), and adults, who took 11.25 seconds (95% CI [7.17, 18.54]) and 3.82 pounds (95% CI [2.80, 5.05]). Juveniles taking more seconds and more pounds to open an item than subadults and adults were credible effects (all $PP > 0 = >0.98$). Subadults and adults did not differ significantly from one another in both models.

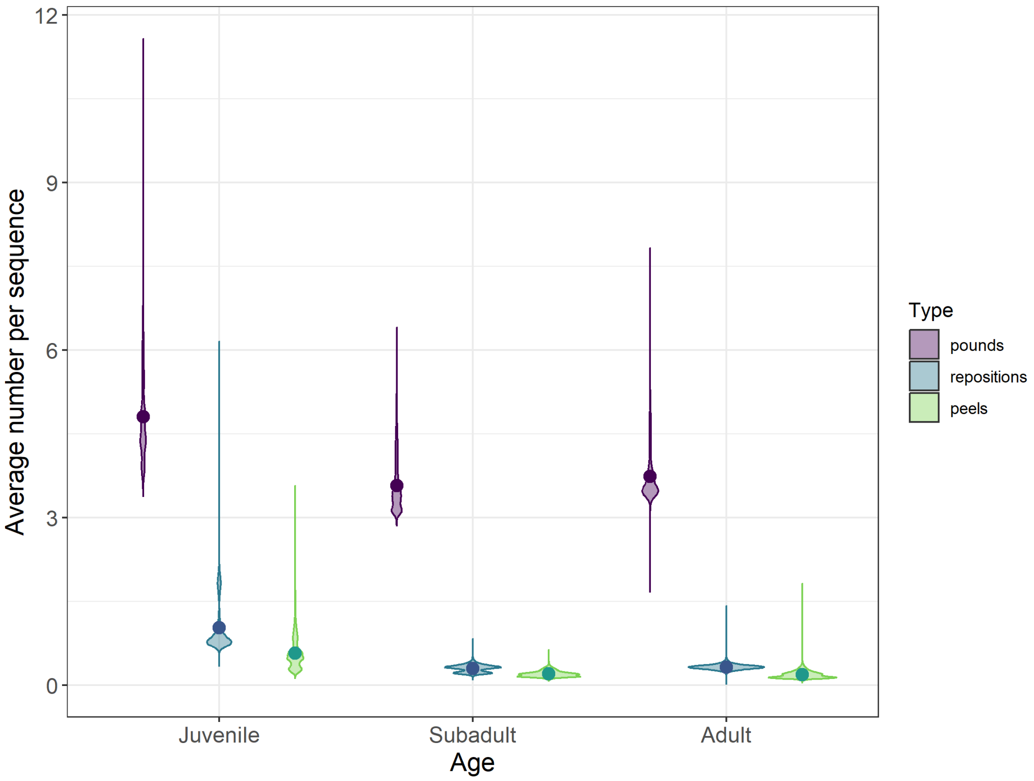

Figure 2.2: Model estimates and mean values of pounds, repositions, and peels in one tool use sequence opening a single sea almond per age-class (juvenile, subadult, adult). Model estimates are reflected by violin plots, and observed means from data are represented as points.

The level of ripeness of the sea almond and the material of the anvil affected both seconds and pounds required to process a sea almond. Fresher sea almonds (green and red in color) took more time and more pounds to open than older (brown) sea almonds. We estimated green almonds to require 1.32 times more seconds (95%

CI [1.27, 1.38], PP $>$ 0 = 1) and 1.26 times more pounds (95% CI [1.21, 1.32], PP $>$ 0 = 1) than brown almonds. Red almonds 1.49 times more seconds (95% CI [1.34, 1.65], PP $>$ 0 = 1) and 1.31 times more pounds (95% CI [1.17, 1.45], PP $>$ 0 = 1). Red and green sea almonds did not differ considerably from one another in processing times or number of pounds. The material of the anvil did not affect processing times, but the number of pounds was slightly higher (1.09 times, 95% CI [1.06, 1.14], PP $>$ 0 = 1) at the stone anvil than at the wooden anvil. The relationship between the number of pounds and the sequence duration (so the speed at which individuals pound) was positive between age classes (Figure 2.3). However juveniles showed a 0.75 times lower rate of pounding (number of pounds per second) than adults (95% CI [0.62, 0.93], PP $>$ 0 = 0.98) and 0.74 times lower than subadults (95% CI [0.61, 0.89], PP $>$ 0 = 0.99, for all estimates see Table B.6).

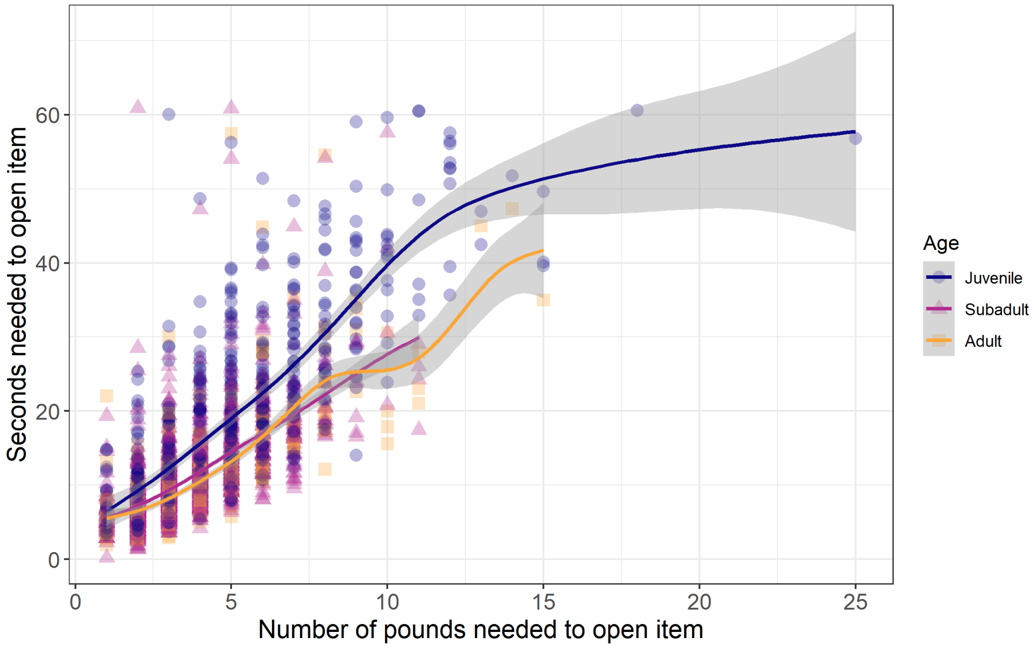

Figure 2.3: Relationship between number of seconds and number of pounds needed to open a single item using stone tools, separately for each age class.

Repositioning and peeling

All age classes showed repositioning of the item on the anvil during a tool use sequence, or picking it up and peeling it before continuing to strike, but juveniles did it more than adults and subadults (Figure 2.2, for model estimates see Tables B.7 & B.8). Juveniles showed considerably higher incidences of repositioning and peeling ($\text{mean}_{\text{n\_reposition}}$ = 1.11, 95% CI [0.64, 1.80]; $\text{mean}_{\text{n\_peel}}$ = 0.43, 95% CI [0.27, 0.68]) than subadults ($\text{mean}_{\text{n\_reposition}}$ = 0.33, 95% CI [0.16, 0.79]; $\text{mean}_{\text{n\_peel}}$ = 0.18, 95% CI [0.09, 0.37]) and adults ($\text{mean}_{\text{n\_reposition}}$ = 0.32, 95% CI [0.15, 0.79]; $\text{mean}_{\text{n\_peel}}$ = 0.18, 95% CI [0.09, 0.40]). Juvenile tool users repositioning and peeling more than subadults and adults were credible effects (all PP>0 = >0.98). Tool users peeled fresher sea almonds, in particular green ones, more often than brown, older sea almonds (1.48 times more, 95% CI [1.23, 1.75], PP>0 = 1). The material of the anvil made no difference in the number of repositions or peels.

Mistakes

Tool users rarely made mistakes during tool use sequences (occurring 323 times in the sample of 2900 tool use sequences), and in 47% of cases the tool user making a mistake was juvenile. The most common type of mistake was the item flying off the anvil after being struck (occurring 161 times), followed by misstrikes (106 times), and dropping the hammerstone (occurring 56 times). Juvenile tool users were more likely to make misstrikes or send the item flying off ($\text{mean}_{\text{n\_misstrikes}}$ = 0.14, 95% CI [0.03, 0.51]; $\text{mean}_{\text{n\_itemflies}}$ = 0.32, 95% CI [0.18, 0.52]) than subadults ($\text{mean}_{\text{n\_misstrikes}}$ = 0.04, 95% CI [0.01, 0.26]; $\text{mean}_{\text{n\_itemflies}}$ = 0.07, 95% CI [0.05, 0.14]) and adults ($\text{mean}_{\text{n\_misstrikes}}$ = 0.06, 95% CI [0.01, 0.35]; $\text{mean}_{\text{n\_itemflies}}$ = 0.06, 95% CI [0.03, 0.13]). Juveniles making more mistakes than subadults was a credible effect (misstrikes PP>0 = 0.91, items flying PP>0 = 1) as was juveniles sending more items flying than adults (misstrikes PP>0 = 0.83, items flying PP>0 = 1, for model estimates see Tables B.9 & B.10).

The material of the anvil also affected the likelihood of the item flying off: a sea almond was 3.42 times more likely to fly off of a stone than wooden anvil (95% CI [2.56, 4.62], PP>0 = 1). Green and red sea almonds were also 3.49 (95% CI [2.53, 4.81], PP>0 = 1) and 2.46 times (95% CI [1.27, 4.62], PP>0 = 0.99) more likely to fly off when struck than brown, dried out, sea almonds.

2.4.2 Tool use development

We observed little change in tool use proficiency over the year for all age classes. Adults' performance was the most stable, but juveniles and subadults also did not show considerably changes in the number of pounds (for model estimates see Table B.11), repositions, and misstrikes over time (Figure 2.4). The reduced sampling near the end of the observation period, combined with some individuals (mostly adults) showing clustered activity rather than activity spread over time, means that there is more uncertainty at certain times of the year.

In light of tool use skill development as a function of age, it is important to mention one individual who was absent as a tool user in our sample: ABE. This adult male is estimated to be at least 30 years old, and the likely alpha male of the group, inferred by his size, him being recruited by other group members in conflicts, and the absence of him receiving aggression. While he was observed using tools 73 times in data collected 2017-2019, he never used tools in the current observations. However, 13 times ABE displaced a tool user from the anvil (out of 175 total displacements), and then consumed the item they opened. No other individuals 'stole' from tool users in this manner.

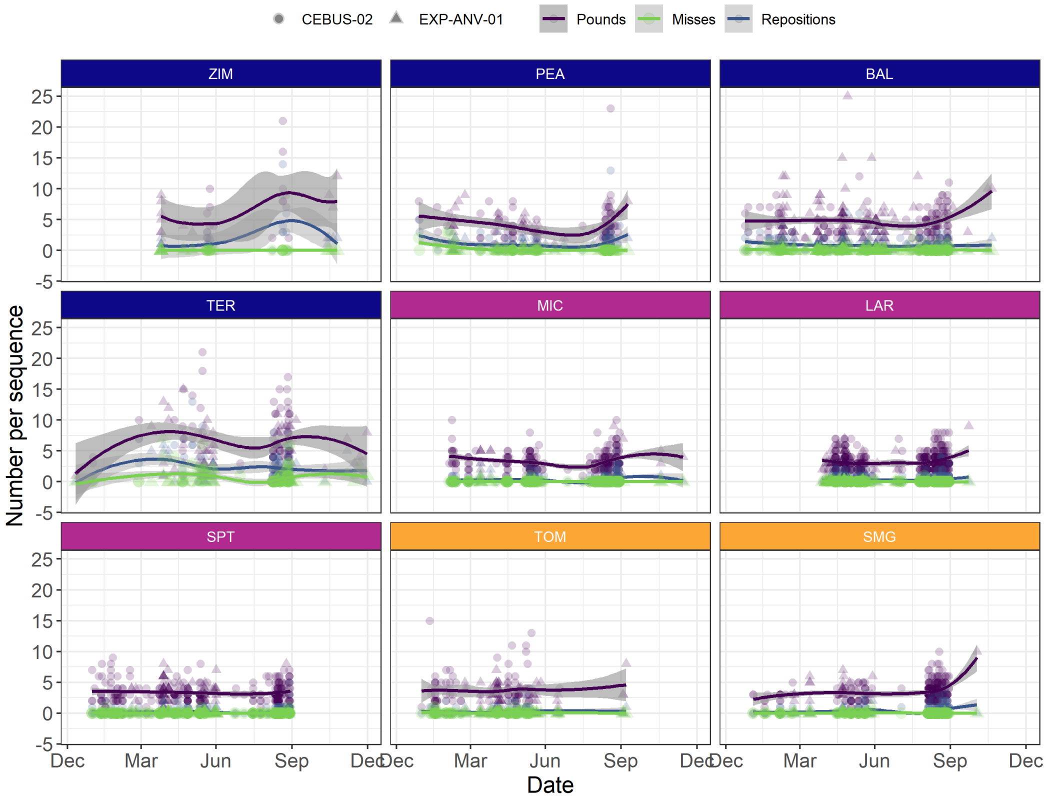

Figure 2.4: Development of number of pounds (purple), misstrikes (green), and repositions (blue) per individual over the full observation period for brown sea almonds only. The color of the box with the individuals code represent their age class (blue for juveniles, lilac for subadults, orange for adults). Points are raw data, with point shape corresponding to anvil location. The smooth curve is estimated using method `loess` and formula "y~x".

Social attention

After filtering, our sample contained 844 sequences that were completely captured within a single video, during which other capuchins aside from the tool user were present, who could all be assigned an age-sex class. The majority of other capuchins present were juveniles (833 out of 1346 capuchins present, 62%), followed by subadults (269, 20%) and adult males (135, 10%). Adult females were most rarely present during tool use sequences (109 times, 8%). In this filtered sample, social attention occurred in 183 (22%) of the sequences with capuchins present.

Individuals paying social attention were overwhelmingly juveniles, an adult male was observed paying social attention once, adult females five times and subadult males 18 times. Of the 208 occurrences of juveniles paying social attention, 23 were identified as known tool-using juveniles. The remaining unidentified juveniles were likely not tool users, as they were too young (<3 years) to easily be identified and we have not observed regular tool use by any individuals of this age.

Our model exploring factors predicting the probability of social attention also found juveniles to be the age class most likely to pay social attention. Given an adult male tool user at the most frequently used location (CEBUS-02), juveniles had a

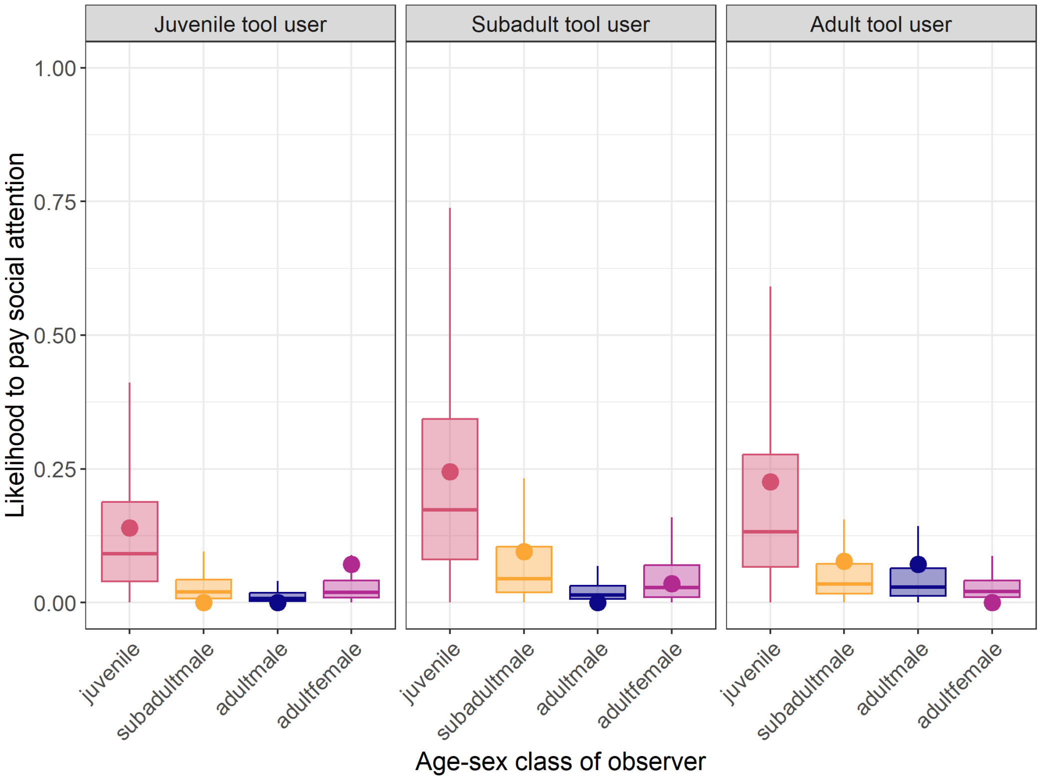

Figure 2.5: Likelihood of paying social attention to a tool user, presented per age-sex class of the observer and age of the tool user. Model estimates are reflected by box plots, and observed means from data are represented as points.

probability of showing social attention of 0.16 (95% CI [0.09, 0.26]), considerably higher than subadult males (0.05, 95% CI [0.02, 0.10]), adult males (0.02, 95% CI [0.01, 0.05]), and adult females (0.03, 95% CI [0.01, 0.07]). In terms of who received social attention, given a juvenile observer at CEBUS-02, juveniles were less likely to receive social attention [0.07, 95% CI: 0.04-0.10], than subadults [0.18, 95% CI: 0.14-0.23] and adults [0.16, 95% CI: 0.09-0.26], who did not differ significantly from one another (Figure 2.5). Juveniles being more likely to pay social attention and less likely to receive social attention than other age-sex classes was a credible effect (PP $>$ 0 for all contrasts $=$ 1).

When more capuchins were present during a tool-using sequence, the chance of social attention occurring was lower. However, in sequences where more individuals were scrounging, social attention was more likely to occur (Figure 2.6, for model estimates Table B.12). When we consider the type of scrounging (whether it was tolerated by the tool user during the tool use event, or only occurred after the tool user had left), we see that social attention mostly occurred in combination with tolerated scrounging (tolerated scrounging occurred in 106 out of 183 sequences with social attention, compared to scrounging afterwards occurring in 13 sequences). Although sequences with other capuchins present were rarer at the EXP-ANV-01 site than CEBUS-02 (180 compared to 664), social attention was more likely at EXP-ANV-01 (Table B.12). For example, given the most frequently occurring combination of a juvenile paying attention to a subadult tool user, the predicted likelihood of social attention at EXP-ANV-01 is 0.36 (95% CI [0.27-0.46] and at CEBUS-02 0.18 (95% CI [0.14, 0.23]). Paying social attention was not entirely without risks: in one tool use sequence a juvenile observer got too close to the tool user, and was hit on the foot with the hammerstone (Video B.1).

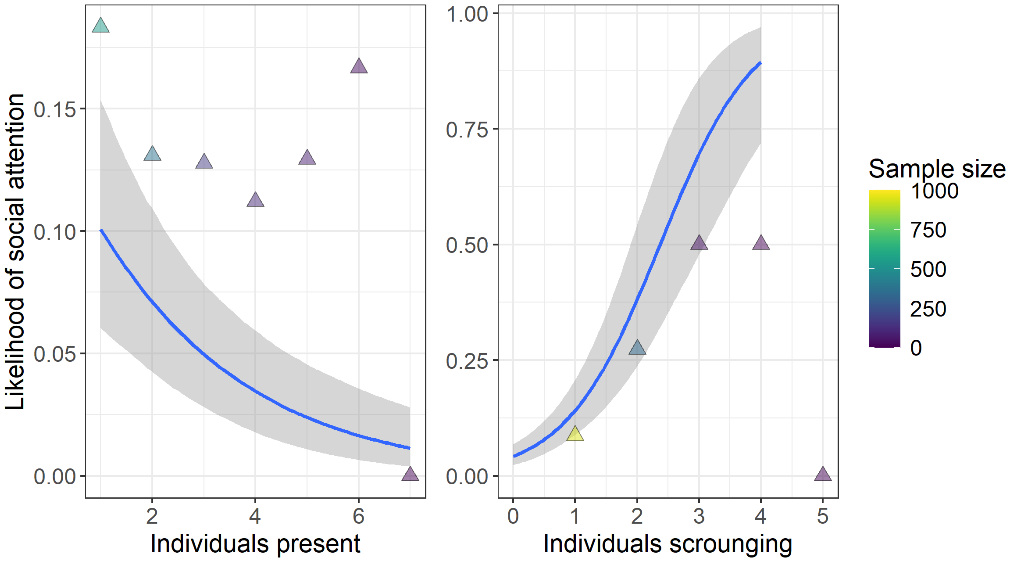

Figure 2.6: Likelihood of paying social attention to a tool user, depending on number of capuchins present (left) and scrounging (right) in the sequence. Model estimates are reflected by the lines, and observed means from data are represented as points. Color of points reflects the size of the sample contributing to the mean.

To consider whether social attention is preferentially paid to more proficient tool users, we limited our sample to sequences where a) the item was successfully opened, b) we could confidently identify the tool user, and c) the tool user had more than 10 tool-using sequences in the sample (n = 1175 sequences). Our model estimated a slight trend of more social attention occurring in more efficient tool-using sequences (where fewer pounds needed to open the item), and this relationship was strongest if observers were juveniles (see Figure B.2 and model estimates Table B.13). Given a juvenile observer of a subadult tool user, the likelihood of the juvenile paying social attention was predicted to decrease with each additional pound the subadult tool user made. The individuals who received most social attention during tool use were the three subadult males, who also showed highest incidence of tool use with other individuals present (Figure 2.7). Individual subadults differed little from each other in how much social attention they received.

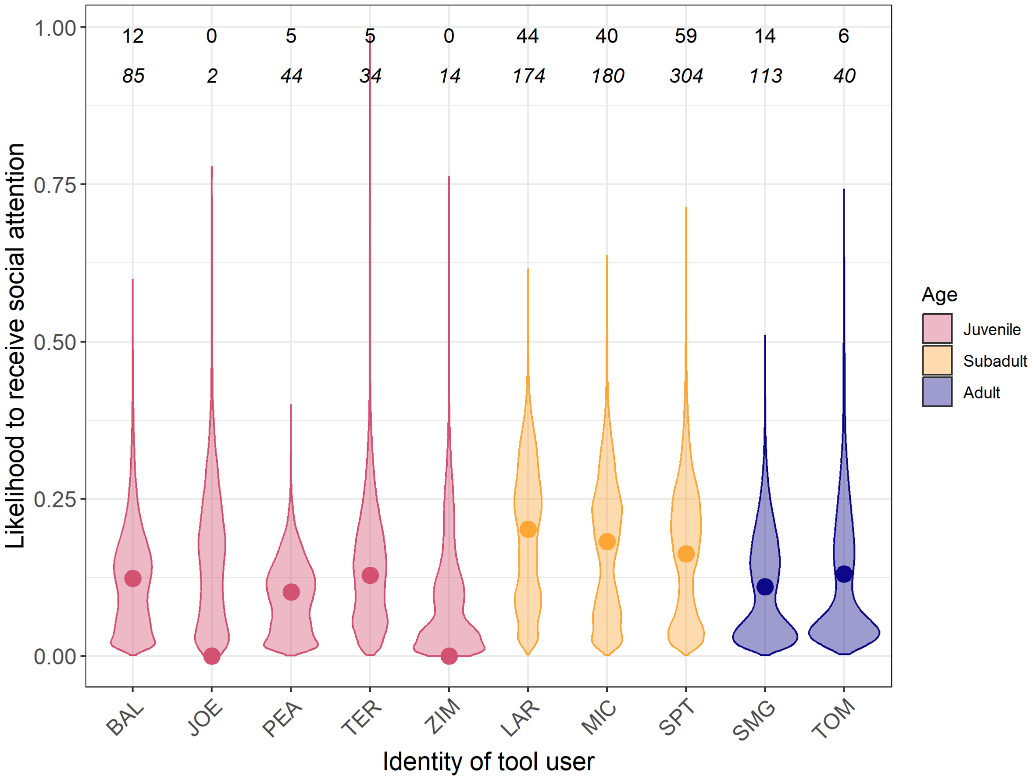

Figure 2.7: Likelihood of receiving social attention for different tool users. Model estimates are reflected by violin plots, and observed means from data are represented as points. Color reflects the age class of the tool user, and the numbers above the number of sequences with social attention (top) compared to the number of sequences with other capuchins present where no social attention occurred (bottom in italics).

2.5 Discussion

Stone tool use by white-faced capuchins on Jicarón is a complex behavior; proficiency takes years to develop. Compared to subadult and adult tool users, juvenile tool users need more time and more pounds to open an item using tools, more frequently reposition the item in between strikes, and make more mistakes. Subadults and adults show comparable levels of proficiency on all measures. Four identifiable tool-using juveniles did not markedly improve in tool use proficiency over the course of approximately one year. No other capuchins were present in the vast majority of tool use sequences and social attention to the tool user was rare (occurring in just 6% of all sequences). Nonetheless, we uncovered some robust patterns in who paid social attention to whom, and in what context. Juveniles were most likely to pay social attention to tool use, and most of these juveniles were too young to be tool users themselves. Social attention was directed at subadults and adults, with a slight preference towards more efficient tool users. Subadults received the most social attention. The more capuchins were present during a tool-using sequence, the lower the probability that social attention occurred. Scrounging showed the opposite relationship: the more individuals scrounging, the higher the chance of social attention.

2.5.1 Differences in tool use proficiency

It is unsurprising that juveniles are less proficient tool users than adults and subadults, regardless of the measure of proficiency considered. This pattern is similar to what has previously been described in macaque stone tool use [49] and for this species of capuchin in other extractive foraging tasks [68]. However, juveniles were still very successful in opening items, and the difference in their efficiency compared with subadults and adults is small. Overall, white-faced capuchins had a slightly higher success rate than what is reported in studies of other nut-cracking primates. The item being abandoned entirely only occurred in 4% of all sequences, much lower than in chimpanzees (failure occurring in 8% of tool use events [150]) and robust capuchins (failure in 2-38% of events depending on population [27, 48, 151]). This does not necessarily reflect higher skill of the white-faced capuchins, but could also be an artifact of their high persistence and tenacity. It is important to note that we excluded tool use sequences that spanned more than one camera trap video from analyses. This was done to ensure no pounds or other behavior were missed between triggers, but also means we likely excluded the very worst tool-using sequences, where individuals took the longest to open the item, and some sequences where successful individuals rapidly opened many items in a row. As both of these variables are linked to age (juveniles are more likely to be less proficient and have sequences spanning multiple videos, while adults might process more rapidly and have multiple sequences in one video), their exclusion is not likely to significantly alter our results.

The clearest distinction between juvenile and (sub)adult tool use proficiency was the much higher incidence of mistakes by juveniles. Mistakes were rare in our sample overall, similar to bearded capuchins [147], but, contrary to their findings, we found that juveniles were considerably more likely to miss the item, or have the item fly off the anvil. Juveniles also more frequently repositioned the food item between strikes. More frequent repositioning by juveniles could reflect poorer control over the hammerstones than adults. This ties in with our surprising finding that at both sites, the same hammerstone was used in over 90% of the sequences, despite multiple other hammerstones being provided. These stones were large and heavy, and thus easier to handle for (sub)adults than juveniles. The (lack of) hammer selectivity relative to body size at the experimental anvils is an interesting avenue for future research, as it stands in stark contrast to findings in chimpanzees [152], macaques [50], and robust capuchins [153]. This may be related to the fact that large hammers might yield large dividends for gracile capuchins, which are the smallest, lightest tool-using primates.

The same hammerstone may have been used so consistently at each site because there was also little variation in the food items being opened. In nearly all sequences, capuchins processed sea almonds. However, the level of ripeness of the sea almond does appear to affect ease of processing: green, fresher, sea almonds required more seconds and more pounds to open than brown sea almonds, were peeled more frequently, and were more likely to fly off the anvil when struck. This likely reflects the harder exocarp of the fruit at this stage, before it is dries out and becomes more brittle. The lack of hammerstone selectivity for sea almond ripeness and higher incidence of peeling with green sea almonds indicates that perhaps the additional step of peeling off the exocarp in between strikes helps overcome the difference in hardness, a technique which juveniles might also need to learn to become a more proficient tool user. However, juveniles also peeled more frequently than (sub)adults, so it is also possible that juveniles lack knowledge/ability to precisely strike the green sea almonds without them flying off the anvil — which green sea almonds are more likely to do — and that peeling the fruit makes it easier to strike. In either case, becoming a proficient stone tool user might not only involve learning *how* to process, but also *what* and *when*. Sea almonds have variable fruiting seasons, and although we know little of seasonal fluctuations in food availability on Jicarón, our data does show sea almond processing peaking bimodally (Figure B.1). Additionally, (sub)adults seem to focus more of their tool-using efforts at specific times of the year (see Figure 2.4), whereas juveniles use tools at a more consistent rate throughout the year. Future studies can elucidate the cause of these seasonal fluctuations in tool use, and also explore whether adults indeed concentrate their tool-using efforts when sea almonds are most abundant or, alternately, when other, easier to consume food resources are unavailable.

2.5.2 Development of proficiency

The lack of change in tool use proficiency by juveniles over the course of our study period suggests that honing these skills to adult levels of proficiency is likely a slow process, or one limited by physical features (like strength) which only mature in adulthood. White-faced capuchins are a long-lived species, with a lifespan up to 50 years [19], similar to chimpanzees, where it has been shown that becoming a proficient nut-cracker can take 3-7 years of practice [44, 154]. Our results, though not yet sufficiently longitudinal for a full understanding of tool use ontogeny, suggests that in white-faced capuchins, becoming a proficient stone tool user may be a similarly extended process. Furthermore, our finding that the oldest tool-using male in the group, Abraham, did not use tools at all during the 1 year period of this study, hints at a potentially upper age limit for stone tool use in white-faced capuchins, as has been documented in chimpanzees [148]. Abraham is the only individual to displace tool users from the anvil to steal the item they opened, which suggests he is still interested in the resources, but perhaps no longer able or willing to invest the energy and time to use tools himself. Here, too, a more longitudinal approach would be very valuable to examine the fluctuations in tool use proficiency across the lifespan.

2.5.3 The role of social attention in tool use acquisition

Stone tool use at the experimental anvils appeared to be a largely solitary activity. As such, opportunities for social attention seem limited, and even when other capuchins were present, social attention only occurred in 20% of the sequences. Data from camera traps may underestimate social attention, as individuals out of frame could be looking at the tool user without this being captured. However, attention from a distance likely only provides the observer with coarse information on the tool use behavior. The low frequency of close social attention in our sample is surprising compared to other nut-cracking primates. In one study on tufted capuchins, conspecifics observed 36% of all nut-cracking events [12], and in chimpanzees, juveniles observe hundreds of nut-cracking events from their mothers [145]. Yet on Jicarón, juvenile capuchins have no opportunity to learn tool use from their mothers, as females do not use tools [84]. Individuals paying social attention to tool use were mostly juveniles too young to be tool users themselves, suggesting that social observation may be most important for the acquisition of the tool use behavior [68]. Although scrounging was not as common as in tufted capuchins [12], the more individuals were scrounging, the higher the likelihood of social attention occurring. Furthermore, when scrounging did occur together with social attention, it was nearly always tolerated by the tool user. The tool users who received the most social attention, subadult males, are also known to be tolerant of juveniles [155]. Our results echo the idea that inter-individual tolerance plays a crucial role in social learning of complex behaviors [39]. Furthermore, capuchins might also rely on local enhancement and interaction with temporally enduring artifacts of tool use to learn about the tool use behavior [146]. In the absence of many opportunities for direct social learning, debris left on the anvil after a tool use sequence, such as partially processed food items, and wear on the hammerstone and anvil may provide important information to individuals visiting the site. Capuchins on Jicarón using this physical evidence of tool use as a cue could also explain the 'burn-in period' at the novel anvil, EXP-ANV-01, since perhaps regular tool use by many individuals only started once enough debris had accumulated from sporadic tool use events, marking this location as a suitable anvil for tool use.

2.5.4 The importance of location

Here, we report on data collected from only two anvils in the tool-using groups' range. However, we have identified at least 10 different anvils that are habitually used for stone tool use, and over 300 ephemeral locations. While CEBUS-02 is the most frequently used anvil, which has, to the best of our knowledge, been in use for the longest time (at least since 2004), it is possible that most social learning of tool use occurs elsewhere, for instance during tool use in the intertidal zone [122]. We do see a difference in the likelihood of social attention between the two experimental anvils: CEBUS-02 has more opportunities for social attention, but social attention is more likely at EXP-ANV-01. This could be due to CEBUS-02 being an established, well-used anvil prior to the current study. We infer that this anvil is used so frequently because it is located in a productive foraging area (next to a stream), leading to more capuchins being present at the same time. In contrast, we purposefully placed the experimental anvil EXP-ANV-01 in a location without evidence of prior tool use, meaning this location likely held less interest for the capuchins. This inference is supported by the fact that it took capuchins taking several months to start regularly using this anvil. The availability of ripe sea almonds at this location may have also influenced the latency to capuchins visiting this anvil. Another, non-exclusive, possibility is that, either due to anvil material or other properties of the site, CEBUS-02 is simply a 'better' anvil. In this case, there may be more competition over this site, and lower tolerance for observers. We found that on average, capuchins used more pounds at the stone anvil than the wooden anvil, and that items were more likely to fly off the stone than the wooden anvil, further supporting that the wooden anvil at CEBUS-02 has better properties for tool use. Anvil selectivity by tool users and the notion of 'wear in' time of new anvils is another interesting avenue for future research, in order to examine what exact physical properties drive these differences in tool use efficiency.

2.5.5 Spread of tool use to other groups

The seemingly slow mastery of stone tool use by white-faced capuchins also has implications for the spread of this behavior. Despite being persistent over time, the stone tool use behavior on Jicarón is incredibly localized [30]. In mainland populations of white-faced capuchins, males are the dispersing sex and first dispersal occurs on average at 4.5 years of age in Santa Rosa [156] and 7 years of age in Lomas Barbudal [71]. On Jicarón, males of this age would not yet be proficient tool users based on our data, and as such, might cease using tools post-dispersal, limiting the spread of the behavior. However, it is unclear whether the typical pattern of male dispersal holds on Jicarón, or if, instead, both sexes, or only females disperse. Switches in dispersal tendency are known to occur under high density conditions [89]. It appears likely that at least some males remain in the natal group, as we have tracked some individuals from juvenile to (sub)adulthood. Further elucidating the dispersal tendency of these capuchins is crucial to better understand the maintenance and spread of the tool use behavior.

2.6 Conclusion

We present a first description of variation in and development of stone tool use proficiency in white-faced capuchin monkeys. Using camera traps placed at two experimental tool use anvils on Jicarón island, Panama, we collected nearly a year of tool-using sequences, mostly of capuchins processing sea almonds. Similar to other primates that show percussive stone tool use, white-faced capuchin juveniles are less proficient tool users than adults (in terms of efficiency and technique), and development of proficiency appears to be a slow process. Ripeness of the sea almond affected processing times and efficiency, with less ripe green sea almonds requiring more time and peeling of the skin in between pounds, and generating more mistakes. In contrast to findings from other tool-using primates, tool-using appeared to be a largely solitary activity, with limited opportunities for social learning and even fewer actual occurrences of close social attention. However, when social attention to tool use did occur, there were clear patterns to it that echoed studies in other primates. Social attention was mostly paid by juveniles to proficient subadults, who were tolerant of scrounging. We also found an effect of location on the likelihood of social attention occurring, suggesting social learning opportunities differ between sites. In short, we lay the groundwork for both comparisons between stone tool-using primate species, as well as future research on other aspects of white-faced capuchin stone tool use like seasonality and hammerstone and anvil selectivity.

2.7 Data availability

Details of model output are available in section B.3. All code and data necessary to replicate analyses are publicly available [157].

2.8 Acknowledgments

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Chapter 3

Coupling of coastal activity with tidal cycles is stronger in tool-using capuchins

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Code	https://doi.org/10.5281/zenodo.8129505

3.1 Abstract

[1] Terrestrial mammals exploiting coastal resources must cope with the challenge that resource availability and accessibility fluctuate with tidal cycles. Tool use can improve foraging efficiency and provide access to structurally protected resources that are otherwise unavailable (e.g. molluscs and fruits). To understand how variable accessibility of valuable resources shapes behavioral patterns, and whether tool use aids in the efficient exploitation of intertidal resources, we compared the relationship between tidal cycles and activity patterns of tool-using versus non-tool-using groups of white-faced capuchin monkeys on Jicarón Island in Coiba National Park, Panama. Although tool use on Jicarón is localized to a small stretch of coast (approx. 1 km), all coastal groups forage on intertidal resources. Using more than 5 years of camera trap data at varying distances from the coast, we found that capuchins on Jicarón showed increased coastal activity during specific parts of the tidal cycle, and that this relationship differed between tool-using and non-tool-using groups, as well as between seasons. Activity patterns of tool-using capuchins were more strongly and consistently tied to tidal cycles compared with non-tool-users, indicating that tool use might allow for more efficient exploitation

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[1] Spanish translation of abstract can be found in section C.3

of tidal resources. Our findings highlight the potential of tool use to aid niche expansion.

3.2 Introduction

Animals that are dietary generalists are buffered against the negative consequences of environmental change and fluctuating resource availability [158]. Dietary generalists have been shown to be more innovative and better at spatial reasoning than specialist congeners, helping them to access patchy resources [159, 160], and have also fared better than specialists in the face of anthropogenic change [161]. Maritime mammals (*sensu* [162]) are one example of dietary generalists: these are populations of mammalian foragers who exploit resources in the intertidal zones, despite intertidal areas being an unlikely selective pressure in their evolutionary past, and who typically also forage in other habitats.

While all animals must deal with spatio-temporal variability in choosing when and where to forage, terrestrial foragers exploiting intertidal resources face additional challenges. Tidal cycles are asynchronously cyclical: tidal peaks occur predictably, but the timing of low and high tides shifts daily and the magnitude of tidal change is affected by a myriad of interacting processes. Resource accessibility also varies depending on season and weather. Different prey species may show intra-annual variability in abundance due to migration or breeding patterns [163, 164]. Prey accessibility can be limited by sunlight and temperature, which can heat substrates to greater than 45°C and impact tidal pool salinity causing prey to conceal themselves or move towards the ocean [165–167]. Further, the intertidal zone in tropical regions is often exposed and hot, which potentially puts individuals with reduced adaptation to cope with hot substrates at risk of thermal stress when traversing the intertidal zone. Although a taxonomically diverse set of mammalian taxa are known to exploit intertidal resources (e.g., primates [24, 168], carnivores [169–171] and rodents [172]), it is unclear *how* this variable accessibility of valuable resources affects the daily activity patterns of these maritime mammals.

3.2.1 Tool use improves efficiency of intertidal foraging

The importance of intertidal resources and the extent to which maritime mammals alter their activity patterns to tidal cycles may depend on their ability to exploit the resources in these dynamic habitats. Intertidal resources, such as marine invertebrates and fruits with ocean dispersed seeds, are physically protected and therefore require time-consuming processing (e.g., bivalves, crabs). One way in which maritime mammals could exploit intertidal resources more efficiently and access resources that are otherwise inaccessible to them is by using tools. Tool use facilitates more efficient resource consumption through faster processing, and provides access to structurally protected foods [5], and as such allows animals to expand their effective environment. Rocky intertidal areas exposed by low tides provide a wealth of anvil and hammerstone material, in the form of bedrock, driftwood and smooth stones.

A behavior is considered tool use when an animal manipulates an object that is not part of their own body in order to reach a useful outcome [6, 17]. Examples of animal tool use in foraging contexts are widespread, ranging from chimpanzees (*Pan troglodytes*) using sticks for termite fishing [8] and robust capuchins (*Sapajus* spp.) using stone tools to crack nuts [26, 27], to dolphins (*Tursiops* sp.) protecting their rostra with sponges while foraging on the seafloor [9] and New-Caledonian crows (*Corvus moneduloides*) crafting and using hooked as well as unhooked twig tools to forage on embedded insects [38].

3.2.2 Maritime mammals face challenges in timing foraging with tidal cycles

How intertidal foraging impacts a maritime mammal's behavior depends on the importance of these resources in their diets. Carlton & Hodder [162] distinguish between opportunistic and obligate foraging in the intertidal zone. Opportunistic omnivores can exploit the intertidal zone whenever it is advantageous to them. By contrast, obligate reliance on intertidal resources can be a result of seasonal or systematic impoverishment of terrestrial resources which drives maritime mammals to intertidal resources as an essential addition to their diet [162], making intertidal resources a type of fallback food [173, 174]. Opportunistic exploitation of the intertidal zone has different effects on maritime mammals' activity patterns. An example of opportunistic maritime mammals are Japanese macaques (*Macaca fuscata*), who feed on seafood and only show intertidal foraging linked to tidal cycles in months when terrestrial resources are scarce [175]. By contrast, black legged kittiwakes (*Rissa tridactyla*)—who are more obligate maritime foragers as they systematically rely on intertidal resources—choose to forage in the intertidal zone and leave their chicks unattended when low tide overlaps with their nesting period [176]. Furthermore, island-living arctic foxes (*Alopex lagopus*), whose diet is dominated by fish caught in tidal pools, shape their daily activity pattern around the tides: they forage at low tide and sleep at high tide [177]. Animals that exploit resources in the intertidal zone may thus benefit from adjusting their daily activity to the tidal cycles.

3.2.3 The role of tool use in intertidal exploitation

Tool use might aid intertidal exploitation, as many intertidal resources are structurally protected (e.g., snails, bivalves, coconuts). An example of animals using tools to forage in intertidal zones with greater efficiency are bearded capuchins (*Sapajus apella* and *Sapajus libidinosus*) in mangroves. These capuchins exploit intertidal resources, including crabs and snails, with and without tools [178]. Notably, while crabs can be eaten without using tools, it appears that snails can only be consumed by tool-using capuchins. Island-living Burmese long-tailed macaques (*Macaca fascicularis aurea*) exploit both terrestrial resources (palm nuts) and tidal resources exposed at low tide, such as oysters, by using stone tools [24]. Intertidal resources may be of differing importance to tool-using and non-tool-using maritime mammals, as tool use can provide access to novel foraging niches [179] or otherwise inaccessible items [37]. Thus, tool-using maritime mammals may access more marine prey items than non-tool-using mammals. Alternatively, tool-users might have *less* need for intertidal resources than non-tool-users as they can access more nutrient-rich foods inland as well. In this case, non-tool-using maritime mammals might exploit intertidal resources to a greater extent as they have fewer terrestrial resource options.

3.2.4 Coiban capuchins are tool-using and non-tool-using maritime mammals

White-faced capuchins in Coiba National Park, Panama (hereafter Coiban capuchins), have been reported to habitually conduct first-order (e.g., pounding of coconuts on anvils [180]) and second-order tool use (e.g., hammerstone and anvil stone tool use [30, 31]). This habitual tool use behavior provides the opportunity to explore: (i) if capuchins adjust their patterns of activity to coincide with the tides and (ii) whether this relationship differs between tool-using and non-tool-using capuchins. White-faced capuchins are exploratory dietary generalists who rely heavily on extractive foraging to access structurally protected resources in varied neotropical forests [63, 64, 181]. Many of these extractive foraging behaviors are socially learned [66–68]. Despite decades of studies across multiple field sites [70, 71], habitual stone tool use by white-faced capuchins has only been documented in at least one group of capuchins on the island of Coiba [31] and one group on the island of Jicarón [30] in Coiba National Park, located approximately 30 km off the Pacific coast of Panama. Recently, stone tool use was also described in an urban population of *Cebus albifrons* in Ecuador [32]. Coiban capuchins use hammerstone and anvil tool use to access a variety of food items, including sea almonds (*Terminalia catappa*), coconuts (*Cocos nucifera*), Halloween crabs (*Gecarcinus quadratus*), palm fruits (*Bactris major* and *Astrocaryum spp.*), hermit crabs (*Coenobita compressus*), nerite snails (*Nerita sp.*) and other freshwater molluscs. Coiban capuchins differ from well-studied mainland populations in showing increased terrestrial activity, likely due to the lack of mammalian predators on the island [76] and live at high population densities [30, 75]. Additionally, both Coiba and Jicarón have lower plant richness than similar mainland ecosystems [81, 121]. On Jicarón, this tool use tradition is highly localized along the coast and mostly limited to one social group [30], despite similar ecological circumstances and no physical barriers between the tool-using capuchin group and other groups of non-tool-using capuchins on the island. Further, both tool-using and non-tool-using capuchins on Jicarón are maritime mammals—that forage on (structurally protected) marine prey items along the coast and in the intertidal zone, such as crabs and snails [30] (electronic supplementary material, video S1). Coiba National Park experiences mixed tides; two low tides of different heights occur every approximately 12.5 h. Thus, the timing of the low tide(s) experienced by capuchins shifts approximately 30 min each day (see Figure C.1 for the timing of low tides for one month). As such, visits to the intertidal zone at a repeatable time each day are insufficient for capuchins to regularly exploit coastal resources.

Here, we investigate how the pattern of Coiban capuchins' activity varies with shifting tidal cycles, by using camera trap data collected from March 2017 to January 2023. We compare how the patterns of activity, relative to distance from the coast and tidal cycles, differ between tool-users and non-tool-users. As exploitation of intertidal resources likely has a seasonal component (e.g., red deer [182] and baboons [168]), we examine differences in tidal patterns for tool-using and non-tool-using capuchins between the wet and the dry season. Lastly, capuchin activity at the coast can be affected by diurnal activity and space use patterns, which are likely shaped by temperature and sleeping site location. To gain a more complete picture of capuchins' activity at the coast, we also consider intra-diel capuchin activity (i.e. are capuchins more likely to be at the coast at a specific time of day). By jointly examining these questions in a system with tool-using and non-tool-using capuchins, we provide a first exploration of the relationship between tool use and tidal cycles for a non-human animal in a coastal habitat. This provides insights into how an ecological generalist copes with complicated cycles of resource availability in a non-typical habitat, and provides a much needed comparative study to help understand potential hominin behavior in coastal environments where tool use is unlikely to be preserved [183, 184].

3.3 Methods

3.3.1 Subjects and site

Coiba National Park consists of nine islands and over 100 islets located off the Pacific coast of Veraguas Province, Panama. It is a designated UNESCO World Heritage site with endemic animal and plant species [80]. White-faced capuchins (*Cebus capucinus imitator*) live on the islands of Coiba (50 314 ha), Jicarón (2002 ha) and Rancheriá (125 ha). These islands are estimated to have been geographically isolated from mainland Panama for 14 000–18 000 years [77]. The terrestrial mammalian communities in Coiba National Park are depauperate in comparison to forests on the mainland, and mammalian predators are entirely absent. Coiba and Jicarón were used as a penal colony from 1919 until 2004, prior to which the islands were inhabited by indigenous people from 250 CE until about the sixteenth century [78]. In recent years, only the island of Coiba and Rancheriá see constant human occupation at two research stations and a police station; the other islands (including Jicarón) are largely undisturbed by humans in recent centuries [30]. Average annual temperature in Coiba National Park is around 26 °C. Rainfall varies seasonally. In the dry season (mid-December to mid-April), there is less than 60 mm of precipitation, while in the wet season there is over 3000 mm of precipitation [185].

Stone tool use on Jicarón has been documented at three types of sites, distinguished by the degree of accumulation of debris and tools due to activity intensity and site erasure [30]: (i) elusive sites with low to no accumulation, such as the intertidal zone where debris is washed away, (ii) sites in streambeds, with low to medium accumulation due to more sporadic tool use, and (iii) high accumulation sites—referred to as 'anvils' from here on out—further away from streambeds, where large amounts of debris and tools can accumulate over time as capuchins habitually use tools. Since the start of data collection on Jicarón in 2017, habitual tool use at high accumulation anvil sites has only been observed to occur along an approximately 1 km stretch of coast, likely occupied by a single group of capuchins as documented by camera trap data. In 2022, in-person observations confirmed the occurrence of tool use in the intertidal zone by the two groups neighboring the approximately 1 km stretch of coast (C. Monteza-Moreno, pers. comm. 2023). However, extensive camera trapping and surveys of the coast and in riparian areas yielded no evidence of tool use (both at high accumulation anvil sites and streambeds) outside of this stretch of coast. Therefore, we refer to the other surveyed groups on the island as non-tool-using groups.

3.3.2 Data collection and processing

Data collection

We analyzed images and videos collected using unbaited camera traps on the island of Jicarón between 25 March 2017 and 24 January 2023 (with a gap in data collection in 2020 due to the COVID pandemic) in 11 deployments of about approximately four months (three to six months). Both still (Reconyx Hyperfire HC600 & HF2X) and video (Reconyx Ultrafire XR6 & XP9) camera traps were used. Camera traps are not fully non-invasive, as they are visually incongruent with the surroundings, and produce sounds or light which may disturb animals (and some individuals/species more than others) [83]. We purchased infrared rather than white flash camera traps to minimize disturbance to the animals.

Still-image camera traps recorded 10 images per trigger event without any between-trigger delays (approx. 1 s between images). Video cameras recorded over a 24-h period and captured one image and a dynamic video per trigger, which means that the camera trap stops recording after 3 s of inactivity, and retriggers if additional movement is detected within 27 s. This results in videos of varying lengths, with a maximum length of 30 s (however, we deployed two video cameras with a static video length of 30 s per trigger). We surveyed 61 camera sites within the range of the Jicarón tool-using group, of which 11 targeted anvil sites, 26 were placed at untargeted locations in the streambeds and forest interior and 24 were placed as a 100-m spaced grid. We also surveyed 43 other camera sites in non-tool use areas on Jicarón, of which 18 were placed at untargeted locations, and 25 in a 100-m spaced grid comparable to the one in the tool-using group's range.

We can reliably identify most members of the tool-using group (due to their unique tool-using behavior and increased sampling and coding efforts), allowing us to be confident about which cameras were placed in the tool-using group range. For the non-tool-using capuchins, based on co-occurrence of identifiable individuals we are confident that the 25 grid cameras all capture one non-tool-using group. However, the 18 untargeted cameras capture multiple non-tool-using groups due to their spread across the island (see tables C.1 and C.2 for details on camera trap deployments). Table 3.1 details our estimates of size and composition of the tool-using group and non-tool-using group sampled by the grid cameras.

In total, 137 cameras (117 stills and 20 videos) were deployed during the accumulated sampling period at 104 sites. Out of these deployments, 89 had a single sampling period. The remaining 15 sites were repeatedly sampled (ranging from 2

Estimated numbers	*Tool-using group*	*Non-tool-using group*
Adult females	5-6	5-6
Adult males	5-6	5-6
Subadults	2-4	2-3
Juveniles	6-10	7-9
Total	20-25	19-23

Table 3.1: Estimated average group size and composition of the tool-using group and non-tool-using group sampled by grid cameras throughout our sampling period. Estimates are based on a) identifiable individuals, b) the maximum number of capuchins observed in a sequence, and c) the maximum number of individuals of a particular age-sex class observed together. No exact numbers are known because of the nature of data collection via camera trapping and fluctuation throughout our sampling period.

to 6 deployments in the same location). Average duration of sampling nights per camera was 145.30 (range 9–260), totaling 12 748 sampling nights for the tool-using group and 7152 nights for non-tool-using groups. Camera traps were deployed at various distances from the coast (meaning the coastal vegetation boundary, for more information see below), and grid cameras were placed further inland than other cameras (for the tool-using group non-grid cameras 0.8 m–140.4 m, grid cameras 11.7 m–328.3 m; for non-tool-using groups non-grid cameras 0.5 m–39.2 m and grid cameras 6.1 m–469.7 m). Few camera traps were placed on the beach directly targeting the intertidal zone due to challenges in mounting (i.e., tree availability and seawater) and vandalism.

Coding of images and data processing

Still-images were compiled into sequences based on the time between triggers: all bursts of images triggered less than 30 s apart were considered part of the same 'sequence'. Each video of 30 s was considered a single sequence. All sequences were coded in Agouti, an online platform for archiving and annotating camera trap data [123]. In each sequence, we identified the animal species visible and the number of individuals per species. For analyses, we only considered sequences with capuchins in them ($n = 22\,185$). We did not include any 0's in our models because an absence of capuchin detections does not necessarily mean an absence of capuchins (e.g., camera traps do not always trigger fast enough to capture a traveling animal). Our analyses thus focus on comparing differences in patterns of detection rates in capuchin activity rather than the absence or the presence of capuchins. Further, our focus is not to estimate activity patterns as is commonly done for multiple species, using timestamps from camera trap pictures [186–188]. Instead we are modeling the non-random, spatiotemporal patterns of animal detection, which we refer to as *capuchin activity*. We excluded deployment set-up and collection days from all analyses, as on these days the human presence may have altered capuchin behavior.

Tidal data, i.e., timing of low and high tides, were obtained from http://www.tides4fishing.com for Cébaco island, which lies approximately 90 km from Jicarón, and is used locally by fishermen in the area and digitized into a `.csv` using the software Tabula (https://tabula.technology). As the intertidal zone is maximally exposed around the peak of low tide, we calculated the time difference between the initial timestamp of each photo sequence and the time of the nearest low tide. These values ranged from approximately -6 to 6 h, with 0 indicating the peak of low tide and around -6 and 6 the peaks of high tides. Negative values indicate times where the tide is receding, positive values indicate that the tides are approaching the coast.

We calculated the distance of each camera site to the coast by taking the distance from a camera's GPS point to the nearest coastal vegetation boundary. To determine the coastal vegetation boundaries, we used high-resolution satellite imagery from Planet Labs [189]. We used 3 m resolution, four-band surface reflectance Planet imagery from 29 January 2021. On this date, cloud cover was near zero and the image was collected at low tide. We used a normalized difference vegetation index threshold of 0.7 to determine the boundary between coastal vegetation and sand or rock. Data were processed in Google Earth Engine and using the `terra` package in `R` [190]. We split the data into dry and wet season based on known rainfall and temperature differences, with the months December–April being part of the dry season and May–November being the wet season.

3.3.3 Statistical analyses

We used hierarchical generalized additive models (GAMs) fit using Bayesian regression modeling with Stan via the `brm` function in the `brms` package v. 2.17.0 [127]. All statistical analyses were done in `R` v. 4.2.2 [124]. GAMs are extensions of generalized linear models that allow estimation of nonlinear patterns in data without any prior knowledge of the shape of the expected relationship. Inference is done on the basis of a sum of smooth functions, which are penalized regression splines [191, 192]. GAMs are especially useful for seasonal and cyclical data where relationships are unlikely to be linear, such as capuchin activity and tidal cycles. While GAMs are well suited for identifying nonlinear patterns in data, they require caution when used for forecasting based on new data [191].

We fit five different GAMs: three including capuchin activity in relation to time to nearest low tide and two considering diurnal activity. For the tidal models, we ran an initial model (model MT_1) on all of the data comparing the effect of tidal cycles on activity between tool-using and non-tool-using groups. Then we considered differences in tidal pattern between the dry and wet season for the tool-using (MT_2) and non-tool-using groups (MT_3) separately. The diurnal activity GAMs examined how spatial spread of activity patterns varies depending on the time of day, also separately for the tool-using (MD_1) and non-tool-using groups (MD_2).

GAM specifications

To compare tool-users to non-tool-users (model MT_1), we fit a Poisson GAM. Our outcome variable was the count of unique capuchins annotated in a sequence. For predictors, we estimated the effects of (i) temporal difference from nearest low tide, (ii) distance of camera trap from coast, and (iii) an interaction of temporal difference from nearest low tide and camera distance from coast. We used tensor product smooths for this interaction, which allows one to model responses of the outcome variable to interactions of multiple variables with different units.

We used a cyclic cubic spline for time to nearest low tide, as 6 h before a given low tide matches up to 6 h after the previous low tide. We also estimated varying smooths of this tensor product for the tool-using and non-tool-using groups, and included if a group were tool-users (1) or non-tool-users (0) as an index variable. As we have uneven sampling between the tool-using and non-tool-using groups, we include a global tensor smoother for distance to coast and time to low tide, and a tensor smoother considering the tool-using group and non-tool-using groups separately as smooth deviations from that overall surface. We included camera trap location as a random effect.

Secondly, to assess seasonality in a possible tidal effect, we fit two more GAMs with the same structure: one for the tool-using group (MT_2) and one for the non-tool-using groups (MT_3). In these models, we estimated varying smooths of the tensor product for the wet and the dry season, and included the season, wet/dry, as a fixed effect.

Lastly, to investigate the relationship between coastal activity and temperature, we used time of day as a proxy, since temperature varies depending on the time of the day. We used a proxy rather than the actual temperature as camera trap measurements of ambient temperature are unreliable and we lack independent measurements (e.g., from a weather station) to validate them. As such, we fit the same structure GAMs as for the seasonality question, one for the tool-using group (MD_1) and one for the non-tool-using group (MD_2). However, we used hour of the day (from 0 to 23) rather than time to low tide.

We z-transformed time to low tide, distance from coast, and hour of the day to improve computational speed, model fit, and ease parameter interpretation. All models were fit with mild regularizing priors, using Normal(0,2) for the intercept and estimates, and exponential(1) for standard deviations. We performed a prior predictive simulation to visualize the priors. We ran the final models with three chains, each having 4000 iterations, including a warm-up period of 2000 iterations per chain. Our model was stable with large effective sample sizes (Bulk_ESS and Tail_ESS over 1000 for nearly all estimates) and Rhat values smaller than 1.01. For all models, Pareto k estimates were below 0.5. We used the posterior predictive check function to visually assess model fit and confirm our choice of priors. For full model specifications and details, see section C.2 and associated reproducible R code.

Assessing reliability of model estimates

Tensor smooth products were visualized into two-dimensional heatmaps (filled contour plots) using the `ggplot2` package v. 3.3.6 [193]. To assist in interpretation of these patterns, we used the 'method of finite differences' to estimate the first derivative of the spline, which allows for identification of periods of change along a fitted spline. Previous implementations of the method of finite differences on GAMs, were done on single-dimension splines in a frequentist context [194, 195]. We have built upon this by developing a Bayesian extension of this method for two-dimensional interaction splines [196]. To accomplish this, we first used the `posterior_smooths` function in `brms` to obtain posterior predictions. Then we recomputed posterior predictions after adding or subtracting a small offset, 0.001, for both predictors in the tensor smooth. As predictors were z-transformed, 0.001 represents 1/1000th of 1 s.d. for each predictor, a comparable change in both predictors despite their different scales. The first derivative of the two-dimensional tensor smooth can be approximated as follows:

$$f_{td} \sim \frac{\begin{array}{c} f(t + eps_{h,d} + eps_k) - f(t + eps_{h,d} - eps_k) \\ - f(t - eps_{h,d} + eps_k) + f(t - eps_{h,d} - eps_k) \end{array}}{4 * eps_h * eps_k} \tag{3.1}$$

where t and d represent the two predictors in the tensor smooth interaction (e.g., time to low tide and distance to coast). Here eps_h and eps_k represent the small offset that is added or subtracted to each estimate. With the first derivative approximation, we could identify regions of the two-dimensional surface where the slope was non-flat in all four directions represented in the numerator of Equation 3.1. If 89% of the posterior uncertainty interval of the first derivative was on one side of 0, then we interpreted it as reliable evidence for a non-zero rate of change. This conservative criterion allows us to identify areas of the two-dimensional surface of model estimates where we have the most evidence that: (i) the model reliably predicts a nonlinear change (ii) this change is consistently (greater than 89% of the time) in the same direction even with small perturbations to the model. Contourplots showing the proportion of the derivatives above and below zero are provided as electronic supplementary material (figures C.4, C.7, C.10, C.12, and C.14).

3.4 Results

Capuchins live at high densities on Jicarón, but use different locations with varying intensity. We observed capuchins at least once on every camera trap within each deployment (sequences with capuchins range: 4–1346). On average, 2 ± 1.51 (range 1–22) capuchins were observed per sequence. All models indicated considerable variation between camera locations (see figures C.2, C.5, C.8 for model estimates of capuchin activity per camera location).

3.4.1 A guide to interpreting two-dimensional heatmaps of derivatives

We present the best predictions of our model in Figure 3.1. We guide the reader through how to interpret these types of graphs using Figure 3.1 as an example. In these figures, the y-axis represents the distance from the coast in meters. The x-axis represents hours until and after nearest low tide, where 0 indicates low tide and the boundaries of the graph around -6 and 6 represent high tides. Observations are indicated in the margins of the axes by translucent gray hash marks. In these heatmaps, color reflects capuchin activity: 0 is the mean number of capuchins from z-score transformed raw data. Light colors indicate a greater number of capuchins than the mean, while dark colors indicate a lower number of capuchins. For example, in Figure 3.1b, the orange peak at all distances around low tide (0) indicates highest capuchin activity. The small dark purple trough at 2 h after low tide indicates lowest capuchin activity. We use color saturation to represent evidence for a reliable nonlinear change in the number of capuchins as represented in Equation 3.1. Color-saturated areas have more than 89% of the derivative being non-zero, indicating that estimated changes in capuchin activity are consistently in the same direction (i.e., positive or negative). In Figure 3.1, no areas are color-saturated, which shows that we do not see strong, reliable evidence for changes as defined by our 89% criterium. Figure C.4 shows exactly how much support there is for specific areas of the two-dimensional heatmap by estimating the mass of the derivative of the posterior on either side of zero. This shows the area with most support is from low tide until 4 h after at less than 50 m from the coast for tool-users (the lighter area in Figure 3.1a). However, the proportion of the posterior on one side of 0 here is between 75% and 80%, and thus does not meet our 89% cutoff criterium, which is why it is not saturated.

3.4.2 Tool-users versus non-tool-users (Model MT_1)

The influence of tides on space use patterns differed for tool-using and non-tool-using groups. While we observe little difference between tool-users and non-tool-users in the number of capuchins present per sequence (tool-users: 1.60 [95% CI 1.36–1.95], non-tool-users: 1.65 [95% CI 1.42–1.90]; see Table C.3 for estimates), the patterns of capuchin activity relative to the tidal cycle vary.

For the tool-using group (Figure 3.1a), our model estimates a higher number of capuchins near the coast compared to further inland, although the difference is

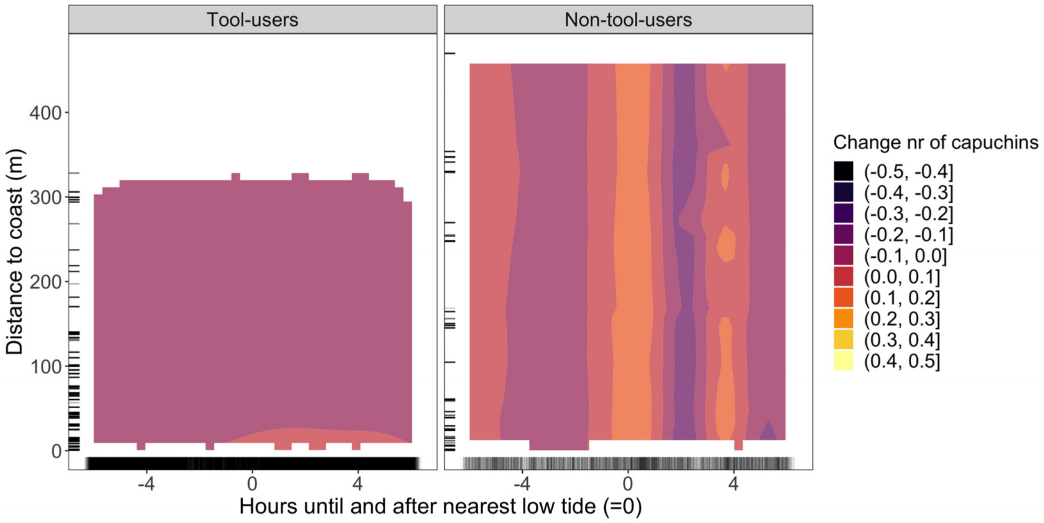

Figure 3.1: *Tidal activity of tool-using versus non-tool-using capuchins.* Two-dimensional heatmap showing capuchin activity (color) at various distances to the coast (y-axis) and hours until and after nearest low tide (x-axis), for the (a) tool-using group and (b) non-tool-using groups separately. More color-saturated areas indicate where greater than 89% of the posterior distribution of the derivative of the tensor smooth interaction lies on one side of 0. Note the rug showing the density of sampling, which reflects the greater density of sampling close to the coast and sparser sampling further inland.

small (change of less than 0.2, see Figure C.3 for a zoomed in plot of the area 0–50 m from the coast). We see more capuchin detections close to the coast (0–30 m) at and after the peak of low tide (0–6 h) compared with before (-4–0 h). We do not see reliable evidence (greater than 89%) for a nonlinear change in the number of capuchins, but the increase of capuchins close to the coast after low tide is observed 75–80% of the time, based on the derivative of the tensor smooth interactions (Figure C.4).

By contrast, for the non-tool-using groups (Figure 3.1b), our model estimates larger changes in capuchin activity related to the tidal cycle, but consistent across all distances from the coast instead of concentrated closer to the coast. Based on the heatmap, non-tool-using capuchins show more activity around the peak of low tide, less activity after (around 2 h), and greater activity 4 h after low tide. There are no areas of the heatmap where there is reliable evidence for a change in capuchin activity (Figure C.4).

3.4.3 Seasonality: tool-using group(Model MT_2)

We considered seasonality in separate models for the tool-using group and non-tool-using groups. Although for the tool-using group we find comparable numbers of capuchins per sequence between the dry and wet season (dry season: 1.54 [95% CI 1.30–1.79], wet season: 1.63 [95% CI 1.49–1.80]; see Table C.4), the patterns of capuchin activity in relation to the tidal cycle differ.

The activity of the tool-using group varies with the tides throughout the year, but stark differences exist between the patterns observed in the dry and wet seasons.

In the dry season (Figure 3.2a), capuchin activity at all distances peaks around high tide (-6 and 6 h) and is lowest around low tide (-2 to 2 h). Changes in when and where capuchins are active are smaller in the dry season than in the wet season. Based on the derivative of this model, there are no combinations of distance and time to low tide where we have reliable evidence for differences in activity (Figure C.7). By contrast, in the wet season (Figure 3.2b), we see the opposite pattern. Our model estimates that capuchin activity near the coast is lowest after the peak of high tide, and is highest near the coast immediately preceding and following low tide (-2 to 4 h). Additionally, capuchins are most active further inland (250–300 m from the coast) around high tide (-6 and 6 h). This is also the time period when capuchin activity near the coast is lowest. The derivative highlights large areas where we have reliable evidence for a strong, nonlinear change in capuchin activity, concentrated around the peak of low tide and cameras closer to the coast (less than 30 m). See also Figure C.6 for a zoomed in view of predicted capuchin activity between 0 and 50 m from the coast.

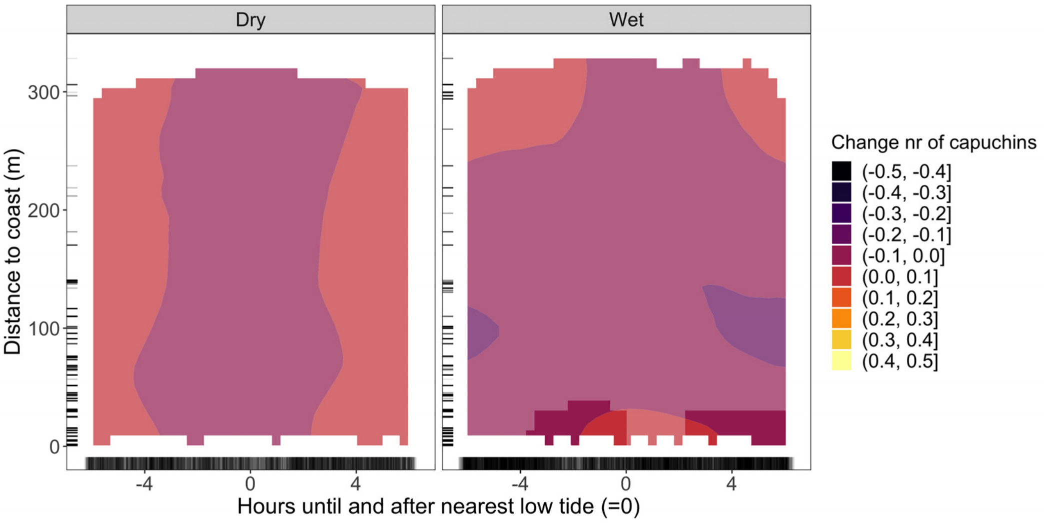

Figure 3.2: *Tidal activity of tool-using capuchins: dry versus wet season.* Two-dimensional heatmap showing capuchin activity (color) of the tool-using group at various distances to the coast (y-axis) and hours until and after nearest low tide (x-axis), for the (a) dry and (b) wet season separately. More color-saturated areas indicate where 89% or more of the posterior distribution of the derivative of the tensor smooth interaction lies on one side of 0.

3.4.4 Seasonality: non-tool-using groups (Model MT_3)

Tidal influence on the space use patterns of the non-tool-using groups is most pronounced during the dry season, which is opposite to our findings for the tool-using group, whose activity near the coast is estimated to peak around high tide in the dry season and around low tide in the wet season. As with previous models, we found no change in the average capuchin activity between seasons (dry: 1.63 [95% CI 1.39–1.92], wet: 1.58 [95% CI 1.39–1.84]; see Table C.5), but rather changes in the timing of capuchin activity at different distances from the coast.

In the dry season (Figure 3.3a), the pattern estimated by our model is similar to the predictions of our first model comparing tool-using and non-tool-using groups (Figure 3.1b). The model estimates higher capuchin activity near the coast in the hours around low tide (-2 to 2 h, Figure C.9 for a zoomed in view of the predictions near the coast). The peak of capuchin activity as estimated by the model lies further after low tide and slightly inland (3-4 h after low tide at 20–40 m). We see no reliable evidence for a change in capuchin activity in any regions further of the heatmap (greater than 89%), although at the areas with the largest predicted changes in capuchin activity up to 70–80% of the derivative is on one side of 0 (see Figure C.10). In the wet season (Figure 3.3b), changes in capuchin activity are much smaller than in the dry season. The model estimates a slightly lower number of capuchins near the coast before and after low tide (-4 to 5 h) than around high tide (-6 to -4 and 4 to 6); however, this difference is small (less than 0.1). There are no regions of the heatmap where we have reliable evidence for a change in activity for non-tool-using groups.

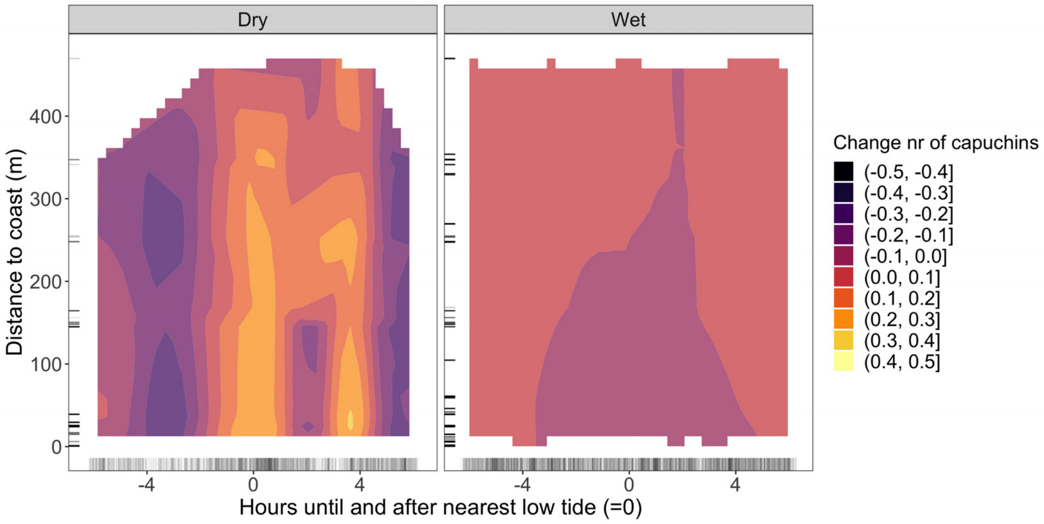

Figure 3.3: *Tidal activity of non-tool-using capuchins: dry versus wet season.* Two-dimensional heatmap showing capuchin activity (color) of the non-tool-using groups at various distances to the coast (y-axis) and hours until and after nearest low tide (x-axis), for the (a) dry and (b) wet season separately. More color-saturated areas indicate where 89% or more of the posterior distribution of the derivative of the tensor smooth interaction lies on one side of 0.

3.4.5 Daily activity: tool-using group (Model MD_1)

Consistent daily shifts in temperature or capuchin movement patterns are possible explanations for varying capuchin detection rates at the coast relative to the tides. For the tool-using group, we see a consistently different activity pattern between the dry and wet season in relation to distance to the coast and time of day.

In the dry season (Figure 3.4a), our model estimates that capuchin activity near the coast is lowest in the morning, and higher only after 17.00 (see Table C.6 for model estimates). Based on the derivative, we have reliable evidence for a change in capuchin activity in a small region close to the coast around 11.00 (see figures C.11 and C.12). In the wet season (Figure 3.4b), we see higher coastal activity throughout the day, with the peak of activity occurring between 11.00 and 19.00. Before 11.00, capuchin activity inland (greater than 200 m) is higher than coastal capuchin activity. In the dry season, we observe capuchin activity until later in the day (21.00) than in the wet season (19.00). In one small region of the heatmap (approx. 11.00 at approx. 200 m inland), we have reliable evidence supporting a change in the number of capuchins. However, the increase in capuchins' coastal activity in the afternoon is supported with over 80% of the derivative being positive (see Figure C.12).

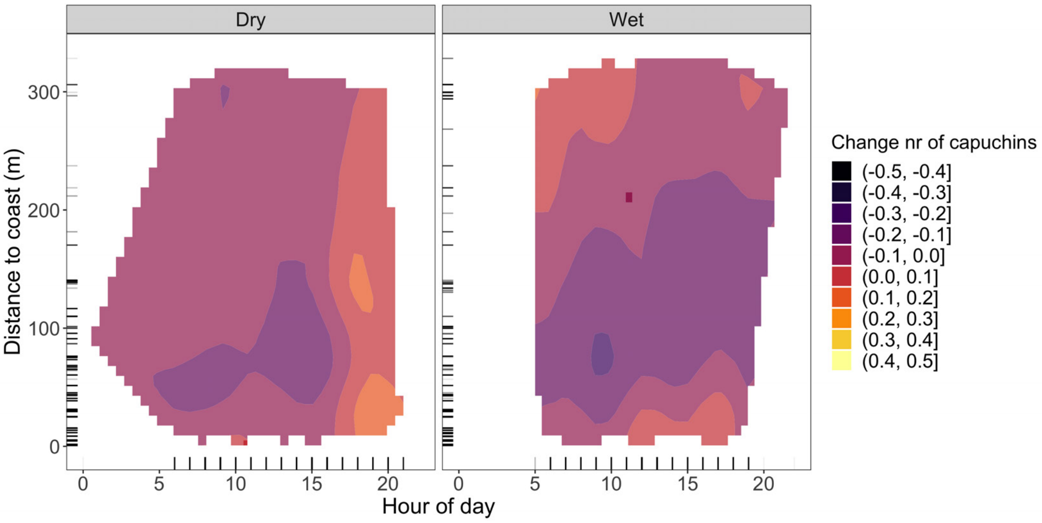

Figure 3.4: *Diurnal activity of tool-using capuchins: dry versus wet season.* Two-dimensional heatmap showing capuchin activity (color) of the tool-using group at various distances to the coast (y-axis) and hours of the day (x-axis), for the (a) dry and (b) wet season separately. More color-saturated areas indicate where 89% or more of the posterior distribution of the derivative of the tensor smooth interaction lies on one side of 0.

3.4.6 Daily activity: non-tool-using group (Model MD_2)

For the non-tool-using groups, we observed an opposite pattern to the tool-using group when considering activity at varying distances to coast in relation to time of day (Figure 3.5; see Table C.7). In the dry season (Figure 3.5a), our model estimates highest capuchin activity at cameras near the coast (0–70 m) in the morning until 12.00 (see Figure C.13 for a zoomed in view of predicted coastal activity). Estimated capuchin activity is lowest in the afternoon (13.00–18.00) from near the coast until as far as 300 m inland. We do not have reliable evidence for a change for any areas of the heatmap, but there is up to 85% support for the decrease in capuchin activity in the afternoon (Figure C.14). In the wet season (Figure 3.5b), estimated changes in capuchin numbers are smaller than in the dry season, and there are again no areas of the two-dimensional heatmap where the derivative provides reliable evidence for a change. The model estimates a slightly lower number of capuchins near the coast than further inland throughout the day, until the late afternoon, when capuchins' coastal activity increases slightly. Highest capuchin activity lies inland (300–400 m) in the morning.

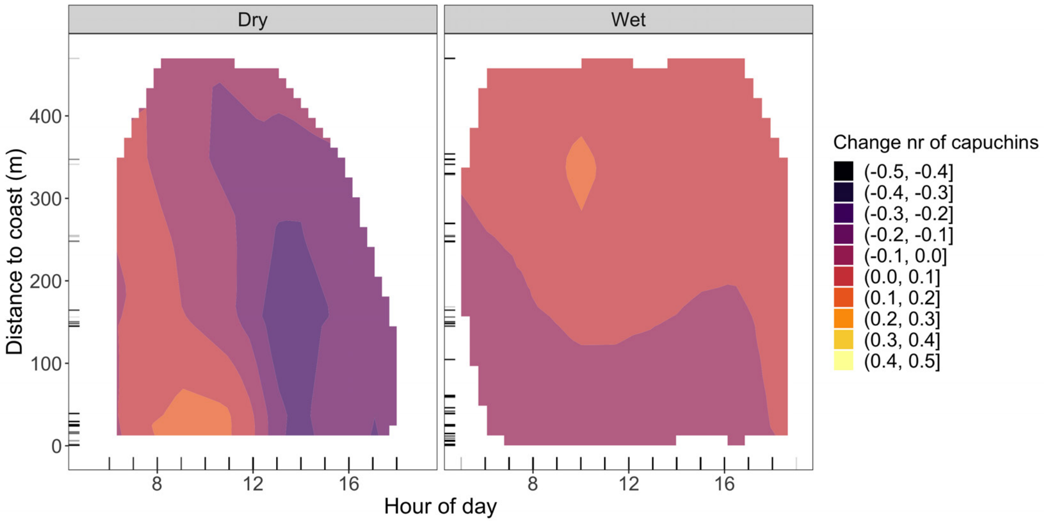

Figure 3.5: *Diurnal activity of non-tool-using capuchins: dry versus wet season.* Two-dimensional heatmap showing capuchin activity (color) of the non-tool-using groups at various distances to the coast (y-axis) and hours of the day (x-axis), for the (a) dry and (b) wet season separately. More color-saturated areas indicate where 89% or more of the posterior distribution of the derivative of the tensor smooth interaction lies on one side of 0.

3.5 Discussion

White-faced capuchins living on Jicarón island adjust their activity patterns in correlation with tidal cycles. Our findings are consistent with the hypothesis that availability of intertidal resources plays an important role in shaping patterns of movement and habitat use. We find seasonal variation in the relationship between capuchin activity and the tidal cycle, as well as in capuchins' daily activity patterns. Tool-using and non-tool-using capuchins are seen less frequently near the coast in the dry season during the hottest times of the day (approx. 13.00–17.00), suggesting that high temperatures likely limit capuchins' activity near the coast and potentially in the intertidal zone. Although capuchins in both tool-using and non-tool-using groups consume intertidal resources, they show different patterns of activity in relation to tidal cycles. Activity of the tool-using group near the coast increases around high tide in the dry season, and around low tide in the wet season. Patterns are more pronounced in the wet than the dry season, when differences in estimated capuchin activity are larger and we have more reliable evidence supporting these changes. By contrast, non-tool-using groups' activity near the coast is higher around low tide in the dry season and around high tide in the wet season, with more pronounced differences in capuchin activity in the dry season.

3.5.1 Capuchin activity varies in relation to tidal cycles

By showing that tool-using and non-tool-using capuchins' activity at the coast is related to the tidal cycle, we provide additional evidence that exploitation of intertidal resources by maritime foragers shapes the rest of their activity patterns, similar to seabirds [176] and arctic foxes [177]. While from our data, we cannot conclude whether exploitation of the intertidal zone is opportunistic or obligate [162], the tight coupling between Coiban capuchin's coastal activity and tidal cycles indicates that Coiban capuchins likely exploit intertidal resources regularly. Tool-using and non-tool-using capuchins consistently spend time near the coast at either low or high tide, depending on the season. While there are multiple factors that could attract capuchins to the coast (e.g., coastal resources which are not linked to the tides, like coconuts, crabs and sea almonds), because the timing of low tide shifts each day, the observed patterns cannot arise from intermittent activity near the coast irrespective of the tidal cycle. These findings indicate that Coiban capuchins are timing their activity at the coast to coincide with specific parts of the tidal cycle.

3.5.2 Temperature limits coastal activity

Tool-using and non-tool-using capuchins show increased coastal activity at different periods of the tidal cycle (Figure 3.1). To understand these differences, we first have to consider differences in coastal activity between seasons. If seasons are jointly analysed, signatures of seasonal variation in coastal activity can be weakened or masked if a pattern is only present in one season and absent in the other, or if seasonal patterns are opposite to one another. Higher temperatures and lack of rainfall in the dry season affect capuchins' daily activity and, potentially, their exploitation of the intertidal zone. During the hottest times of the day, capuchins prefer resting rather than energy-expending activities like foraging and travelling [197], and presumably, tool use. This is supported by both the tool-using group and non-tool-using groups showing lower activity in the dry season during the hottest time of the day (approx. 15.00) at all distances to the coast (Figure 3.4a and Figure 3.5a). Capuchins might compensate for missed daylight activity by staying active later in the evening. We see this for the tool-using group who shows activity up to 2 h later in the dry season than in the wet season (Figure 3.4b).

Temperature regulation might also be a driving force to spend time near the coast in general, or at varying moments of the tidal cycle. Overall, the microclimate at the coast is cooler than inland, due to the atmospheric phenomenon of sea breezes which carries cool air to the coast [198]. At high tide, this cooler microclimate would be more pronounced than at low tide, when the water has further receded. While hot temperatures might push capuchins to the coast where it is cooler, heat might also repel them from the intertidal zone. When it is hot, capuchins might be less inclined to venture into the intertidal zone, where there is no shade, the rocks and sands heat up in the sun, and water in tidal pools and crevices evaporates more quickly. This rapid evaporation increases water temperature and salinity, which reduces the number of species that survive in tidal pools. Thus, at high temperatures, capuchins might be attracted to the cooler coast, but avoid the exposed intertidal zone where it is hotter with less available prey.

3.5.3 Seasonality in capuchin activity: tool-users versus non-tool-users

The tool-using group shows decreased activity at all distances from the coast in the dry season around low tide (Figure 3.2a), which supports the idea of temperature limiting their (coastal) activity. Immediately after high tide, the sand is still wet and cool from the receding water and the capuchins can remain close to the shade of the tree line, making it possible to consume snails, such as *Nerita scabricosta*, which migrate to the top of the intertidal zone at high tide [199]. However, the lack of differences in activity between coastal and inland cameras suggests this pattern might be more related to temperature regulation aspects of the coast rather than potential intertidal foraging. In the wet season, when temperature is not a limitation, we see reliably high coastal activity of the tool-using group up to 2 h before and 4 h after the peak of low tide (Figure 3.2b). This group may exploit the full intertidal range that is exposed in the hours before and after low tide. In contrast, the non-tool-using groups show highest coastal activity in the dry season around low tide and 4 h after low tide (Figure 3.3a), which is unexpected if temperature is a major limitation. However, increased capuchin activity is not localized at the coast but rather extends far inland. One possible explanation is that non-tool-using capuchins are at the coast during low tide only for some low tides of the day, while for others they are resting or further inland. Some low tides will be cooler than others: the intertidal zone is likely colder during a low tide at 9.00 than one at 14.00. Non-tool-using capuchins might be near the coast in the dry season when it is not the hottest time of the day, and only venture into the intertidal during these cooler low tides, which could lead to the observed pattern. The non-tool-using groups do not appear to consistently be closer to the coast around low tide, but rather only after high tide (Figure 3.3a). Additionally, differences in capuchin activity near the coast are less certain than for the tool-using capuchins, indicating that non-tool-using capuchins show less consistent activity patterns with the tidal cycles.

3.5.4 Seasonality in food availability as a driver of intertidal exploitation

Despite temperature limiting activity in the dry season, this appears to be when non-tool-using capuchins show the strongest tidal pattern (Figure 3.3a). The contrasting pattern of tool-using capuchins showing most coastal activity correlated with the tidal cycle in the wet season raises the question: what role does seasonality in food availability play in intertidal exploitation? Resource scarcity is likely experienced differently by tool-using and non-tool-using groups, as tool-using groups can access structurally protected resources more efficiently [5]. Additionally, the tool-using group is located on the side of Jicarón facing the open sea, where exposure effects are more severe and possibly fewer resources are available than at the other side of the island. We have no direct information on seasonal fluctuation in food availability on Jicarón, but tool use occurs more frequently in the transition periods between wet and dry seasons, which might be in response to a limitation in terrestrial resources [30]. This would be in contrast to tool use in *Sapajus* capuchins, which was found to be driven by opportunity rather than necessity [27, 200]. It is important to consider that capuchins are dietary generalists who not only consume fruits but also insects and other invertebrates, which have their own seasonal fluctuations. Additionally, oceans are also seasonal and, as such, resources in the intertidal zone likely vary spatially and temporally across seasons (e.g., snails [201]). However, for tool-using capuchins, exploitation of intertidal resources might not be driven by a scarcity of terrestrial resources: in the wet season, there is likely peak availability of one of the tool-users most consumed resources, *Terminalia catappa*, which bears fruit from January to April and from May to September [149]. This coincides with high rates of coastal activity around low tide and the possible exploitation of intertidal resources.

3.5.5 Tool-users versus non-tool-users: why such different patterns?

Why do we observe a difference in the relationship between activity and tidal cycles for the tool-using group and non-tool-using groups? The non-tool-using groups show more activity at the coast during low tide in the dry season, when temperature likely constraints coastal activity, and no clear tidal pattern in the wet season (Figure 3.3). The tool-using group's coastal activity is clearly consistent with exploitation of tidal resources around low tide in the wet season (Figure 3.2b). We propose two explanations for why non-tool-using groups might exploit intertidal resources more opportunistically or more rarely than tool-using capuchins.

First, the spatial fixedness of both materials and resources for tool use might drive tool-users to spend more time near the coast. Stones large enough to serve as anvils and hammerstones are more abundant at the coast and the mouth of streams than further inland and may also be prevalent in the intertidal zone itself. Further, important resources, including bivalves, crabs and sea almond trees are restricted to the coast [149]. Because of these constraints, the tool-using group's important foraging spots and anvils are all close to the coast, giving tool-users more opportunities to pick up visual and auditory cues of low tide and more opportunities to exploit tidal resources. Non-tool-using groups, who also forage on sea almonds but only eat the less calorically dense exocarp of ripe fruits and not the nut inside [30] (also see [202] for evidence in another population), likely need to forage more widely for resources and do not have a similar reliance on coastal locations as the tool-using group. Thus, increased proximity to the coast due to reliance on coastal tool use resources might allow and encourage the tool-using group to forage in the intertidal zone more frequently.

A second explanation is that tool use allows the tool-using group to exploit intertidal resources more consistently than the opportunistic foraging by non-tool-using groups. By allowing access to encapsulated resources, percussive tool use can both broaden the diversity of consumable food items (such as tool-using *Sapajus* in mangroves gaining access to snails [178], improving diet quality [33], and increase the efficiency of consuming known resources [5]). Both (or either) of these aspects of tool use could explain why the tool-users might show more intertidal foraging than non-tool-using groups. The costs due to energy investment, time lost foraging elsewhere, and risk of venturing out into the exposed intertidal zone might be outweighed by tool-users' ability to open more resources in the intertidal with greater efficiency than non-tool-users.

Differences in sampling between the tool-using group and non-tool-using groups in spatial and temporal coverage (a small area with dense camera trapping versus a larger area with sparse camera trapping) as well as comparing one group to a multitude of groups may have affected our results. This possible limitation implies that while we can be more confident of the presence of a tidal pattern in the tool-using group, we should interpret the tidal pattern in the non-tool-using groups' results with more caution. We only have reliable evidence for a change in coastal capuchin activity in relation to the tidal cycle for the tool-using group in the wet season, results of our other models showed more uncertainty. Given this limitation, we can tentatively conclude that for coastal-living capuchins, investing in consistent exploitation of intertidal resources might be a trade-off between nutrition gained and energy and time expended in which using tools could be a decisive factor.

3.5.6 Opportunities for future research

To disentangle capuchins visiting the coast for temperature regulation versus foraging on intertidal resources, we need data on capuchin activity from the intertidal zone itself. With camera traps, this was not possible, thus we infer visits to the intertidal based on proximity to the coast. We know that both tool-using and non-tool-using capuchins forage on intertidal resources from in-person observations [30] (B.B., M.C. and Z.G. personal observations), and physical evidence of tool use in the intertidal zone (Figure 3.6). Additionally, capuchins on the island of Coiba also consume intertidal resources like snails [180]. However, more than one process could contribute to the patterns of activity we report, for example, capuchins being near the coast to regulate their temperature. We consider this alternative by including spatial patterns depending on time of day, where time of day serves as a proxy for temperature. Our findings that temperature likely constrains capuchin activity near the coast, in particular in the dry season, suggest that in future research this should be examined in more detail. One possibility is to directly measure the ambient temperature at varying distances from the coast. One unexplored factor that might repel capuchins from the intertidal zone rather than attract them is noise created by the breaking waves, which also fluctuates depending on the tidal cycle. Such loud noises could disrupt vocal communication [203] between group members, and consequently be another trade-off faced by capuchins foraging in the intertidal zone.

Additionally, with semi-arboreal species such as capuchins, terrestrial camera traps miss activity: we cannot distinguish an absence of capuchins from capuchins present but in the trees. While the capuchins on Jicarón are highly terrestrial [76], we attempted to further mitigate this concern by focusing solely on fluctuations in the number of capuchins present in a sequence, rather than drawing conclusions based on the absence. We did not place all of our camera traps randomly, but some were placed in targeted locations, such as on anvils or streambeds, as this study is part of research on tool use. By only comparing fluctuations in capuchin

Figure 3.6: *Evidence of tool use in the intertidal zone.* Hammerstones and debris in the intertidal zone at low tide, which will be washed away by high tide. Photos by Meredith Carlson & Zoë Goldsborough.

activity *within* a specific camera location we account for this (and other) variation present between different camera locations.

Our findings of such clear tidal patterns in capuchin activity raise the question of how capuchins are aware of the timing of the tides: do they rely on sensory cues (e.g., auditory, visual or olfactory), cues from other species (i.e., seabird activity) or perhaps even cognitively 'track' the tidal cycle? Movement data would provide insights on the exact timing of capuchins' visits to the coast, and what underlying mechanism(s) allow(s) them to be there at the right time. Additionally, as the spatial scale of this study (0–400 m from the coast) is limited in comparison to typical capuchin home range sizes (e.g., 0.8–1.5 km2 on Barro Colorado Island [204]), tracking of individuals would also allow for integration of our findings into a more comprehensive understanding of Coiban capuchin space use.

There are additional avenues to examine differences in consumption of intertidal resources by the tool-using group and non-tool-using groups, such as DNA barcoding or stable isotope analysis to indicate what proportion of the capuchins' diet is marine resources (*sensu* [205]]). Additionally, a more detailed examination of the variation in daily activity between the tool-using group and non-tool-using groups is needed to explore the effect tool use might have on their behavior aside from allowing access to tidal resources. Lastly, taking a similar approach in other tool-using and non-tool-using maritime mammals would shed light on whether tool use is indeed important for consistent exploitation of intertidal resources.

3.5.7 Broader implications of our findings

We found that capuchins living in coastal ecosystems show changes in their activity near the coast that correspond to tidal cycles. While both tool-using and non-tool-using capuchins show tidal patterns that correspond with potential exploitation of intertidal resources, only tool-using capuchins show a strong, reliable pattern of increased coastal activity around low tide which is limited to the wet season. Our findings suggest that tidal resources may be very important for coastal-living capuchins, but that tool use might be key, or even a prerequisite, for their efficient exploitation. Although we lack mainland data for comparison, it is important to consider that Coiban capuchins in this study live in a coastal, insular habitat. Islands are often resource-limited: species richness decreases with island area and distance to mainland or insular source populations. Additionally, habitual reliance on tool use is observed in many endemic island-living species (i.e., Woodpecker finches [*Cactospiza pallida*; [51]], New-Caledonian crows [*Corvus moneduloides*; [38]], Hawaiian Crows [*C. hawaiiensis*; [52]] and Keas [*Nestor notabilis*; [53]]), or restricted to populations that live on islands (i.e., Burmese long-tailed macaques on islands in the Andaman Sea [54]). Potentially, the presence of such a rich intertidal zone in an otherwise challenging ecosystem might be one explanation for why tool use is more likely to arise on islands: to aid exploitation of the intertidal zone.

Percussive tool use on coastal resources also played an important role in human evolution. Prehistoric *Homo sapiens sapiens* used stone tools to access a variety of marine resources from the intertidal zone [206–208]. Consumption of marine resources is argued to have aided the rapid increase in brain size observed in human evolution, due to their high contents of docosahexaenoic acid as well as iodine and selenium [209, 210]. Modern coastal-living humans do still employ tools to forage in the intertidal zone, and have been found to prefer foods that provide the best nutritious value for the least effort [211]. Ethnoarchaeological work in humans has shown that intertidal foraging is a high-reward type of foraging—*if* the tidal conditions are optimal [212]. Non-human primates like white-faced capuchins provide an interesting parallel to understand the role tool use has played in human evolution, in the absence of clear evidence from the fossil record.

The findings of this study have implications for the conservation of these capuchins, namely highlighting the potential importance for exploitation of tidal resources for both tool-using and non-tool-using capuchins. Exploitation of intertidal resources by tool-using capuchins appears to be less frequent in the dry season, and due to anthropogenic climate change these periods of hot, dry weather are globally becoming longer and more intense [213]. Further, the ocean is becoming increasingly acidified, which negatively affects many marine organisms [214] and as such will eventually affect the capuchins too as they forage on these marine resources. The role intertidal zones play in capuchins' foraging patterns should be included when considering how to best conserve the capuchins on Jicarón and their unique tool use behavior [215].

Overall, our findings both uncover the impact exploitation of tidal resources may have on an animal's general activity pattern, as well as increase our understanding of how tool use may provide access to a new niche. Animals that are dietary generalists can opportunistically complement their diet with valuable resources from the intertidal zone, and tool use might be necessary to make the investment in these fluctuating resources worth the costs of keeping up with the tidal cycle.

3.6 Data availability

All data and code used for analyses in this paper are available via [216].

3.7 Acknowledgments

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Chapter 4

Rise and spread of a social tradition of interspecies abduction

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Code	https://doi.org/10.5281/zenodo.15006912
Data	https://doi.org/10.17617/3.BQW4IY
Interactive timeline	https://www.ab.mpg.de/671374/Capuchin-tool-use/interspecies-abduction-tradition

4.1 Abstract

We describe the emergence and spread of a novel social tradition: interspecies abduction of infant mantled howler monkeys by white-faced capuchins. Using camera traps, we observed eleven abductions by one capuchin group over a 15-month period on Jicarón island, Panama with infants carried up to nine days. Despite continuous monitoring since 2017 to study stone tool use, we first observed this behavior in Jan, 2022. The tradition originated with a single subadult male carrying four howler infants within four months. Later the behavior spread and the number of carriers and simultaneously present infants increased. In total, three subadult and two juvenile males were confirmed carriers, with transfers between carriers occurring multiple times a day. Non-carrier adult capuchins did not interact with infant howlers. Four of eleven howler infants died — likely from starvation and/or dehydration, though no predation was observed, and the fate of the others was not directly observed. The high incidence, and observation of attempted escapes and lost-calling between adult and infant howlers suggests (forceful) abduction and not abandonment. We show how longitudinal camera trapping can document the origin and spread of social traditions in unhabituated wild primates. Our findings support our idea that innovations, both adaptive and non-adaptive, are common on islands due to the direct impacts of relaxed predation and reduced species diversity. Necessity need not be the mother of invention:

increased general innovation propensity might be simultaneously driven by need and ‘boredom’ in intelligent, generalist species whose evolved cognition is deployed in a less stimulating environment.

4.2 Introduction

4.2.1 Cultural traditions in animals

How and when social learning leads to the spread of phenotypes through an extragenetic mode of inheritance — culture — is a central theoretical and empirical focus of researchers spanning both human and animal behavioral sciences and ecology [218–220]. In non-human animals, seminal studies on cultural transmission of birdsong [221, 222] and social learning in largely captive animals comprised most social learning research prior to the 21st century. During this time, social learning research was limited to investigating localized cultural traditions in groups with similar ecologies, genetic admixture, and group overlap — the goal being to simply support the existence of culture in non-human animals, countering the many animal-culture skeptics by demonstrating that some traditions could not exist if not by social learning mechanisms [66, 223–225]. These traditions ranged from seemingly adaptive (foraging tool use), to seemingly pointless traditions like rain dancing [224, 225], and traditions without clear initial purpose, which may be exapted to have a function, e.g., dyadic eye poking and other social games in wild capuchins [223]. Research later developed beyond identifying the existence of traditions into understanding how, why, and from whom individuals acquire traditions via social learning strategies, by exploring within-population heterogeneity [68, 226, 227]. The importance of cultural transmission in animals in relation to wildlife reintroduction and conservation efforts has also recently gained increased focus [228–230], leading to a United Nations Convention on the Conservation of Migratory Species of Wild Animals initiating a working group on the importance of conserving animal culture.

4.2.2 Conditions conducive to innovation

While the diversity and spread of cultural traditions have received considerable attention, how they originate– via innovation– has proved challenging to study. To paraphrase Hoppit and Laland [220], *innovation* leads to the introduction of novel learned behaviors (*innovations*) into a population’s repertoire. From an evolutionary perspective, innovation is a type of phenotypic plasticity which helps animals respond to changing environments, possibly leading to speciation [231, 232]. The ability of individuals to problem solve (i.e., innovative tendency), has been linked, in multiple directions, to various factors including age, sex, and rank (reviewed in [233, 234]). Conversely, overly-predictable environments may induce boredom; this lack of external stimulation leads to neural arousal driving a search for variety– resulting in innovation [235, 236]. Quantitative models support this, showing that experiencing boredom in an unstimulating environment creates conditions to sample the environment in novel ways, as organisms balance pleasure associated with prediction with the negative experience of boredom [237]. How individuals balance this trade off is likely influenced by their evolutionary history. For example, in humans, many innovations have no clear function and fail to spread or spread slowly in a population [238]. In fact, Henrich [238] argues that in humans, ecological necessity, while having importance, does not explain or is not required for the spread of most innovations. Many innovations are incremental or transfer a known solution to a new problem ('low-magnitude' innovations *sensu* [239]) — and if they are adaptive this is likely due to luck, unrelated to the innovator's intent [238]. Models suggest that beneficial 'high-magnitude' innovations, or great leaps forward, evolve if there is some status or social benefit conferred upon the innovator or if social learning is selective [239]. While innovations can be seeded experimentally, it remains challenging to document the rise and spread of a spontaneous innovation in wild animals (but see [65]).

4.2.3 Arbitrary cultural traditions

Non-adaptive (studying *behavior* vs *behaviour*), or even costly (forgoing reproduction to earn a PhD) cultural traditions are exceptionally common in human societies, partially explained by our obligate reliance on social learning and cumulative cultural evolution [240]. Their presence in animals is more puzzling as their behavior is less shaped by culture. Examples of animal innovations lacking clear adaptive benefits include chimpanzees wearing grass in their ears [241] or copying the unusual gait of a group member [242, 243], capuchins grooming porcupines [244], and orcas wearing dead salmon as 'hats' [245]. A unifying framework for the importance of studying these seemingly arbitrary traditions is lacking, and these behaviors are often interpreted as non-adaptive by-products of a species' motivation to learn socially [241, 243] or being adaptive through their social benefits [246], e.g., 'fitting in' post-immigration [242]. It is currently unclear whether the same ecological and social conditions that favor adaptive innovations also drive the development of these non-adaptive innovations.

4.2.4 Innovations by island-living primates

White-faced capuchin monkeys (*Cebus capucinus imitator*) living on Jicarón island in Coiba National Park, Panama are an excellent study system for examining conditions favoring innovation. Capuchins are dietary generalists with a high tendency for innovation and many documented social and foraging traditions [65, 67]. Islands are linked to higher rates of innovation, both genetic [56] and behavioral [57] and on Jicarón island in particular, the ecological and social conditions appear conducive to innovation. Vertebrate communities have low alpha diversity; capuchins and mantled howler monkeys (*Alouatta palliata coibensis*) are the only primate species present and mammalian predators are absent [75], with capuchins living at high densities [30, 75] and showing increased terrestriality compared to the mainland [76]. One group of capuchins on Jicarón has developed a tradition of habitual stone tool use that is unique to *Cebus* [30]), and has been monitored through camera traps since 2017.

Here, we report the rise and spread of an arbitrary social tradition of interspecies abduction in the group of tool-using capuchins on Jicarón island. We reconstruct the timeline of events (Figure 4.1, for full description see section D.2 and interactive timeline) to show the origin, exposure, and spread of this behavior. In doing so, we argue that the same conditions on Jicarón island which favored adaptive cultural innovations like tool use may also have given rise to this non-adaptive social tradition, driven by an evolved propensity to explore the environment and seek external stimulation, in an overly predictable environment.

4.3 Methods

4.3.1 Site and subjects

Jicarón island (2 002 ha) is one of nine islands in Coiba National Park, a designated UNESCO World Heritage site located off the Pacific coast of Panama. Coiba National Park contains multiple endemic animal and plant species [80]. In addition to white-faced capuchins, only a few other mammal species live on Jicarón island, and mantled howler monkeys are the only other primate species. Since 2004, Jicarón island has been uninhabited with little human disturbance. A handful of capuchin groups in Coiba National Park are the only observed populations of this species to habitually use stone tools [30, 31]. On Jicarón, only one group of capuchins habitually uses stone tools at anvil sites, and it is in this group that all howler abductions occurred. This group consists of approximately 20-25 individuals, with at least 5 adult males and at least 5 adult females. We have been studying the tool-use behavior of this group since 2017, using camera traps to monitor their behavior continuously. Capuchins on Jicarón appear to occur at high population densities [30, 75], but we have no precise estimate.

We have limited information on the howler population on Jicarón. Based on preliminary surveys by JL while deploying cameras, howlers appear to be at relatively high density, with a mean group size of 5 individuals (range: 2-13 individuals; number of groups encountered during survey = 29), and 3 adults per group. One in three groups contained at least one infant ($n = 9/29$; $n_{infants} = 10$, range: 0-2). At least 4-5 groups of howlers were observed in close proximity to the range of the tool-using group. Virtually no systematic research has been conducted on the howlers of Jicarón. Hence, we do not have a full picture of the basic demographics of their population, or aspects of their social dynamics, activity patterns, diet, and behavior. However, besides a presumed unusual small group size, this population does not seem to differ drastically from other mainland populations of the same species (JL personal observations).

4.3.2 Data collection protocol

Since the initiation of this project in March 2017 until January 2022, we have deployed 76 cameras in the tool-using group's home range, with near-continuous temporal coverage and, on average, seven cameras deployed simultaneously. During the same period, we also deployed 47 cameras in ranges of non-tool-using groups on the same island. The current observations are from images and videos collected using 86 unbaited camera traps placed in the tool-using group's range between

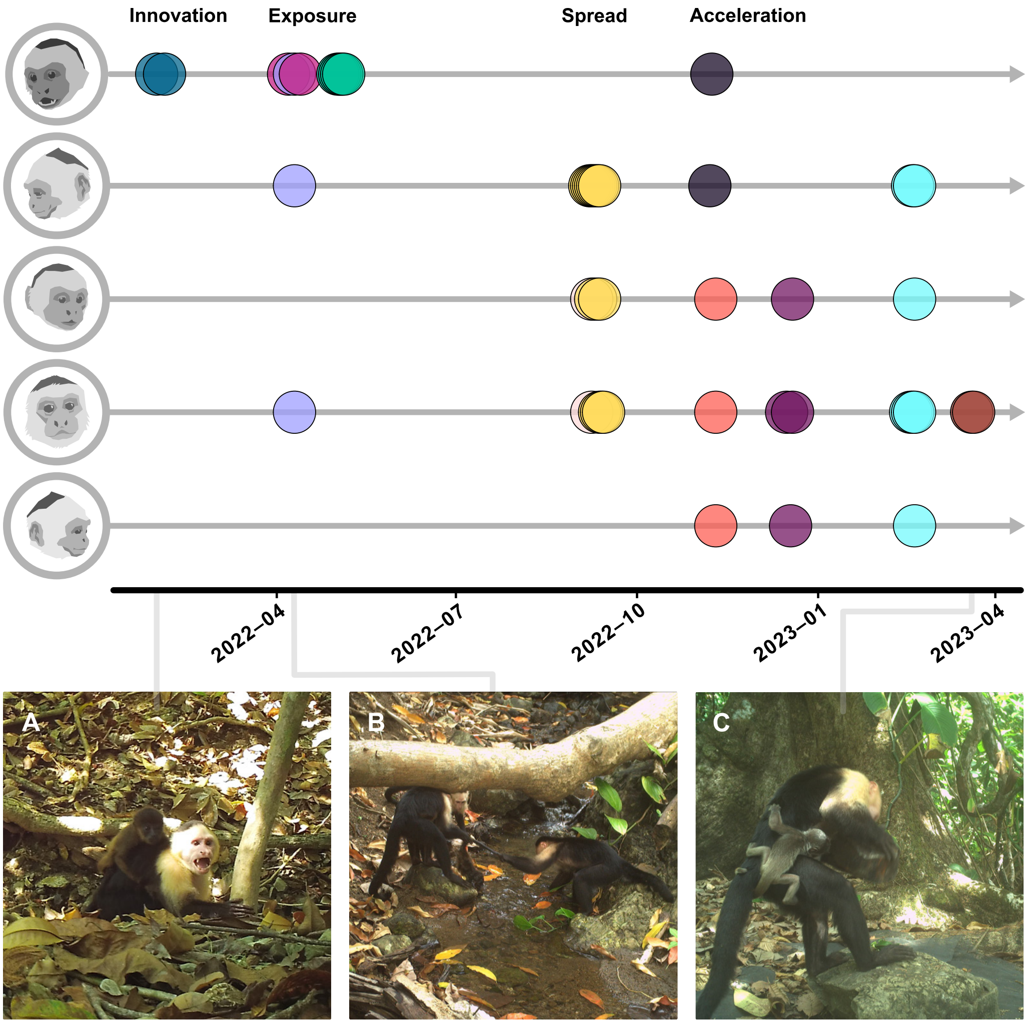

Figure 4.1: Timeline showing the rise and spread of the howler abduction social tradition. Lines reflect capuchin carriers, with the innovator at the top. Colored circles reflect days on which a howler infant was carried by this capuchin and circle color represents howler infant identity. Blue circles, for instance, reflect howler 1 (H1), who was carried the longest—a total of 9 days, and lavender circles H3, who was carried the shortest (one day). Circles at different carriers on the same day, such as light blue for H10 reflect infant transfers between carriers within a single day. Not pictured are 11 observations where individual identification from among the set of five capuchin carriers was not possible due to camera angle or image quality. This includes our very first sighting of a capuchin carrying a howler infant on 26/01/2022. Below the timeline are images of the howler abduction tradition: A) The innovator (Joker) carrying a howler infant dorsally, B) Joker (right) and later carriers pulling on the body of H3, C) a subadult male opening *Terminalia catappa* using stone tools while carrying a 1-2 day old howler infant (H11).

January 2022 and July 2023 in three deployments of approximately six months. We used two types of camera traps: models capturing still images (Reconyx Hyperfire HF2X) and models recording video (Reconyx Ultrafire XP9). Cameras were placed at different locations: 37 (20 video and 17 still images) were placed at targeted locations such as tool use anvils (of which two anvils had two camera traps on them at different angles). Another 11 cameras capturing still images were placed on the streambed, paired with 11 'random' still image cameras placed in a location 15 meters removed from the stream camera. Lastly, 27 still image cameras were placed in a 150-meter spaced grid covering the tool-using group's range.

After discovering the first sighting of an infant howler being carried by a capuchin in our data, we reviewed all images and videos from the cameras deployed between January 2022 and July 2023 (Table D.1). Each time a howler infant was observed on our camera traps, we identified the age-sex classes and behavior of all capuchins present following the ethogram standard in our project [247]. We distinguished individual howler infants based on body size, natal coat coloring, movement patterns, and overall appearance of alertness. The sex of infants was unknown as the testes in male mantled howlers do not descend until they reach sexual maturity [248]. Additionally, we recorded any behaviors directed at the infant howler and the howler infants' own behavior. We also coded images and videos immediately preceding or following howler sightings for context.

4.4 Results

4.4.1 Origin

Due to the extensive monitoring of the tool-using group since 2017, we are confident we captured the tradition's origin on January 26, 2022, with the sighting of a juvenile capuchin carrying a howler infant. In the following four months until May 4, 2022, a single individual (a subadult male named Joker, Figure 4.1a) emerged as the main howler infant carrier, carrying four different howler infants for up to nine days each (Table 4.1 & Table 4.2). All howler infants were between 2-4 weeks old. Joker carried infants dorsally, ventrally, and — when they were unable to cling — in his hand. Joker showed no aggressive behaviors towards howler infants, and was affiliative towards one by embracing it. Some howler infants lost-called, and all appeared to remain present in the capuchin group for consecutive days until they weakened (and likely died) from starvation and/or dehydration.

4.4.2 Exposure

While Joker was the main carrier of the first four howler infants, other capuchin group members were present in 14/20 howler infant sightings and exposed to this behavior. Their interaction with Joker and the howler infants was minimal, aside from several adult capuchins threatening Joker as he carries H2 (howler infant 2), and individuals inspecting H4 when it was seemingly close to dying. Multiple adult capuchins sniffed and visually inspected the infant, and a juvenile capuchin bit and pulled on the howler's tail, corresponding to primates' general responses to dying or deceased individuals [249]. Notable is H3, who we never observed alive but only in one sighting, dead in a streambed and being pulled on by Joker and three other juvenile/subadult capuchins (Figure 4.1b), two of whom later become carriers of howler infants themselves.

4.4.3 Spread

In September 2022, the howler carrying behavior spread to other capuchins in the group, all juvenile or subadult males. Until March 2023, we observed seven different howler infants (ranging from 1-2 days to 4 weeks old), who were present in the capuchin group between 2-8 days. H5 and H6 were present simultaneously (Figure 4.1 & Table 4.2). We saw an explosion in the number of carriers, rapid switching between carriers, and a greater diversity of behaviors to and from howler infants. In September, three new individuals carried infants, and in December, a fifth carrier emerged (Table 4.1). Infants switched between carriers up to several times a day. We recorded one transfer between carriers: occurring passively as the infant climbed off its carrier, was abandoned, and picked up by another capuchin. The new carriers also carried infants dorsally and ventrally, but, unlike Joker, the majority used stone tools while carrying (Figure 4.1c). During tool use, howler infants sometimes fell off, or were squished between the carrier's abdomen and legs. Furthermore, all four new carriers showed some aggressive behavior towards the howler infants, mostly nipping/biting or swatting when the infants attempted to nurse. Only one other carrier, a subadult male, Terry–who carried the most (6) unique howler infants and is observed carrying the most (12) days– showed affiliative behavior by embracing one infant. Joker was only observed carrying one more infant, H7, who was in poor physical condition.

Howler infants continued to lost-call, and adult howlers were heard responding to their calls on two instances. We also observed howlers traveling on the ground without capuchins present three times: single adults (one male and one female) on November 3rd and 30th, and a juvenile on December 15th. Further, some older howler infants climbed off their carriers and ran off, only to be retrieved by the capuchins, in one instance involving aggression (Video D1: https://youtu.be/s3Y3JWVvB9Q). Non-carrier capuchins in the group continued to show no interest in the howlers, aside from sporadic inspections by juveniles, and an adult female threatening two different howler carriers. However, when adult howlers were present in the canopy, other capuchins were vigilant and threatened upward toward the howlers. Most howler infants appeared healthy when first sighted, and visibly deteriorated after days of carrying. Four infants certainly died, as we observed them being carried while deceased. In one sighting, we saw H5 lying immobile next to an anvil and being hit multiple times on the side of the head with a stone during tool use by the carrier on a sea almond. We observed no evidence of predation on the infant howler monkeys.

Carrier name	**Age-sex class**	**Number unique howlers**	**Number days observed carrying**	**Aggressive behaviors towards howler**	**Affiliative behaviors towards howler**	**Other behaviors towards howler**
Joker	Subadult male	5	11	None	Embracing	Carrying in hand when too weak to cling, no tool use observed while carrying
Balthasar	Juvenile male	3	9	Nipping and biting, swatting at	None	Abandons howler at least once, uses tools while carrying
Terry	Subadult male	6	12	Nipping	Embracing	Uses tools while carrying, howler once falls off during tool use, carrying in hand when too weak to cling
Mick	Subadult male	5	6	Throwing by tail, nipping & pushing down (after howler attempts escape)	None	Uses tools while carrying
Zim	Juvenile male	3	3	Nipping and biting, swatting at	None	Not observed using tools while carrying

Table 4.1: Information on capuchin carriers. Overview of all capuchins who carried howler infants, in order of when they were first observed carrying. For each carrier, we include their age-sex class, how many unique howler infants they were observed carrying on how many days total, and what behaviors they showed towards the howler infants.

	Dates	**Days in group**	**Age (weeks)**	**Number of days seen**	**Number of carriers**	**Carried**	**Behaviors**
1	Jan 26 until Feb 3 2022	9	2-3	4	2	Ventral & dorsal	Lost-calling
2	Apr 7 until 13 2022	7	3-4	2	1	Dorsal	Lost-calling, mobile
3	Apr 10 2022	1	2-3	1	2	In hand	Deceased
4	May 1 until 5 2022	5	2-4	5	1	Dorsal, in hand	Small, largely immobile. Appears deceased on May 5, 2022
5	Sep 7 until 14 2022	8	3-4	8	3	Ventral & dorsal	Attempts to nurse, lost-calling (response on Sep 7), runs away, recorded carrier transfer, dead on Sep 14 2022
6	Sep 8 until 12 (maybe Sep 7) 2022	5 (or 6)	1-2	4	2	Ventral & dorsal	Appears weak from first sighting, dead on Sep 12 2022
7	Nov 7 until 8 2022	2	2-4	2	3	Ventral & dorsal	Poor physical condition
8	Dec 9 until 10 2022	2	2-3	2	3	Dorsal	Climbs off, eating coconut
9	Dec 16 until 19 2022	4	2-4	4	3	Dorsal	Attentive, lost-calling
10	Feb 17 until 19 2023	3	3-4	3	4	Dorsal	Lost-calling (with response on Feb 19), attempting escape
11	Mar 20 until 21 2023	2	<1 (perhaps 1-2 days)	2	1	Ventral & on side (also upside down)	Very small, eyes still closed, mostly clinging to carrier. No vocalizations observed.

Table 4.2: Information on abducted howler infants. Overview of all eleven howler infants in order of appearance, including when each howler infant was first and last observed, its approximate age, how many capuchins carried it, and which behaviors the howler infant showed (aside from clinging).

4.5 Discussion

Our report is not only the first instance of capuchins abducting howler infants and carrying them for extended periods of time— to our knowledge it is the first documentation of non-predatory interspecific abduction becoming a cultural tradition in any non-human animal. Howlers and capuchins are both well-studied species [70, 250], whose species' ranges largely overlap [251]. Yet, recorded interspecific interactions are mostly aggressive (from capuchins to howlers), with a few exceptions of infant play and grooming [252], and no carrying whatsoever. Furthermore, the distinctiveness of our finding lies not in the nature of the interspecific interaction, but its spread through the capuchin group to only immature males to be established as a cultural tradition.

4.5.1 Abduction not abandonment

A central question is how capuchins are procuring howler infants, who are still dependent on their mothers (in one case mere days old). We can rule out abandonment of infants by adult howlers due to: i) the high rate of novel infants appearing (even two simultaneously), ii) infants being forcibly held by carriers when attempting to flee, iii) our observations of adult howlers calling back and forth with infants for extended periods of time, and iv) the good health of most howler infants upon first sighting. Abduction appears the most likely explanation, although it is unclear how capuchins take howler infants from their mothers. Mantled howler mothers will rescue their infants when they fall or are 'kidnapped' by other howler females ([253]; L. Corewyn, personal observation). While capuchins in other field sites harass howler monkeys [252], and a tufted capuchin adult male (genus *Sapajus*) abducted, and potentially predated, a howler infant with minimal resistance from attending adults [254], all carriers in our report are significantly smaller than adult howlers. Abducting infants likely involves risks, yet we observe no injuries on the carriers, suggesting they employ an effective infant-stealing tactic. How exactly the capuchins abducted the howlers infants remains unknown, because our camera traps do not capture activity in the trees, where abductions likely occurred. However, non-carrying capuchins did aid in preventing adult howlers from retrieving infants, evidenced by capuchins threatening an adult howler during an attempted escape by H10 (Video D1).

4.5.2 Carriers do not benefit

What is the driver of this behavior? Food competition is unlikely, since howlers are largely folivorous while capuchins are generalists, and they show little dietary overlap [252]. Extended interspecific carrying has been observed in anecdotes of interspecies adoption in primates [255–257], cetaceans [258–260], and felids [261]. However, it is always *females* who carry infants, when we *only see immature male carriers.* Female capuchins show no interest in the howler infants. While in white-faced capuchins, males exhibit a high degree of alloparental care, males' interactions with juveniles are usually limited to short carrying and playing [62]. We observed no play at all. Four out of five carriers showed annoyance and mild aggression towards the infants, making alloparental care an unlikely explanation for all individuals. Our finding of immature males being the only carriers could be due to their high tendency to innovate [65] and socially learn from others [68, 244], also evidenced by this age-sex class being prolific tool-users [84]. Despite observed mild aggression, we observed no predation of howler infants (unlike reported by [262] in a different field site). Howler infants appear to die of starvation or dehydration after being carried for up to 9 days, and some infants are carried post-death with no visible damage. Another possible benefit of infant carrying could be infants functioning as 'status symbols' or way to avoid conflict, termed agonistic buffering [263] and observed in *Cercopithecines* [264]. However, carriers do not receive positive social attention from group-mates (i.e., grooming). We did see adult capuchins threatening carriers, and juveniles observing them from a distance. Carrying does not seem to prevent agonism. Furthermore, the single observed transfer was not competitive as one would expect over a prized resource, but the result of the carrier losing interest and another carrier picking up the discarded infant. In sum, abducting and carrying howler infants appears to be devoid of obvious fitness benefits or positive reinforcement.

4.5.3 Animal 'fads'

The motivation to innovate is not necessarily the same as the motivation to socially learn. After the behavior has spread to other carriers, we only observe the innovator Joker carrying a howler infant once, who is in poor physical condition. Potentially, Joker is a low-ranking individual who, when the behavior became 'trendy' no longer had access to infants and was outcompeted by other carriers. The innovator is also the only carrier to show no aggression or annoyance to infants, suggesting that alloparental care could have been a possible driver of his behavior. In contrast, later carriers all engage in behaviors risking harm to the infant, such as tool use where infants fall off, and respond negatively whenever the howler infant behaves infant-like, such as when it tries to nurse. The behavior of later adopters may be best understood as a fashion trend or fad, similar to the 'grass-in-ear' behavior observed in chimpanzees [241]; they appear to carry the infants for carrying's sake, with little genuine interest or care for the infant itself. It is important to note that howler infants are not entirely passive, due to their palmar grasp reflex they actively cling to the carrier [265], making it less costly to carry them around [266].

4.5.4 Under-stimulation and innovation

What could explain this tradition originating in this particular group of capuchins? Across the human cognitive and behavioral sciences, boredom and cognitive under-stimulation have been argued to be drivers for innovation [235, 237]. Innovative propensity is shown to arise as a tradeoff between desiring predictability in the environment and a need for stimulation– the lack of which leads to boredom. In non-human animals, boredom is thought to have adaptive value in motivating exploration, learning, and the use of novel resources. Thus, generalist and opportunistic species may be more susceptible to boredom-like states as a result of their adaptations to explore and exploit a variety of habitats and foods, both known and novel [236]. Moreover, in species with advanced cognitive abilities and neophilic tendencies, boredom-like states might motivate innovation [267]. In addition to being habitat and dietary generalists, white-faced capuchins are known for their large brains and highly developed cognition. Their reliance on extractive foraging, innovative propensity, high neophilia, and intense interest in con- and hetero-specifics are consistent with a desire and interest in myriad stimuli [19]). Generalist species with advanced cognitive abilities, such as capuchins, seem to have a low threshold for boredom-like states. This tendency may be a proximate driver of exploratory tendency and favor innovation, permitting them and other similar primate species, like humans, to survive in a range of diverse environments.

4.5.5 Island ecology conducive to innovation

Islands are hotbeds of evolutionary innovation, which often arises due to islands lacking in specific contexts relative to the mainland. For instance, islands have lower species richness affected by area and geographic isolation [58], affecting diet diversity, predation risk, and the diversity of other species with whom island-dwellers may interact [268]. These factors directly and indirectly affect behavior including territoriality, social learning, and social organization [72, 269, 270]. All of these factors apply to capuchins on Jicarón. The absence of predators on Jicarón island has two effects: it lowers the direct fitness costs of survival related to predation, and reduces the need to associate with group members for protection from predators and time spent on vigilance. As a consequence, capuchins on Jicarón experience a reduced-risk environment, less conspecific social interactions due to increased group spread from predator release (chapter 5), and fewer interspecific interactions, both in foraging and non-foraging contexts [271]. The reduced risk and less stimulating social and physical environment are remarkably similar to conditions in captivity, suggesting that an extension of the 'captivity effect' —characterized by increased innovations and cognitive performance [272] —may also occur in this wild setting. We argue that the evolutionary drivers of exploration and innovation that have made generalist capuchins such a successful radiation of primates, coupled with a low risk, under-stimulating, island environment, create optimal conditions for innovation. This is driven by a proximate desire to minimize boredom and maximize stimulation; which can drive both adaptive, and seemingly arbitrary, innovations.

4.5.6 Implications for conservation

Our findings have important conservation implications, demonstrating that longitudinal camera trapping can do more than just quantify species richness; it can successfully document the origin and spread of social traditions in unhabituated wild primates -– something that typically requires habituation and near-continuous direct observation. Nonetheless, there is a concerning side to this story: mantled howlers in Coiba National Park are considered taxonomically distinct and are listed as endangered [273]. Given the frequency and rate of howler infant abductions, it seems likely that this tradition may persist, which could pose a serious risk to their conservation. We demonstrate how one species' culture can harm another species' well-being, in line with tool-using macaques driving down shell size through over-exploitation [274], chimpanzees hunting red colobus to near-extinction [275], and countless examples of human traditions at the detriment of animals. These patterns highlight that cultural behaviors and innovations, whether originating by humans or by other species, can have far-reaching consequences for vulnerable populations coexisting within the same ecosystem.

4.6 Data availability

Our coding of all sightings is available [276]. Raw images and videos are available on https://doi.org/10.17617/3.BQW4IY.

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Chapter 5

Habitual tool use on monopolizable resources affects group cohesion

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Code https://github.com/ZoeGold/capuchingroupcohesion

5.1 Abstract

Tool-aided extractive foraging changes animals' interactions with their environment by expanding access to novel and/or high-quality foods. If and how habitual reliance on tool use impacts animals' social dynamics is less understood. If materials for tool use are monopolizable, tool use might increase intragroup competition. While higher intragroup competition encourages greater group spread, this lower cohesion comes at the cost of increased vulnerability to predation and intergroup competition. We examined how use of spatially fixed, monopolizable resources (i.e., anvils) influences group cohesion by comparing groups of tool-using and non-tool-using white-faced capuchins (*Cebus capucinus imitator*) living on Jicarón island in Coiba National Park, Panama. Jicarón lacks terrestrial mammalian predators and habitual stone tool use at spatially fixed anvils is locally restricted to a ∼1.5 km coastal stretch. We deployed two grids of 24-25 camera traps to compare daily activity patterns, as well as temporal variation in party size, party composition, and spatial cohesion between tool-using and non-tool-using capuchins. We found that tool-using capuchins were more likely to exhibit smaller and less variable party sizes than non-tool-using capuchins, and that adult females and adult males were less likely to co-occur in a sequence. Tool-using and non-tool-using capuchins showed different spatiotemporal cohesion; consistent with a more cohesive non-tool-using group and fission-fusioning or less cohesive tool-using group. Although only male capuchins use tools, the entire tool-using group appears to show reduced cohesion, suggesting that increased competition experienced by one sex can have cascading effects on all group members. Our findings suggest that habitual tool use relying on spatially fixed, monopolizable resources incentivizes higher group spread, creating

differences in the social environment of tool-using and non-tool-using animals sharing the same habitat.

5.2 Introduction

While hammerstone and anvil tool use has been observed in multiple primate species (chimpanzees [*Pan troglodytes* [23]], macaques [*Macaca fascicularis* spp. [24, 25]], tufted capuchins [*Sapajus* spp. [59]], and white-faced capuchins [*Cebus capucinus imitator* [30, 31]]), there is great behavioral variation. For example, hammerstone and anvil tool use for nut-cracking has only been observed in 22 of 144 studied wild chimpanzee communities [47]. In white-faced capuchins, another species that has been the subject of numerous studies across its distribution range, habitual stone tool use only occurs on two neighboring islands in the Pacific ocean [30, 31]. On one island, tool use is entirely male-biased [84]. Tool use can be valuable from an individual fitness perspective. It allows access to novel and/or high-quality food items [33, 40], and can spread between individuals via social learning [9, 12–14]. Several hypotheses have been proposed to account for the observed variation in the emergence of tool use across populations [35]: i) *necessity*: tool use emerges as a response to decreased resource availability, ii) *opportunity*: tool use develops in environments with appropriate conditions for tool use (e.g., stones that can be used as a hammer, decreased predation), and iii) *limited invention*: tool use may only emerge rarely and relies on observational learning to spread. The last hypothesis was proposed by Fox and colleagues [35] to account for variation in the emergence of tool use between populations in the absence of any ecological explanation. Furthermore, the *relative profitability hypothesis* combines the opportunity and necessity hypothesis, stating that tool use will arise when it is more profitable than strategies without tools [38]. In later expansions of these hypotheses, it was proposed that the social and cognitive factors influencing (the transmission of) tool use are crucial to its emergence, with social tolerance mentioned as being most important [39].

5.2.1 Tool use and intragroup competition

Social tolerance and social demography play important roles in the spread of tool use behavior as they structure opportunities for social learning. The influences of social demography and tolerance on cultural transmission have been considered theoretically [278] and experimentally [279–281]. However, what is less well-understood is how the existence of a social tradition like tool use can affect the social dynamics of the group in which it occurs. Particularly in the case of hammerstone and anvil tool use, a habitual reliance on tool use at anvils might result in increased intragroup competition as anvils and many food resources are both *spatially fixed* and *monopolizable*,. One study in bearded capuchin monkeys (*Sapajus libidinosus*) found evidence for this hypothesis. For females of this species, using tools to crack nuts at fixed anvil sites was linked to an increase in intragroup contest competition, even though the social structure of the study population was comparable to that of non-tool-using populations [114]. The authors predicted that, in group-living species, tool use that results in usurpable food resources will increase contest competition.

This hypothesis has not yet been evaluated in other species, perhaps due to the difficulty of ruling out ecological factors driving the (non-)emergence of tool use and thus finding suitable comparisons. If tool use can indeed increase intragroup competition, how could this competition be mitigated, and what effect would it have on the social dynamics of a group? Living in a social group is beneficial in a myriad of ways, including better outcomes of intergroup competition, decreased predation risk, higher discovery rates of novel habitats and resources, and increased mating opportunities [282, 283]. However, living in groups also comes with drawbacks, which, in addition to more resource competition within the group, also includes higher risk of disease and infanticide [282].

5.2.2 Intragroup competition and cohesion

A possible route to reduce intragroup competition is to be less socially cohesive. While higher intragroup competition encourages greater group spread, lower cohesion comes at the cost of increased vulnerability to predation and intergroup competition. One way to still enjoy the benefits of a smaller group, while also still profiting from those of a larger group, can be to be more flexible in spatiotemporal associations with group-members. The extent of variation in spatial and temporal cohesion of group members are called fission-fusion dynamics, which is a multi-dimensional, flexible concept reflecting *temporal variation* in i) spatial cohesion among group members, ii) party size and, iii) party composition [284]. Fission-fusion behavior is characterized by fission (a group splitting into smaller subgroups) and fusion (subgroups coming together into a larger group) events [285]. It is flexible and not necessarily consistent within species [284]. A higher degree of fission-fusion behavior can occur in response to environment, such as reduced predation risk, or more dispersed food resources. One study comparing two species of *Sapajus* capuchins found that the species living in an area with less predation and more dispersed, low-quality resources foraged in subgroups more frequently (i.e., showed a higher degree of fission-fusion behavior) than the species with more predation and clumped, high-quality resources [61]. In various primate species, fissioning was found to occur more frequently when food resources were scarce [286–288].

5.2.3 Linking tool use and cohesion

One study system where all these factors may be disentangled from one another is white-faced capuchins (*Cebus capucinus imitator*) living on Jicarón island, Coiba National Park, Panama. It and the neighboring island of Coiba are the only two sites in the world where white-faced capuchins are known to habitually show hammerstone and anvil tool use [30, 31]. On Jicarón, tool use is localized to an approximately 1.5 km stretch of coast, occupied by a maximum of three capuchin groups [122]. Despite there being no physical boundaries, differences in material availability, or other clear ecological differences, habitual hammerstone and anvil tool use does not occur in capuchin groups living in other parts of the island [30].

It is therefore possible to directly compare tool-using and non-tool-using groups of the same species sharing the same habitat. Furthermore, since tool-use is entirely male-biased on Jicarón (though not on Coiba) [84], it means that only males would be expected to experience this increase in intragroup competition, which could have cascading effects on both within- and between-sex social interactions. The absence of terrestrial predators (i.e. large cats and mustelids) and large venomous snakes on this island reduce the constraint of group spread imposed by predation risk.

5.2.4 Differences in cohesion between islands and mainland

Several unusual features of the environment on Jicarón are expected to affect the social dynamics of the capuchins that live there. Terrestrial mammalian predators are entirely absent on Jicarón, and there is only one predatory snake species (*Boa constrictor*) which appears to occur at low densities. Perhaps as a result of this reduced predation risk, capuchins on Coiba and Jicarón are more terrestrial than mainland populations[75, 76]. Capuchins also live at high density [30, 75], something which may lead to more relaxed intergroup interactions [289] — though on Barro Colorado Island, capuchins occur at high density yet have more intense intergroup encounters (M. Crofoot, pers. comm.). Predation pressure and intergroup competition are two major factors driving group cohesion [283, 290]. Their absence may relax these pressures on Jicarón, leading to capuchins here having lower group cohesion than mainland capuchins. In long-term study sites on the mainland, white-faced capuchins are generally described to forage as a group, moving from food patch to food patch and resting together (e.g. grooming, playing) at the hottest part of the day [19]. White-faced capuchins are known to scatter widely while foraging [73, 291], but individuals do not travel independently of other group members and remain in contact via frequent vocalizations [291]. As such, they are not generally described as a species with a high degree of fission-fusion behavior. Similar to the comparison of two *Sapajus* species [61], reduced predation pressure on Jicarón may favor more frequent fission-fusion behavior and lower social cohesion. As such, we expect that capuchins on Jicarón might overall be less socially cohesive than mainland capuchins. However, there might also be differences within the island, namely between tool-using and non-tool-using groups. Comparable to findings by Verderane and colleagues in *Sapajus* [114], there might be increased competition over spatially fixed, usurpable anvil sites. Competition over fixed sites may favor foraging solo or in less cohesive groups, as it allows individuals to reduce competition over anvils with group mates. The stone tool use on Jicarón appears to be a largely solitary activity (chapter 2), which would support the hypothesis that individuals reduce competition over anvils by reducing social cohesion.

5.2.5 Hypotheses and predictions

Here we test the hypothesis that the use of spatially fixed, monopolizable resources (i.e., anvils) influences group cohesion by comparing one group of tool-using and one group of non-tool-using white-faced capuchins (*Cebus capucinus imitator*) living

Hypotheses	*Predictions*	
	TU males split off from cohesive main group	*TU overall less cohesive/splits into multiple subgroups*
H1 — **Party size**: More cohesive groups have larger party sizes on camera traps	**P1a_males**: TU more single party detections than NTU **P1b_males**: NTU larger average party size than TU	**P1a_group**: TU more single party detections than NTU **P1b_group**: NTU larger average party size than TU
H2 — **Party size variability**: Variation in daily part size conditional on group cohesiveness	**P2a_males**: TU has higher standard deviation in party size per day than NTU (due to whole group vs single captures)	**P2a_group**: NTU has higher standard deviation in party size per day than TU (due to subgroups captures in TU)
H3 — **Party composition**: More cohesive group has more diverse party composition	**P3a_males**: TU parties fewer adult males and females together than NTU parties **P3b_males**: TU parties fewer adult males than NTU parties **P3c_males** — No difference in number of adult females in TU and NTU party	**P3a_group**: TU parties fewer adult males and females together than NTU **P3b_group**: TU parties fewer adult males than NTU parties **P3c_group**: TU parties fewer adult females than NTU parties
H4 — **Spatial cohesion**: Cohesive group higher correlation between close distance sightings, rapid decay at greater distances	**P4_males**: TU group has both a high correlation at close distances, and high correlation at distant cameras	**P4_group**: TU group has a slower decay of correlation between sightings with distance than NTU group
H5 — **Spatiotemporal cohesion**: Cohesive group has strong spatiotemporal correlation between sightings	**P5_males**: TU group has both high frequency of sightings close in space and time, as well as occurrence of sightings close in time but far apart in space	**P5_group**: TU group has fewer sightings close in space and time, and occurrence of sightings close in time but far apart in space

Table 5.1: Overview of hypotheses and predictions for dimensions of fission-fusion behavior, differentiating between expected patterns of the tool-using (TU) and non-tool-using (NTU) group in two scenarios. First, if males split off from a cohesive group to use tools, or second, if the whole tool use group is less cohesive and splits into smaller subgroups.

on Jicarón island in Coiba National Park, Panama. Using two grids of camera traps, we compare daily activity patterns and fission-fusion dynamics between tool-using and non-tool-using capuchins. Following Aureli and colleagues [284], we measure degree of fission-fusion dynamics through temporal variation in three dimensions: 1) party size, 2) party composition, and 3) spatial cohesion. We expect that — if tool use increases intragroup competition the tool-using group will be less cohesive and/or show more fission-fusion behavior than the non-tool-using group. If competition is limited to the tool-using males, they might split off from the group to go use tools at specific times of day. However, changes in capuchin males' movement and motivation can also affect overall group cohesion. Thus it is also possible that the whole tool-using group will be less cohesive and/or splits into multiple subgroups throughout the day. In Table 5.1 we detail how these different possibilities translate to explicit predictions for each of the dimensions of fission-fusion dynamics.

5.3 Methods

5.3.1 Site

Jicarón island (2002 ha) is located in Coiba National Park, an UNESCO World Heritage site 60 kilometers off the Pacific coast of Panama. It is uninhabited and only sees infrequent human activity in the form of scientific research and, rarely, ecotourism.

Capuchins on Jicarón use hammerstones and anvils to access a variety of resources, ranging from fruits like sea almonds (*Terminalia catappa*), coconuts (*Cocos nucifera*) and palm fruits (*Bactris major*) to invertebrates like Halloween crabs (*Gecarcinus quadratus*), hermit crabs (*Coenobita compressus*), and nerite snails (*Nerita sp.*)[30]. Tool use occurs at three types of sites, distinguished from one another through activity and intensity of tool use, and how debris accumulates at the site: 1) ephemeral sites, such as the intertidal zone, with low accumulation, 2) sites in streambeds with sporadic tool use resulting in low to medium accumulation, and 3) high accumulation sites, also known as 'anvils', away from streambeds where tool use activity is high and consistent, resulting in large amounts of debris accumulating over time [30]. Habitual stone tool use is limited to a ∼1.5 km stretch of coast inhabited by an estimated 3 social groups [122]. Of these three groups, only one shows tool use at high accumulation sites. The other two neighboring groups have recently been observed to use tools in the intertidal zone (C. Monteza-Moreno, pers. comm., 2023).

The group of capuchins who use tools at anvil sites, who from here on out will be referred to as the 'tool-using group', have been showing hammerstone and anvil tool use since at least 2004 [30]. They have been monitored using unbaited camera traps since 2017, with most sampling efforts focusing on 10 frequently used anvil sites.

5.3.2 Grid deployment

To compare the cohesion of the tool-using group to a non-tool-using group, we placed two grids of 26 camera traps with 100 meter spacing in both the tool-using group's range and a location on the other side of the island (approximately 3 kilometers away) between May 2022 and January 2023. We planned the grid placement by creating a 100-meter raster and overlaying this over satellite imagery of the field site (in `R` using the packages `sf` [292], `raster` [293] and `mapview` [294]). For the tool-using group, due to the high sampling since 2017, we had some information about their home range, and placed the grid to fall within their expected range. For the non-tool-using group, we had very limited information on their movement patterns, and thus placed a grid in an area where we had previously captured photos of capuchins during camera trap surveys. After placement we evaluated whether we captured a single group or the boundary between several groups (see detailed methods below). We selected this area to be as far away from the tool-using group's range as possible, while still sharing similar features (bordering the coast near streams and almendra trees), resulting in a location 3 kilometers away on the opposite shore of the island. We oriented both grids to be parallel to the coast.

From the 100 meter raster, we generated coordinates of 40 possible camera locations using the center coordinates of each cell, of which 30 were preferred placement locations and 10 back up locations. Due to the very challenging and steep topography on Jicarón, we did not know which locations would be physically possible to reach, and as such we aimed to have a range of randomly selected, equally spaced camera locations to try, and see how many would be possible to place. The placement went as followed: we navigated to a pre-designated grid location stored on a handheld

GPS (Garmin GPSMAP66i), and located a tree on which the camera could be mounted, ideally within 15 meters of the intended GPS coordinates. Each camera was placed on a tree at the same height (around 0.6 meters), facing a random direction (not facing into a hill or other obstacle). Cameras were tested using the Walktest function to see if it would trigger from movement on the ground. In the end, we successfully placed 26 cameras in the tool-using group's range, and 26 cameras in the non-tool-using group. Each grid camera was placed on average 10.63 meters (range 0.96-31.41) from the intended point, on a tree facing a random direction. All cameras were still cameras (Reconyx Hyperfire HF2X), and programmed to take to take 20 pictures per trigger with no delays between-triggers (approx. 1 s between images).

5.3.3 Annotation

Following collection of all cameras, triggers within 30 seconds of one another were clustered together into a single sequence. Each sequence was coded on www.agouti.eu [123], coding how many animals were present and of which species. For each capuchin present, we determined their age and sex when possible, attempted to assign an individual ID, and coded their behavior following the ethogram standard to our project [247]. Three cameras had malfunctioned or were not placed correctly, resulting in 24 cameras in the tool-using group, amounting to 4508 trapping days, with a mean of 187.8 days per camera (range 44-256). In the non-tool-using group, we ended with 25 cameras, amounting to 5330 trapping days, with a mean of 213.2 days per camera (range 96-260). For all analyses presented here, we only considered sequences containing capuchins ($n = 3807$).

5.3.4 Group size of tool-using and non-tool-using group

Before proceeding with analyses, we had to verify that the grids actually each captured a single social group. Due to the long-term monitoring of the tool-using group, we can reliably identify most group members, allowing us to be confident that nearly all of our cameras in their range only captured individuals from their social group. Two grid cameras placed on what we expected was the edge of their range had some triggers of unfamiliar individuals, not belonging to the tool-using group. To be conservative, we excluded all sequences with clearly unfamiliar individuals from analyses (3 sequences in the tool-user grid and 2 sequences in the non-tool-using grid), resulting in a total of 3802 sequences for analyses.

For the non-tool-using capuchins, we identified as many individuals as possible based on visual appearance ($n = 14$). We then constructed a social network using the `sna` package [295] based on the co-occurrences of these identifiable individuals in the same sequence (Figure E.1). Since all identified and repeatedly sighted adult males and females were connected to one another in the resulting social network, we are confident that the non-tool-using grid captures a single social group of capuchins.

Our estimates of the size and composition of both capuchin groups are based on a) identifiable individuals, b) the maximum number of capuchins observed in a sequence, and c) the maximum number of individuals of a particular age-sex class observed together in a sequence. Due to the nature of data from camera traps and its inherent uncertainty from the limited visual field, plus the difficulty of identifying juvenile capuchins from images alone, we cannot provide exact estimates of the group size. However, based on this method, the tool-using group and non-tool-using group sampled with the grid appear to be of comparable size and group composition Table 5.2.

Estimated numbers	*Tool-using group*	*Non-tool-using group*
Adult females	5-6	5-6
Adult males	5-6	5-6
Subadults	3-5	2-3
Juveniles	7-10	7-9
Total	20-27	19-24

Table 5.2: Estimated average group size and composition of the tool-using group and non-tool-using group sampled by grid cameras.

5.3.5 Statistical analyses

We ran all analyses in R v. 4.3.1 [124]. All Bayesian regression models were fit via the `brm` function in the `brms` package v. 2.16.1 [127]. To evaluate the credibility of the difference between categories we used the `hypothesis` function in `brms` and estimated means on the response scale using the `emmeans` package[296]. We considered what proportion of the posterior probability (PP) of the contrast was greater than 0, using a cut-off of 0.89 to reflect a strong reliable effect. For each model, we performed a prior predictive simulation to compare our chosen priors to default priors, and to evaluate parameter identifiability. For the final models, we ran three chains of 3000 iterations each, with a 1500 iterations warm-up per chain. Our models were stable with Pareto k estimates below 0.7 and large effective sample sizes (Bulk_ESS and Tail_ESS over 1000 for all estimates [127] and Rhat values ≤ 1.01 [128]. We visually assessed model fit and confirmed our choice of priors using the posterior predictive check function.

Intra-diel activity

First, we compared intra-diel activity of tool-users and non-tool users using the `activity` package v. 1.3.4 in R [187]. We expressed capuchin activity relative to sunrise, and then fit an activity model for the tool-using and non-tool-using groups separately, with 1000 repetitions. We estimated the overlap between the two activity curves using the coefficient of overlap method [186], where 0 reflects no overlap and 1 complete overlap.

Party size

With the term ‘party size’ we refer to the number of capuchins captured in a sequence together. Data was heavily 1-inflated — 68.94% of sequences only contained a single capuchin. Capturing larger parties of capuchins was rare at both sites. To account for this skew in analyses, we subtracted 1 from the party size to create a variable where 0's reflect captures of individuals alone (no social partners), and numbers above reflect the number of partners present. From here on we will refer to this variable as 'social party size' in order to differentiate it from the normally used 'party size' for the total number of individuals present. To compare mean social party size between the tool-using and non-tool-using group, we ran a hurdle Poisson GLMM (*model sps_ bm1a*). For the non-zero component of the model, the outcome was the number of partners in the sequence (total number of capuchins minus 1), and the predictor variables the grid location (tool-using or non-tool-using group, with non-tool-using as reference) as well as a random effect for each camera. For the zero-component of the model, we included the predictors of grid location and varying effects of camera location, under the assumption that both could affect single capuchin detection frequency.

To consider temporal variation in party size, we examined party size variability within a single day as well as fluctuations in party size depending on the time of day. First, to examine variability in party size, we calculated the standard deviation in party size per day for each camera, as cameras differ in their likelihoods to capture large parties due to their varying detection distances. We excluded data when only one party was detected at a camera on a given day, and thus no standard deviation could be calculated. Due to the high occurrence of standard deviations of 0 (mostly resulting from two parties of the same size being observed at a camera in one day), we ran a hurdle-gamma GLMM (*model ps_ bm1b*), with the same predictors for the zero and non-zero component of the model. The outcome was the standard deviation in party size, and the predictors were the grid location (tool-using or non-tool-using group), a random effect of the camera location, and as an offset the log of the number of parties observed at the camera that day. Second, we considered how party size fluctuated depending on the time of day to test the hypothesis that the tool-using group was sleeping together (larger party sizes in the morning and evening) and splitting up during the day. To model this, we ran a hurdle-poisson GAM (*model sps_ gam1*), using the social party size (where 0 reflects a party of one) as the outcome. For the hurdle (zero) part, we used the grid location and a random effect of camera location as predictors. For the non-zero part, we included the same predictors as for the hurdle part, with the addition of a smooth of the hour of day, estimating a separate smooth for each grid location. Additionally, we considered the locations of the first and last sightings of the day, to examine if the sleep site of the capuchins was likely captured in our grid.

Party composition

Due to the limited view of the camera traps and quick passage of many individuals, reliable aging and sexing of individual capuchins was not feasible in all sequences. We were unable to reliably estimate age or sex in 23% of the capuchins observed, mostly because only part of the capuchin was visible, or because it was not possible to determine if they were subadult or juvenile. Adults were easiest to identify — we reliably classified their sex in 94% of cases. Therefore, to compare party composition between the tool-using and non-tool-using group, we focused on adult males and adult females as these age-sex classes could be identified most reliably.

We hypothesized that the number of adult females and number of adult males occurring together in a party would differ depending on the cohesion of the group. As these variables contained many 0s (ranging from 66-81%), and these 0s could both reflect true absence as well as be a result of sampling (i.e., an unknown capuchin is actually an adult female), we decided to use zero-inflated models, since these models assume the presence of both 'true' and 'sampling' zeros. To compare the number of adult females in a party between the tool-using and non-tool-using group, we ran a zero-inflated Poisson GLMM (*model pc_ bm1*). The outcome was the number of adult females in a sequence, and the predictors grid location and an interaction of grid location with the number of adult males in a sequence. Camera location was fit as a random effect. We ran another zero-inflated Poisson GLMM (*model pc_ bm2*) with the same structure except the number of adult males as the outcome, and the number of adult females as a predictor.

Spatial cohesion

We quantified temporal variation in spatial cohesion in several ways. Firstly, we ran two regressions where we modeled camera trap location as a Gaussian process for each grid location (*model gp_ tu* and *model gp_ ntu*). This permits us to estimate a unique intercept for camera trap location that models the spatial autocorrelation between traps. From this we can statistically compare how covariance of party sizes decays as a function of the distance between camera trap locations. We posited that in more cohesive groups we would see a higher covariance between camera traps at closer distances and a quick decay at greater distances, whereas with a fission-fusion or less cohesive group covariance would be lower at closer distances and decay slower. These models were fit in R using the `rethinking` package v. 2.13 [297, 298]). We created distance matrices per grid calculating the distance between each pair of cameras in hectometers. In our models, we estimated the party size (number of capuchins detected in a sequence) depending on the camera and distance between cameras. Each Gaussian process regression was run on 4 chains, with 5000 iterations per chain. We then compared posterior estimates of how covariance between cameras decayed depending on distance between the tool-using and non-tool-using group.

To compare covariance in time as well as space between the grid locations, we made several visualizations of subsequent capuchin sightings within the same day. Assuming both cohesive and less cohesive capuchin groups likely sleep together at night, we first separated all detections by day. Within a day, we assigned an increasing number to each observation of capuchins (so the first observation of the day a 1, the second a 2, and so on). The first sighting of a day served as the starting point. From this we calculated for each subsequent sighting i) how far away in space this observation was from the previous observation (0 meters for the same camera, and otherwise the distance between the cameras in meters) and ii) how far away in time this observation was from the previous (how many seconds passed). We then assessed the relationship between time and space between sightings for the tool-using and non-tool-using group separately, assuming that a cohesive group and less cohesive group would show different patterns. In a cohesive group, subsequent sightings would be expected to occur close in both time and space to the previous sighting. In contrast, a fission–fusion group would also show subsequent sightings that are close in time but far apart in space.

When individuals of the same group are detected close in time but far apart in space at cameras at a great distance, this can indicate that they are fissioned into sub-parties. For instance, triggers of 150 meters apart within 2 minutes would be very unlikely to originate from one cohesive group of capuchins, based on capuchins' travel speed [19]. We identified what we term as 'co-occurrences' by extrapolating this rule (so 300 meters in 4 minutes, and so on) and flagging observations that occurred within these criteria. For both the tool-using and non-tool-using group, we considered the frequency of co-occurrences, as well as how many individuals were present in each of the observed parties. Lastly, we visualized capuchin sightings within 10 days at the two grids. We selected a period when both grids had multiple capuchin sightings within a day, and animated these sightings using the `gganimate` package [299].

5.4 Results

5.4.1 Intra-diel activity

Tool-using and non-tool-using groups had a coefficient of overlap of 0.90 of their daily activity (Figure 5.1). The non-tool-using group showed more activity in the morning, and the tool-using group in the afternoon. A striking difference is the presence of night (after sunset and before sunrise) activity by the tool-using group, which was entirely absent in the non-tool-using group. We had a total of six sequences showing capuchins from the tool-using group traveling on the ground between 19:00 and 05:00.

5.4.2 (Social) party size

In the tool-using group, we never observed a total party size larger than 10 individuals, while at the non-tool-using group the largest party size was 16. When comparing the social party size (where parties of 1 are reflected as a 0, and each number above 0 reflects the number of other partners available), we found different results for the zero and non-zero component of the model (Figure 5.2 and Supplemental Figure E.2, for model estimates see Table E.1). Singletons were slightly more common in the tool-using group than the non-tool-using group, although this effect was not reliable (i.e., less than 89% of the posterior was on one side of 0). The model estimated a 1.8% increase ($PP > 0 = 0.69$) in the likelihood of observing single parties in the tool-using group (estimated probability of $0 = 0.73$, 95% CI [0.68, 0.78]) compared to the non-tool-using group (estimate $= 0.71$, 95% CI [0.66, 0.76]). However, when parties larger than a single individual were observed, they were likely to be larger in the non-tool-using group than the tool-using group. The non-zero component of the model reliably estimated larger social parties ($PP > 0 = 0.96$) in the non-tool-using group (estimate $= 1.36$, 95% CI [1.10, 1.64]) than in the tool-using group (estimate $= 1.05$, 95% CI [0.83, 1.28]).

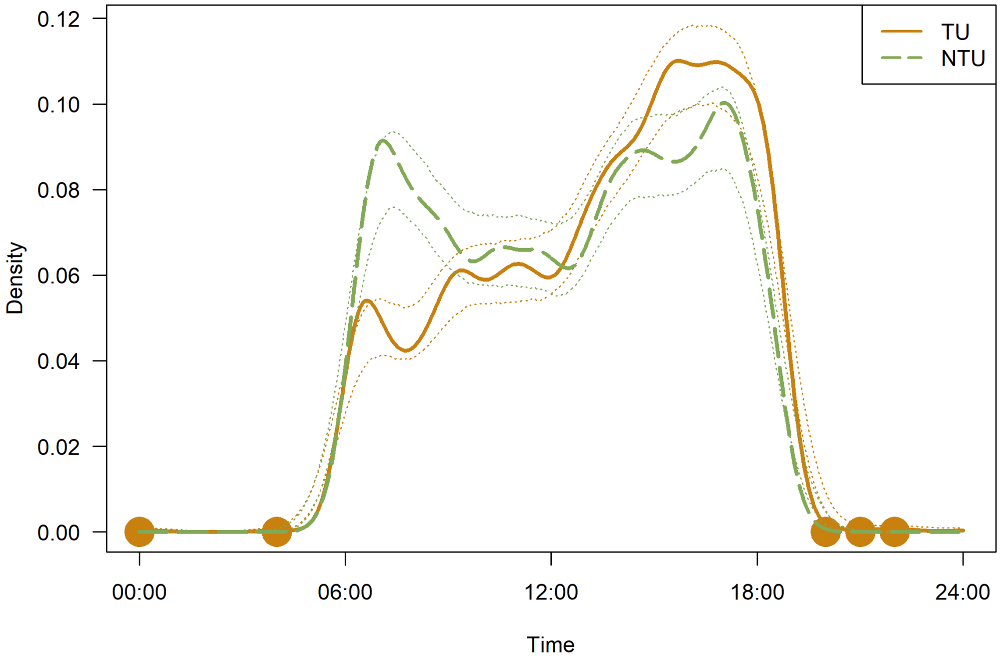

Figure 5.1: Density plots of daily activity of tool-using group (in orange) and non-tool-using group (in green). The thick line reflects the model estimates, and the dotted lines the 95% confidence intervals. Circles are used to represent the observations of capuchins during the night.

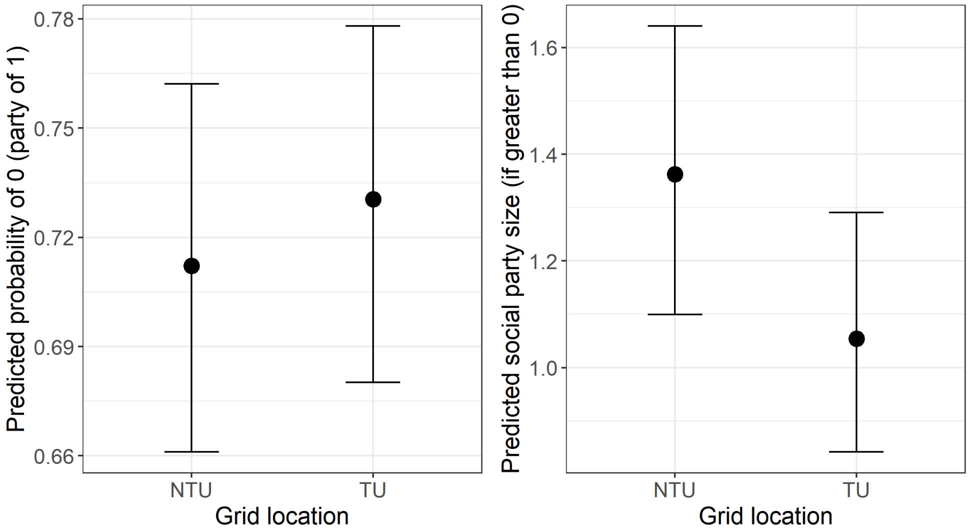

Figure 5.2: Model estimates from hurdle-Poisson model comparing mean social party size between the tool-using (TU) and non-tool-using group (NTU). On the left are model estimates of the zero (hu) component of the model, and on the right of the non-zero (mu) component. Points reflect averages estimated by the model, and the whiskers the 95% confidence interval.

The non-tool-using group showed more within-day variation in party size than the tool-using group (for estimates Table E.2). Our model estimated a reliably (PP $> 0 = 0.95$) larger standard deviation in party size in the non-tool-using group (estimate = 1.50, 95% CI [1.29, 1.72]) than the tool-using group (1.27, 95% CI [1.08, 1.45]). Taking a closer look at how social party size fluctuated within a day, we found that the non-tool-using group had a slightly higher social party size during the day than in the mornings and evenings (Figure 5.3 for model estimates see Table E.3). The tool-using group showed a slight increase in social party size as the day progressed, with highest estimated social party sizes in the evening. For the tool-using group, there was also one camera location where capuchin sightings were two times higher in the morning (< 7:00) and evening (> 17:00) than at other cameras, suggesting that this is likely a sleep site captured within the grid. For the non-tool-using group there was no single camera location with much greater capuchin activity in the early morning and late evening.

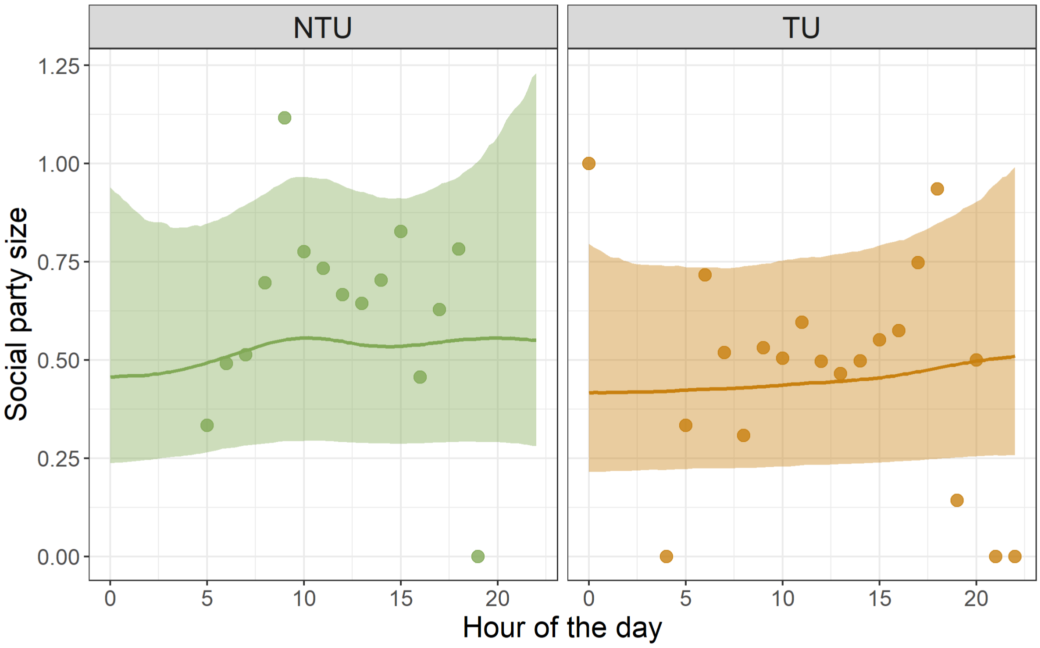

Figure 5.3: Daily fluctuation in social party size for the non-tool-using group (left in green) and tool-using group (right in orange). Lines reflect the social party size estimated by the hurdle-Poisson GAM, with the shaded area representing the 95% confidence interval. Points reflect the true means from the data.

5.4.3 Party composition

Adult females were more likely to be seen together in the non-tool-using group than in the tool-using group (for model estimates see Table E.4). Our model estimated a higher mean number of adult females present in a sequence in the non-tool-using group (0.26 95% CI [0.31, 0.42]) than in the tool-using group (0.26, 95% CI [0.22, 0.31]), and this effect was reliable (PP $> 0 = 0.98$). Adult males were also more likely to be seen together in the non-tool-using group than in the tool-using group (for model estimates see Table E.5). Our model comparing the number of adult males estimated a higher mean number of adult males present in a sequence in the non-tool-using group (0.32 95% CI [0.26, 0.38]) than in the tool-using group (0.18, 95% CI [0.14, 0.22]), and this effect was reliable ($PP > 0 = 1$). Both models estimated a different relationship between the number of adult females and number of adult males present for the tool-using and non-tool-using group (Figure E.3). In the non-tool-using group the models estimated a positive relationship: the more adult males were observed, the more adult females were observed. In the tool-using group, the relationship was negative: the more adult males observed, the fewer adult females.

5.4.4 Spatial cohesion

Covariance in space

Our Gaussian process regressions estimated greater covariance between party sizes at neighboring cameras for the tool-using group than the non-tool-using group (Figure 5.4 and Table E.6 for model estimates). The covariance also decayed slower at the tool-using group than the non-tool-using group, the latter showed little covariance at cameras close together which quickly dropped to no covariance at cameras more than 200 meters apart. The tool-using group also showed greater posterior correlation between camera traps than the non-tool-using group (supplemental figures E.4 & E.5)

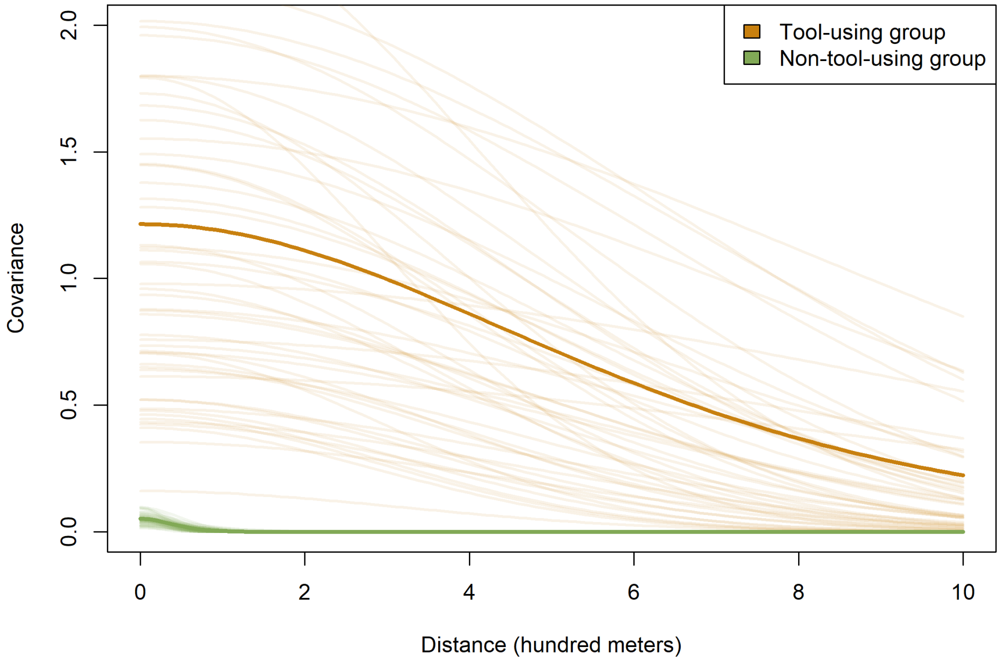

Figure 5.4: Posterior distribution of the spatial covariance for the tool-using group (in orange) and non-tool-using group (in green). The thick line represents the posterior mean covariance at each distance. The thin curves show 60 functions sampled from the posterior distribution.

Covariance in space and time

When examining the time and space between subsequent sightings of capuchins within the same day, a different pattern emerged for the tool-using and non-tool-using group (Figure 5.5). For both groups, if the subsequent sighting was at the same camera, in most cases only little time had passed. We observed slightly more occurrences of longer times at the non-tool-using group than tool-using group, but overall the distributions look very similar. However, we observed clear differences when considering when the subsequent sighting occurred at a different camera. For the non-tool-using groups, most subsequent sightings at a different camera were at cameras both close in space and in time, with subsequent sightings at great distances but close in time occurring less frequently. For the tool-using group, we see a greater frequency of detections that are far in space but close in time. These different patterns are also visible in our animation of capuchin sightings (online supplement). For the non-tool-users, capuchin detections often occurred at cameras neighboring the camera of the previous sighting, in line with cameras being triggered by a group traveling in a specific direction. In contrast, for the tool-using group, we see that subsequent detections are not usually at a neighboring camera, but rather somewhere else on the grid entirely, more in line with capturing several subgroups rather than one big group. Using a cut-off time of 60 seconds at 150 meters, we found 26 co-occurrences in the tool-using group and 15 in the non-tool-using group (Figure E.6)

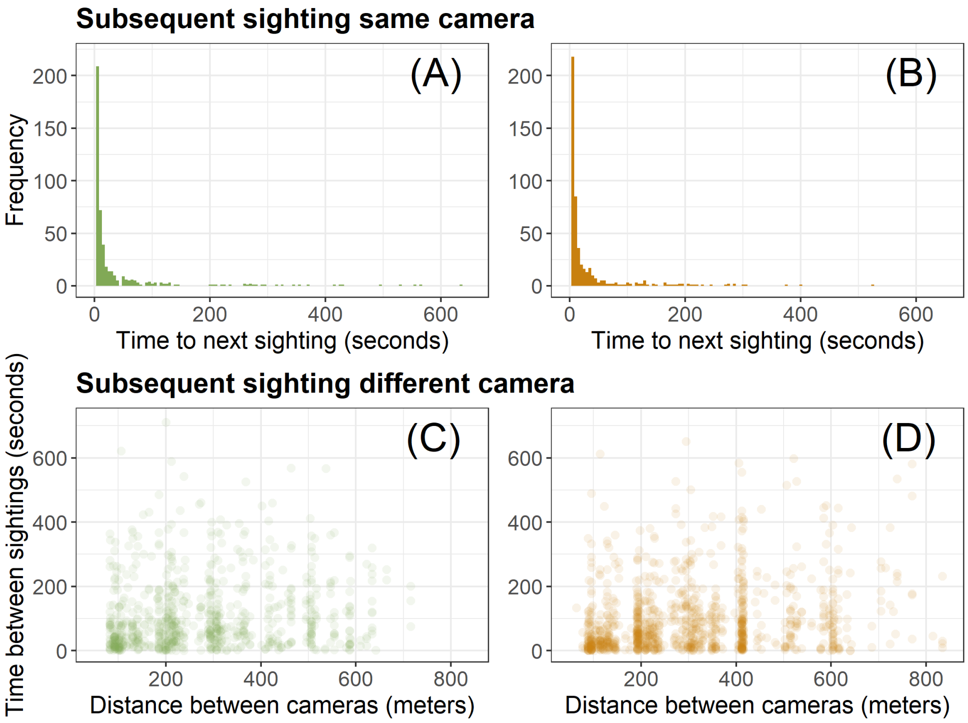

Figure 5.5: Subsequent capuchin sightings within a day for non-tool-using (green) and tool-using groups (orange). (A, B) show time to next sighting at the same camera; (C, D) show time and distance to next sighting at a different camera. Each dot represents one sighting.

5.5 Discussion

We investigated whether increased intragroup competition from habitual tool use in white-faced capuchins is linked to reduced group cohesion. Using two grids of camera traps, we compared the social cohesion of one group of tool-using and one group of non-tool-using white-faced capuchins sharing the same habitat. Following our hypotheses (Table 5.1), we suggested two ways in which the tool-using group could be less cohesive to avoid competition over anvils: tool-using males could split off from a cohesive main group to use tools, or the entire tool-using group could be less cohesive and/or split into smaller groups. We found that, despite large overlap in daily activity patterns and only 3 kilometers of distance between them, there are marked differences in group cohesion between the tool-using and non-tool-using group.

We measured cohesion following Aureli and colleagues [284] as temporal variation in i) party size, ii) party composition and iii) spatial cohesion. Our findings regarding party size all support the entire tool-using group being less cohesive and/or splitting into smaller subgroups. The tool-using group had a higher likelihood of party of one detections, and smaller and less variable party sizes than the non-tool-using capuchins. Our finding of the tool-using group showing higher party sizes in the evening suggests that they likely still sleep together. The differences in party composition between the two grids — despite comparable group composition — also supported the hypothesis of a cohesive non-tool-using group, and tool-using group which is less cohesive or splits. Capuchin parties in the tool-using group had fewer adult males, fewer adult females, and fewer adult males and females present together than parties in the non-tool-using group. Spatially, the tool-using group showed stronger covariance in party sizes between cameras at all distances, while the non-tool-users only showed little covariance at close cameras and none at distant cameras. The spatiotemporal patterns of detection and co-occurrences further qualitatively support a more cohesive non-tool-using group and a more fragmented tool-using group.

5.5.1 Tool use linked to reduced group cohesion

Our findings provide the first evidence for a potential link between habitual tool use at monopolizable anvils and reduced group cohesion. The tool-using group and non-tool-using groups sampled here are of comparable group size and composition, inhabit the same habitat with only 3 kilometers between them, and both border the coast, where similar resources are available (e.g., coastal species like sea almonds, as well as intertidal resources). Yet they differ behaviorally, since the tool-using group has a habitual stone tool use tradition which has persisted over two decades [30], and here we also show how the social cohesion of these two groups also differs. It seems plausible that, on Jicarón, similar to what has been observed in bearded capuchins [114], tool use on usurpable food resources has led to increased contest competition, which in turn was alleviated through reduced group cohesion. In the range of the tool-using group on Jicarón, there are at least 10 heavily used anvil sites close to sea almond or coconut trees, which can only be used by one individual at a time [30]. The fixed location of these anvils, combined with their potential to be monopolized suggests these areas are expected to be a source of intragroup contest competition. In a mainland study site, white-faced capuchins of higher rank had higher energy intake than lower ranking individuals due to their success at winning contest competition interactions and ability to displace others from feeding patches [113]. While we do observe individual capuchins displacing others from the anvil and/or hammerstone, displacements are rare in the Jicarón tool-using group [84] (chapter 2). Thus, it appears as if the increased contest competition at anvil sites is either not present — which is unlikely given the high intensity of use — or is alleviated in some other way than through behavioral agonism.

Reduced group cohesion is one way to reduce the intensity of intragroup competition [300, 301]. However, reduced group cohesion can also result from a diminished need for social proximity when the benefits of group living are lower. On Jicarón, where predators are absent and capuchins are more terrestrial as a result [76], the selective pressure to maintain tight social cohesion may be relaxed. As both the tool-using group and non-tool-using group live in this predator-free environment, it is feasible that they are both less cohesive than mainland populations. However, predator absence alone cannot account for the *difference*s in cohesion between the tool-using and non-tool-using group described here, since they share the same ecological context. The most parsimonious explanation for this observed difference in behavior is the presence of habitual tool use at monopolizable anvils. To fully understand the relative contribution of tool use, predation pressure, and effects of island-living on capuchin group cohesion, comparative data from mainland populations and other islands are needed.

5.5.2 Cascading effects of a sex-biased tool use tradition

Despite tool use on Jicarón being restricted to males [84] — and thus only males experiencing contest competition at anvils — our results suggest the whole tool-using group shows reduced group cohesion. Rather than males splitting off from a cohesive group to use tools at an anvil and avoid competition, it appears as if either the entire tool-using group shows fission-fusion behavior and/or has greater group spread than the non-tool-using group. This has several important implications for the social system and behavior of the tool-using capuchins. First, in well-studied populations of white-faced capuchins at mainland sites, female-female social bonds are of great importance, and males are the dispersing sex [19, 302]. While we did not consider social behavior and grooming in this study, we do see that adult females are much less likely to be seen together in the tool-using group than in the non-tool-using group, thus seemingly having fewer opportunities for social contact. It is unclear how social bonds within- and between-sexes in the tool-using group differ from both non-tool-using capuchins on Jicarón, and from what we know from well-studied mainland populations, but this is a fruitful area for future research. Second, the male-exclusive nature of the tool use behavior combined with reduced cohesion likely results in some degree of sexual segregation, at least at anvil sites, where females are observed less frequently than other age-sex classes [84]. This affects social learning opportunities for immature individuals who are still dependent on their mothers, as it limits their observations of tool use and interactions with male group members. Our previous research found that social attention during tool use events is relatively rare (chapter 2), yet the continued persistence of the tool use tradition suggests young individuals are capable of acquiring the behavior.

5.5.3 Implications for intergroup dynamics

One benefit of high group cohesion is more success during competitive encounters with other groups. The reduced group cohesion in the tool-using capuchins may make them less competitive in intergroup encounters. In mainland sites, white-faced capuchins are known to be xenophobic with hostile intergroup encounters [19, 74, 303]. On Jicarón, we know little about the nature of interactions between groups. We have observed (sub)adult males with injuries, but have no evidence whether these were caused by intra- or intergroup aggression, and personal observations suggest intergroup competition is likely more relaxed on Jicarón, as on other islands [269, 270]. Due to the small size of the island and its genetic isolation, it is possible the capuchins have a high degree of inbreeding, and, as a result are less capable of differentiating ingroup from outgroup members, resulting in lower outgroup aggression [304]. However, higher relatedness would again be able to account for differences in behavior between capuchins on Jicarón and mainland capuchins, not between tool-using and non-tool-using capuchins within Jicarón island. More information is needed on intergroup encounters on Jicarón in order to assess whether they are comparable to those between mainland capuchin groups, and to see whether the tool-using group suffers a competitive disadvantage from reduced group cohesion. One possible way to obtain information on these rare events could be to use Passive Acoustic Monitoring (PAM) devices placed at several locations on the island to capture audio data of intergroup encounters, or playback experiments of calls from unknown individuals to see how the capuchins respond. The observed difference in group cohesion within such a small geographic scale (a 2002 ha island) also raises interesting questions regarding dispersal. While the details of the dispersal system on Jicarón are still unclear [30], dispersal between the tool-using and non-tool-using group is likely possible as they are only 3 kilometers apart. As such, a non-tool-using capuchin migrating into the tool-using group would not only be faced with the novel behavior of tool use, but also a less cohesive social group — potentially with more fission-fusion occurring — than it was used to. Whether migrants would adapt to the cohesiveness of their new social group is a question that has not previously been explored, but could provide fascinating insights into the flexibility of social systems.

5.5.4 Estimating cohesion using camera traps

There are several challenges to estimating group cohesion using camera traps, some of which can be addressed using statistical methods. Each camera trap has its own detection distance, where an animal passing by results in a trigger. Due to the limited view of camera traps, there is always the possibility of animals being present in the party captured but out of view from the camera trap. This bias is greater at camera traps with small detection distances, and to account for this we included the camera trap location as a random effect in all of our models. Nonetheless, while with our current methods we can show that there is a difference in the group cohesion of the tool-using and non-tool-using group, theoretical models will likely be needed to contextualize this difference. Ideally, one would have comparable data from a grid of camera traps placed in a mainland group of white-faced capuchins, but since capuchins are largely arboreal, such data does not exist. Capuchins' arboreality also means that a lack of detections at ground-level camera traps does not necessarily indicate their absence, since individuals may be present in the canopy. Arboreal camera traps placed on Jicarón — though only in areas with non-tool-using capuchins — found that capuchins were more arboreal during the morning [76, 271]. Placing arboreal camera traps in the tool-using group's range is necessary to assess whether patterns of terrestriality, both in timing and extent, differ between tool-using and non-tool-using groups. This information is also crucial for interpreting some of our results, such as the differing daily activity patterns between tool-using and non-tool-using group (Figure 5.1).

In the absence of comparable mainland data, modeling the movement of capuchin groups of different levels of cohesion (e.g., a group that fissions versus a cohesive group which stays together) over a grid of camera traps with varying detection probabilities would help contextualize the spatiotemporal patterns in capuchin detection that emerge. Additionally, identifying individual capuchins from camera trap images, especially from cameras with close detection ranges, is very challenging since images are often blurry with only parts of the animal in frame. If all individuals can reliably be identified, camera traps can be used to reliably assess demography and construct robust social networks, which has been demonstrated in chimpanzees [305, 306]. Our analyses would have greatly benefited from better identification of the individuals that were clearly captured, something which will potentially be possible in the future with the development of deep learning facial recognition algorithms. Given the large proportion of capuchins that we could not assign an age-sex to, it is also possible that some sightings were not of the group targeted with the grid, but one of their neighboring groups. This is especially likely in the non-tool-using grid, where we had to establish identities of capuchins during sampling for this study, rather than were able to rely on identification of individuals from years of prior data collection like in the tool-using group. It is important to keep this limitation in mind, since for instance the pattern observed in co-occurences in the non-tool-using group (Figure E.6) could also reflect capture of two different social groups, rather than subgroups from the same group of capuchins.

Another important consideration given the nature of our data collection is the home range size of the capuchin groups which we studied. Mainland groups of white-faced capuchins tend to have home ranges of around 1 km^2 [307], and on another island, Barro Colorado Island — though here capuchins can swim to the mainland — home ranges are of comparable size [204, 308]. We lack precise data on the home range sizes of capuchin groups on Jicarón, but the camera trap grids offer some insight into their minimum extent, which appears to be broadly comparable to those reported elsewhere. One possible explanation for the detections at night in the tool-using site, while these were entirely absent in the non-tool-using site, could be that the grid covered more of the tool-using group's homerange. Thus, we may have captured their sleep sites with our grid, which is supported by the much higher frequency of capuchin sightings early in the morning and late in the evening at a specific camera in the tool-using grid. If the tool-using group is truly fissioning during the day, but sleep together, one may expect they have fewer sleep sites or switch them less frequently to allow the group to more easily come back together. Theoretically, the tool-using capuchins could also have a smaller home range as a consequence of their focus on the 10 heavily used anvil sites, as well as exploitation of the intertidal zone. The greater coupling of the tool-using group's coastal activity to the tidal cycles might also result in different spatiotemporal patterns of detections than the non-tool-using group [122]. Future research incorporating these many different drivers of movement is needed to be able to draw more concrete conclusions about the differences in group cohesion.

5.5.5 The motivation to fission

The advantage of using two similar grids of camera traps at the tool-using and non-tool-using group is that we have comparable data between these two groups. However, this design means that the grid cameras do not capture tool use—the hypothesized driver of the reduced cohesion in the tool-using group. To more directly test this hypothesis, data from camera traps placed at anvils—though not the focus of the present study—can offer additional insights into how competition over tool-use sites may influence group cohesion. By showing detections of individuals using tools at different anvils around the same time, we would have more concrete behavioral evidence of fission-fusion behavior in the tool-using group. Furthermore, previous studies have shown that fission-fusion dynamics are highly flexible [284] and can vary seasonally, for instance in response to fluctuations in food availability [286–288]. Tool use on Jicarón likely also has a seasonal component [30], where we see peaks in tool use frequencies in the transitions between wet and dry season (see chapter 2) The camera traps used in this study were only deployed for about 7 months, overlapping in time with at least one of the peaks in tool use activity. As such, the reduced cohesion we observed by the tool-using group may reflect their cohesion during this time period of increased competition, and cohesion may increase in times when tool use frequency decreases. Further research is needed over larger timescales to shed light on this, also taking into account fluctuations in availability of other food resources which may affect intragroup competition and cohesion for tool-using and non-tool-using capuchins on Jicarón alike.

5.6 Conclusion

Our results suggest that habitual tool use can lead to reduced group cohesion as a strategy to reduce intragroup competition over monopolizable anvils. By comparing two groups of capuchins sharing the same environment, but differing from one another in their tool-use behavior, we provide evidence that tool use itself likely drives this difference in social cohesion. Given that group-living is a balancing act of advantages and disadvantages, this reduced group cohesion can likely only emerge in specific environments where the costs of fissioning are minimized, such as environments with low predation pressure. On Jicarón, the absence of predators may allow the benefits of fissioning to use tools without competition to outweigh the costs of reduced cohesion like increased vulnerability to predation. While tool use is restricted to males, its effects appear to extend beyond males, influencing group-wide dynamics, including adult social bonds and juvenile learning opportunities. Future research should aim to better contextualize the observed patterns by i) comparing island to mainland groups, either directly or through theoretical modeling, to assess the influence of island-living on group cohesion, ii) integrating data from cameras at anvil sites to directly examine the role of tool use, and iii) conducting longer-term monitoring to capture potential seasonal variation in both tool use and cohesion. Studying these dynamics will provide broader insights into the interplay between social structure and cultural behaviors in primates.

5.7 Data availability

Details of model output are available in section E.2. All code and data necessary to replicate analyses can be found at https://github.com/ZoeGold/capuchingroupcohesion.

5.8 Acknowledgments

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General Discussion

6.1 Thesis overview

This thesis presented an investigation of the stone tool-using capuchins of Coiba National Park using data from camera traps. My research explored what makes these islands and the capuchins inhabiting them so different from mainland capuchins, with the goal to elucidate the drivers of their unique tool use tradition. The findings I presented here are but a small piece of the puzzle of what conditions may favor the development of tool use. The chapters in this thesis highlight how animals' social and ecological environments are inherently linked to behavior, and how behavior in turn may also shape their environments. By comparing tool-using and non-tool-using capuchins living in the same habitat, I was able to exclude influence of certain ecological factors, and hone in on what might truly be important for a tool use tradition to develop and be maintained. What can this unique case teach us about tool use in the animal kingdom in general?

6.1.1 Who uses tools?

In chapter 1, I explored the discrepancy between the tool use traditions on the neighboring islands of Coiba and Jicarón. On Coiba, both sexes use tools, while on Jicarón, tool use appears to be restricted to males. By placing camera traps in streambeds and random locations in the forest interior, rather than only relying on data from biased placement at anvil sites, I was able to test several hypotheses for the absence of female tool use on Jicarón. Importantly, I demonstrated that the absence of female tool use is not likely the result of a sampling bias. Furthermore, females are physically capable of tool use and have the opportunity to access tools and anvil sites. However, females on Jicarón do not use tools, and hardly scrounge on items opened by others using tools. This chapter highlights how different tool use traditions can be in neighboring, separate populations, and that sex biases can arise even without apparent physical, environmental, or social constraints.

Due to the difficulty sexing juveniles from camera trap images, we do not know whether females use tools as juveniles and then cease in adulthood or never acquire the behavior to begin with. In chapter 2, I presented what we do know about the development of the tool use proficiency on Jicarón. Similar to other tool-using primates, becoming a proficient tool user appears to be a long process. While acquisition of tool use often relies on exposure to the behavior via close social attention, on Jicarón social learning opportunities seem limited. I found that, when juveniles do pay social attention, they preferentially pay attention to older, more proficient tool users, and that this attention is correlated with the opportunity to scrounge. These findings further highlight the importance of social tolerance in the acquisition of complex behaviors like tool use.

6.1.2 What drives the development of tool use?

My findings of chapter 1 and chapter 2 showcase the great within-group variation in the tool use behavior of the tool-using group on Jicarón. The localized nature of tool use on Jicarón, despite shared environments and no physical boundaries between social groups, remains puzzling. In chapter 3, by exploring intergroup variation between tool-using and non-tool-using groups, I uncovered that a possible function of the tool use might be to exploit resources in the intertidal zone. Tool-users, more than non-tool-users, timed their activity near the coast in accordance with the tidal cycles. Tool use might allow for more efficient exploitation of these ephemeral resources, in line with the proposed importance of intertidal foraging in human evolution. Novel observations of tool use in the intertidal zone by the two groups neighboring the tool-using group on Jicarón further support that one driver to acquire tool use may be exploitation of intertidal resources.

However, necessity may not need be the mother of invention, if free time (or boredom) is sufficient. The findings I presented in chapter 4 highlight how the tool use tradition on Jicarón may also have emerged due to conditions favoring innovation overall. I described a novel social tradition of abduction and carrying of howler infants by capuchins. The same age-sex classes that are fervent tool users are perpetuating this tradition, and it might be another reflection of the unusual characteristics of Jicarón island that made it possible for tool use to emerge there.

6.1.3 What are the effects of tool use?

Lastly, in chapter 5, I took another perspective on the differences between tool-using and non-tool-using groups on Jicarón, by examining how the tool use tradition may have affected capuchins' social cohesion. Habitual reliance on monopolizable anvils possibly altered the social system of the capuchins due to increased intragroup competition, having cascading effects on all the above mentioned questions. I compared the tool-using group to one non-tool-using group using two similar grids of camera traps. I found that tool users appear to fission-fusion or overall be less cohesive, where male capuchins likely preferably exploit anvils alone rather than take turns with group members. The absence of predators on Jicarón island means the costs of reduced group cohesion are lowered, and competition due to tool use might be a driver for capuchins to take advantage of this opportunity.

6.2 The origins of tool use

Collectively, the chapters in this thesis show that the emergence of tool use is likely driven by a complex interplay of factors. While cognitive capacities may be a limiting factor in the development of tool use, complex cognition alone is not sufficient for tool use to emerge. White-faced capuchins are curious, tenacious, and explorative foragers, capable of overcoming the defenses of many food items [19]. Multiple studies at decades-long field sites have demonstrated their remarkable ability to innovate and learn socially [68, 70]. However, these features alone are not enough for them to develop a tool use tradition. White-faced capuchins on the mainland have not developed tool use. Even within Coiba National Park, where tool use does occur, not all groups of capuchins show the tool use tradition. Furthermore, despite females on Coiba using tools, females on Jicarón do not, a difference which cannot easily be explained by common hypotheses (i.e. differences in risk perception or physical ability). This all suggests that there are environmental and/or social factors necessary for tool use to emerge, persist and spread, beyond simply suitability of the animal species to the cognitive tasks of tool use.

6.2.1 Terrestriality and opportunity

In line with the opportunity hypothesis [35], tool use may have emerged in Coiba National Park as a result of greater opportunity to use tools due to capuchins being more terrestrial. The absence of predators has likely contributed to the increased terrestriality observed in white-faced capuchins in Coiba National Park compared to the mainland [76]. This is further reflected in the low rate of vigilance behaviors during tool use, especially when compared to robust capuchins using tools in predator-rich environments [309]. An absence of terrestrial predators means there is less risk in spending time on the ground focused on using tools, also supported by our observations of capuchins napping on the ground during the day (Figure 6.1). Terrestriality is hypothesized to affect three major components of tool use: its innovation, accumulation, and social learning [310]. More terrestrial animals are thought to have a higher chance to innovate tool use, due to increased encounter rates with the materials for tool use. Materials of tool use can also accumulate more easily, since tools used terrestrially usually remain in the place last used, in contrast to tools used arboreally which can fall out of the trees and be lost. Lastly, social learning of tool use is enhanced by terrestriality due to the differences in structural landscape of trees compared to the ground, allowing for closer observation of tool use events by conspecifics on the ground [310]. In some other tool-using animals, this hypothesis seems to hold true. In robust capuchins, a group with a higher terrestriality level also showed more diverse tool use repertoire [112], and this is considered the key factor driving the emergence of tool use in robust capuchins [311]. Furthermore, in chimpanzees, tool use employed in terrestrial contexts tends to be more complex than tool use seen exclusively in arboreal contexts [310]. However, on Jicarón, other capuchin groups that do not use tools are exposed to the same low predation pressure, exhibit similar levels of terrestriality [76], and are afforded the same opportunities to encounter tool use materials [30]. It is possible that innovation of tool use, though more likely with greater terrestriality, is still very rare [35]. Therefore, although reduced predation and increased terrestriality may have been important in enabling and supporting tool use on Jicarón, these factors alone cannot fully explain the observed variation in its occurrence.

Figure 6.1: Camera trap image of an adult female from the Jicarón tool-using group napping on a tool use anvil.

6.2.2 Necessity from environment

While we currently have little information on (seasonal fluctuation in) food availability on Jicarón, previous research indicates that tool use occurs more frequently in the transition between wet and dry seasons [30]. This suggests tool use on Jicarón might partially be driven by necessity, as this is when terrestrial resources would likely be more limited. Tool use has been linked to necessity in a variety of tool-using animals, such as island-living macaques who only began using stone tools when they were faced with food scarcity during the COVID pandemic since human tourists — who normally fed them — were absent [25]. Our finding that tool-using capuchins' coastal activity is tightly coupled to the tidal cycle, and that this effect is stronger in the wet season, suggests that capuchins' intertidal foraging also has a seasonal component. Non-tool-using capuchins show the opposite pattern, with more coastal activity in the dry season, indicating that using tools may make a difference in when intertidal exploitation is either worthwhile or necessary. While more research is needed to see how coastal activity links to actual consumption of intertidal resources, tool use enhancing exploitation of marine resources is in line with theories on human evolution [183]. The novel findings of tool use in the intertidal zone by the groups neighboring the tool-using group on Jicarón further suggests that tool use in this context is likely more cost-effective or adaptive than tool use on terrestrial resources. It also highlights, given the nature of our data collection using camera traps and physical surveys, the limitations to our knowledge of how localized the tool use is, since this opportunistic tool use which leaves no physical traces could be more widespread on Jicarón island. Nonetheless, there are no clear indications that non-tool-using capuchins on Jicarón suffer from malnutrition or starvation, they continue to survive and reproduce, suggesting that necessity alone is not a good explanation for the occurrence of tool use on Jicarón. However, it is possible that while historic environmental conditions on Jicarón made tool use a necessity, these conditions have changed and thus the necessity is no longer clearly observable [312].

Furthermore, an important caveat when considering the variation in tool use behavior between groups is the adaptiveness of tool use. There is currently no clear evidence that tool use is adaptive [5], aside from one study demonstrating that stone tool use improves diet quality among *Sapajus* capuchins [33]. One possible explanation for the lack of spread of the tool use tradition on Jicarón, and the male bias we observed in the tool use behavior, could be that it does not necessarily have fitness benefits. Tool use could have developed in the tool-using group and persisted due to their free time and the costs of tool use being low, not necessarily because it improves their fitness. In this situation, there would be less pressure on it to spread to other groups. Its continued persistence, however, suggests that there is likely some benefit to the tool-using capuchins, perhaps comparable to *Sapajus* capuchins, it may improve diet quality [33]. While our data from the camera traps does capture some feature of diet, data are inherently biased by the placement of the traps and as such do not capture the full picture. In particular consumption of small invertebrates and other items that are encountered opportunistically is likely overlooked, and we have no cameras in the intertidal zone at all. Complementary to the findings of chapter 3, DNA barcoding or stable isotope analysis of feces or hair can uncover in more detail what the capuchins are eating, as well as what proportion of their diet is marine resources [313]. Comparing the diet breadth and quality of the tool-using and non-tool-using capuchins can help elucidate whether tool use has positive effects on fitness, and if it leads to the consumption of more intertidal resources. Even so, our discovery of the rise and spread of a social tradition in the tool-using group that lacks any clear benefit — the abduction and carrying of howler infants — demonstrates that behavior does not necessarily need to be clearly adaptive to be innovated and spread via social learning. It also provides evidence that the conditions on Jicarón might be overall conducive to innovation.

6.2.3 Islands as hotbeds of innovation

The environmental and social conditions on Jicarón which favor innovation could be features of islands more generally, which would also account for the remarkably high occurrence of tool use in island-living populations of animals. Islands are also called ‘hotbeds of innovation’ or ‘natural laboratories’ for a reason [56]. Compared to the mainland, islands tend to have reduced predation pressure, decreased species richness (resulting in more limited diets and reduced resource abundance), higher densities, as well as genetic isolation and limited cultural transmission [56–58]. In response to these conditions, animals living on islands show physical, morphological, and life history adaptations that differentiate them from their mainland counterparts [72, 314]. While this ‘island syndrome’ has been widely studied, the behavioral component of island syndrome is still relatively unexplored and it is unclear how island-living affects personality and cognitive abilities [57]. The findings I present in this thesis provide further evidence that island-living animals differ from their mainland counterparts in a variety of ways, including the innovation and maintenance of a tool use tradition. Furthermore, the release from predation pressure, free time, and understimulating social and physical environment experienced by animals on islands has comparisons to conditions in captivity. Captive animals show an increased rate of innovations — also of tool use by otherwise non-tool-using species [315] — and better cognitive performance [272] than their wild counterparts. On islands we might see a version of this 'captivity effect' occurring in the wild. Future research is needed to pinpoint the role the conditions on islands play in the development in tool use, and to test whether islands are indeed hotbeds of innovation of tool use.

A promising avenue to better understand how capuchins on Jicarón differ from mainland capuchins in term of cognition is by implementing non-invasive experiments in the wild. As part of this thesis, I piloted a setup of an experimental anvil with hammerstones, alongside a 'snail jail' — a jug containing water and a species of snails that are normally consumed by both tool-using and non-tool-using capuchins. The intention of this experiment was to provide a baseline for a later experiment where we would replace some of the snails with another species that cannot be cracked using tools, to compare the conservatism and cognitive flexibility of tool-using and non-tool-using capuchins. This setup requires further refinement to be used in the future, as many snails escaped and the non-tool-users were very wary so rarely interacted with it. An initial investigation comparing the responses of the tool-using and non-tool-using capuchins to this experimental set-up — as well as the camera traps deployed over the years — indicated that tool-using capuchins are more neophilic and less neophobic than non-tool-using capuchins (unpublished data, Figure 6.2). This difference in neophilia and neophobia could be both a cause of or result of the tool use behavior, since neophilia has been linked to innovation [316]. Future experiments which more carefully mimic natural situations — to avoid non-tool-users being too wary to interact with the set up — will allow for direct comparison of cognitive abilities and flexibility between tool-using and non-tool-using groups of animals living in the same habitat. These findings would help shed light both on the evolution of cognition and adaptations to island-living [317, 318], as well as any cognitive abilities associated with habitual tool use.

6.3 The consequences of tool use

6.3.1 Physical landscape and interspecies interactions

The habitual use of tools alters an animal's physical landscape, due to manipulation of tool use materials and accumulation of debris. The physical remnants of tool use contain evidence that can be used to uncover drivers of tool use behavior, and can be complimentary to behavioral analyses. In the still relatively new field of primate archaeology [22], comparison of non-human primate tool sites to archaeological records of hominins allows for better understanding of how behavior translates into archaeological signatures. On Jicarón island, capuchin tool use is also investigated from this archaeological perspective, and several of the chapters

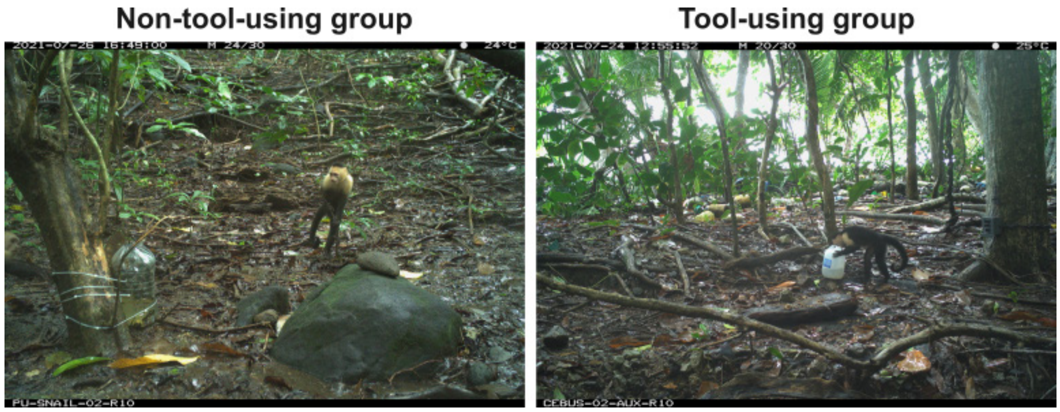

Figure 6.2: Two camera trap images illustrating the initial response of a group of non-tool-using capuchins (left image) and the tool-using group (right image) to the snail trap.

here incorporate archaeological evidence (e.g., physical evidence of tool use in the intertidal zone), or will still have an archaeological perspective counterpart (e.g., hammerstone selectivity to inform variation in tool use proficiency between age classes). Capuchins' tool use activity may create both opportunities and limitations for other species on the island. While one might imagine other animals benefit from scrounging on the debris left behind by tool-using capuchins, agoutis on Jicarón appear to avoid the tool use area more than areas with non-tool-using capuchins, suggesting they are perhaps outcompeted by tool-using capuchins [271]. The variation in tool use behavior within Jicarón island means it is also a suitable location for future investigations of how tool use alters the physical landscape and affects interactions with other species.

6.3.2 Tool use affecting the social environment

An important finding of my thesis is that tool use may not just shape an animal's physical environment, but also its social environment. The described differences in group cohesion between tool-using and non-tool-using capuchins could be a consequence of the tool use behavior. Social learning opportunities and who spends time with whom can be structured by sex-biased attentional preferences [319, 320], which in turn enhance and are enhanced by sex biases in tool use behavior. I present a first exploration going beyond tool use structuring social opportunities to it affecting group cohesion more broadly, also of individuals who do not use tools. The implications of these differences in cohesion warrant further investigation: the social behavior of the capuchins on Jicarón remains largely understudied. Future studies need to consider how their social behavior compares to that of well-studied, mainland populations, and how it differs between tool-using and non-tool-using groups. For instance, how are mating opportunities affected by reduced group cohesion in the tool-using group?

One crucial puzzle piece in this question, as well as in understanding the localized nature of the tool use behavior on Jicarón, is the dispersal tendency of the capuchins. In mainland sites, male capuchins disperse, sometimes several times within their lives [71, 133]. This pattern of dispersal would be expected to lead to the spread of the male-biased tool use behavior. The absence of tool use spreading could be a result of females dispersing rather than males, and such reversal of dispersal tendencies can occur under high density conditions, as is the case on Jicarón [89]. During the project, hair from the tool-using capuchins was collected non-invasively through use of hair traps (tubes with sticky tape and a quail egg inside). Future DNA testing of these samples is much needed to uncover relatedness within and between sexes in the tool-using group, which could clarify the dispersing sex. Additionally, the capuchins on Jicarón might exhibit a high level of inbreeding. Reports of amelanism on the larger island of Coiba [136] suggest increased genetic homozygosity, likely resulting from inbreeding or founder effects. Reduced genetic diversity could also have implications for intergroup competition, as highly inbred animals can struggle to differentiate between familiar and unfamiliar individuals [304]. Assessing the effect of reduced cohesion on intergroup competition is also crucial to better understanding the potential costs and benefits of the tool use behavior.

6.3.3 Comparing Coiba, Jicarón, and the mainland

The work presented in this thesis largely focuses on the tool-using capuchins on Jicarón, since most data was available on this population, and the localized nature of the behavior on the island makes it very suitable for comparative studies. However, tool use also occurs on the island of Coiba [31], and an obvious fruitful avenue of future research is to contrast and compare the tool-using group there to the one on Jicarón. The imbalance in data collection was largely a result of the nature of the tool use site on Coiba: it is harder to access, and as most tool use occurs in stream beds, there are fewer trees to mount cameras on. Innovative solutions like constructing poles to place cameras in the streambed will allow for more detailed data collection on the Coiba tool-using capuchins. In addition to the sex difference, uncovering how tool use behavior on Jicarón differs from that on Coiba, along with identifying environmental variation, will help to further narrow down the drivers of tool use. On Coiba, more research is needed to see if tool use is indeed more limited to streambeds, or if there are also more high accumulation sites, and how these then compare to the high and medium accumulation sites on Jicarón. Furthermore, additional surveys are needed to see if the tool use behavior on Coiba is similarly localized as on Jicarón. If it is not, this could help identify the factors limiting the spread on Jicarón, by examining what differs in the capuchins' environment and social structure between the two islands. Since Jicarón is further from the mainland than Coiba and is much smaller, the islands differ in species richness. Comparing the non-tool-using capuchins on the two islands would thus be incredibly valuable, to examine the effects of environmental conditions on behavior in the absence of tool use.

One major challenge in the interpretation of research on Jicarón is that islands differ from the mainland in so many ways. It is hard to know what would be expected as 'normal' capuchin behavior — the typical picture from decades long study sites on the mainland [70, 71] — and when contrasting tool-users to non-tool-users we lack a clear behavioral baseline from the mainland for comparison. Since

Coiban capuchins are much more terrestrial than mainland capuchins, a direct comparison will always remain difficult. It is for instance not possible to place a similar array of camera traps in a mainland population, since they are simply too arboreal. However, a combination of data from mainland sites with theoretical modeling could allow for some comparison, and there are other methods (such as non-invasive cognitive experiments) which can be conducted in a similar fashion on the islands and on the mainland.

6.4 Implications for conservation

6.4.1 Using camera traps to study complex behavior

My research demonstrates how minimally invasive camera traps can be used for the study of complex animal behavior. Conducting research on animals as minimally invasive as possible is of vital importance to me personally, but also to the well-being of animals being studied, and the quality of the science overall. If animals are disturbed by our research methods, it not only harms their mental and physical well-being, but also alters their behavior and as a consequence, limits the generalizability of our findings [321]. Therefore, in my view, a crucial component of my thesis is that I demonstrate how, beyond measuring species richness [322], or cataloging behavioral diversity [47], camera traps can be used to research something as dynamic as movement related to the tides, and as complex as the rise and spread of a novel cultural tradition.

Camera traps have limitations and are not suitable for all contexts — for instance they are ineffective for strictly arboreal species. When studying semi-arboreal animals like capuchins using ground-based camera traps — as I do in this thesis — it is important to interpret detection rates with the caveat that an absence of detections may reflect capuchins being present, but in the trees. However, continued developments in image processing and statistical analyses allow for many of the limitation of camera traps to be overcome. For example, clustering of images into sequences involves setting a largely arbitrary cut-off time, however, recent research has demonstrated that analyses based on per image annotation and continuous time are also feasible [323, 324]. The rapid advancements in machine learning also mean that processing of data from camera traps is relying less and less on intensive manual labor, as machine learning can accurately classify wildlife in camera trap images [325]. Using camera trap data from Jicarón and Coiba, collaborators developed a Capuchin Detection Algorithm, which in the future, can be used to process data from camera traps much faster than manual labeling. There are also possibilities for pose estimation and behavioral analyses using machine learning algorithms [326, 327], further opening up new avenues for detailed analyses in this rich dataset to gain a better understanding of the tool use behavior. In this thesis, I pioneer several methods, such as the use of Bayesian hierarchical GAMs for modeling activity relative to the tidal cycles, and a Gaussian Processes model to compare group cohesion between grids of camera traps. For every chapter, I shared all data and code necessary to replicate analyses, with the intention of disseminating our findings as widely as possible and facilitating future research that builds on these methods.

6.4.2 Conserving Coiba National Park and animal culture

The impact of the research presented here goes far beyond the white-faced capuchins. All the camera traps placed in Coiba National Park are also used to document the biodiversity in the archipelago, which is a UNESCO World Heritage Site. I coded the data from the camera traps on www.agouti.eu [123], where data is easily shared with researchers across the globe. This can help conserve the animal species living on these islands, many of which are endemic [75]. Coiba National Park faces the same threats as other areas in the world that remain relatively undisturbed by humans: increased pressure from tourism, overfishing, and cascading effects from climate change. Furthermore, massive amounts of plastic waste wash ashore from the Pacific Ocean every single day, leading to a never-ending pollution of these otherwise pristine islands (Figure 6.3). It is as of yet unclear how the presence of all this anthropogenic waste impacts the health and behavior of the animals on Coiba [30], but potentially data from the camera traps described in this thesis can be used to investigate this.

Furthermore, in a world where habitat loss and fragmentation due to human impact is rampant [328] — leading to the increasing prevalence of ecological islands — it is crucial to understand how and if animals adapt to these conditions. Recently the importance of conserving animal culture to overall conservation has gained attention [228–230, 329]. The unique nature of the tool use behavior of the capuchins in Coiba National Park means preserving it is of vital importance. As such, raising awareness among other scientists and the general public of the Coiban capuchins and their one of a kind culture is a key aspect of the work I presented here.

Figure 6.3: Camera trap image of a subadult male capuchin using tools at an anvil, with anthropogenic trash washed up from the ocean visible in the background.

6.5 Conclusion

Research on the capuchins of Coiba National Park is still in its early stages, and a comprehensive understanding of their tool use will require insights from diverse sources and disciplines. Uncovering what drove tool use to arise, persist, and (not) spread in this unique study system can deepen our understanding of the broader factors driving animal tool use and the role islands play in this process. In this thesis, I used camera traps to capture valuable insights into the cognitive, ecological, and social factors that shape stone tool use by wild white-faced capuchin monkeys on Jicarón island.

I demonstrated remarkable behavioral variation within the tool-using group (chapter 1 and chapter 2), as well as between the tool-using and non-tool-using groups on the island (chapter 3 and chapter 5). These results underscore that no single factor can account for the emergence, maintenance, and spread of tool use in animals. However, islands serve as 'natural laboratories' where multiple drivers of innovation may converge. When a tenacious, explorative, and intelligent animal lives in an environment free of predators and abundant in free time, it might innovate behaviors absent in other populations of its species (chapter 4). Future studies are necessary to home in on the driving forces of cultural innovation on islands, and to explore the potential consequences of tool use on social behavior.

If the unique conditions of ecological islands foster the emergence of tool use, ongoing habitat fragmentation due to climate change and human activity might lead to the emergence of tool use in more animal populations. While intriguing, this adaptation pales in comparison to the devastating human impact on animal populations across the globe. Even on this remote, uninhabited island — where capuchins encounter humans only sporadically — our footprint endures in the form of trash washed ashore. Although the capuchins' ability to innovate highlights the remarkable flexibility of animal behavior, such adaptability has its limits. As human-driven changes reshape ecosystems, preserving biodiversity also means protecting the cultural traditions that make each population of animals unique, and the conditions that fostered the development of these traditions in the first place.

Appendices

Appendix A

Supplementary information for ‘Male-biased stone tool use by wild white-faced capuchins’

A.1 Details on methodology

Table A.1: Overview of camera deployments, S reflects a still camera and V a video camera

Location	***R1 Mar-Jul 2017***	***R2 Jul-Dec 2017***	***R3 Dec 2017-Mar 2018***	***R4 Mar-Jul 2018***	***R5 Jul-Dec 2018***	***R6 Dec 2018-Mar 2019***	***R7 Mar-Jul 2019***	***R8 Jul-Dec 2019***	***R10 Jul-Dec 2021***	***R11 Dec 2021-Jul 2022***	***R12 May 2022-Jan 2023***
Anvil cameras											
CEBUS-01	V	S	V		V	V					
CEBUS-02	S	V	S	S	S	S					
CEBUS-04				S	S	S		S			
CEBUS-05			S		S	S		S			
CEBUS-06				V	V	V					
CEBUS-07						V	S				
CEBUS-08		V	V	V	V	V					
CEBUS-09		S	S	S	S	S					
CEBUS-10							S				
SURVEY-CEBUS-07-03			V								
SURVEY-CEBUS-17-03				S							
Streambed cameras											
J-STREAM-01									S	S	
J-STREAM-02									S	S	
J-STREAM-03									S	S	
J-STREAM-04									S	S	
J-STREAM-05									S	S	
J-STREAM-06									S	S	
J-STREAM-07										S	
J-STREAM-08										S	
J-STREAM-09										S	
J-STREAM-10										S	
J-STREAM-11										S	
J-STREAM-12*											
JIC-STREAM-DISC-T-1						S					
SURVEY-CEBUS-15-04				S	S						
Random cameras											
Non-grid											
J-RAN-01										S	
J-RAN-02										S	
J-RAN-03										S	
J-RAN-04										S	
J-RAN-05										S	
J-RAN-06*										S	
J-RAN-07										S	
J-RAN-08										S	
J-RAN-09										S	
J-RAN-10										S	
J-RAN-11										S	
J-RAN-12										S	
SURVEY-CEBUS-08-01	S										
SURVEY-CEBUS-16-01		S									
Grid											
TU-135											S
TU-137											S
TU-141											S
TU-151											S
TU-153											S
TU-154											S

TU-155	S
TU-156	S
TU-157	S
TU-158	S
TU-166	S
TU-169	S
TU-170	S
TU-171	S
TU-172	S
TU-173	S
TU-182	S
TU-183	S
TU-184	S
TU-185	S
TU-186	S
TU-187	S
TU-188	S
TU-190	S

* Indicates a camera that was deployed but lost or destroyed

Table A.2: Ethogram of relevant behaviors (part of larger ethogram).

Behavior	Description
BS: Aggression	Aggressive towards another capuchin (or species). Fight, bare teeth threat, stacked coalitionary aggression, open mouth threat. This includes when an individual supplants another (specified in comment if supplanting from anvil, tool, or food).
BS: Infant Care	Nursing or caring for infant, including dorsal or ventral carrying of an infant.
BS: Submissive	Being fearful or submissive toward an aggressive individual (also code when being supplanted by another)
BS: Visually foraging	Looking around leaves/sticks/stream/leaf litter for food, without any physical interaction
BS: Tolerated scrounging	Individual takes food to eat from another individual (both tool use and regular foraging) and is tolerated. Specified in comment whether food sharing appears intentional (i.e., handing over food)
F: Almendra flesh	Consuming almendra exocarp, no tools used or endocarp eaten
F: Anvil debris	Foraging opened food at anvil when tool user not there (also applies to other species)
F: Coco flesh	Consuming coconut meat (white part), no tools (but smashing the coconut on an anvil is part of this).
F: Coco water	Drinking coconut water, typically smaller coconuts.
F: Fruit	Foraging fruit (comment if known)
F: Insect	Foraging insects (searching leaf litter using hands, chewing sticks for embedded insects, straight up eating an insect).
F: Other	Foraging other (comment if known)
F: Unknown	Foraging unknown object
TAF: Almendra	Foraging w/ stone tool: Terminalia catappa/sea almond
TAF: Coconut	Foraging w/ stone tool: coconut
TAF: Embedded insect	Foraging w/ stone tool: embedded insect in stick
TAF: Halloween crab	Foraging w/ stone tool: Halloween crab
TAF: Hermit crab	Foraging w/ stone tool: hermit crab
TAF: Other	Foraging w/ stone tool: other (comment if known)
TAF: Palm fruit	Foraging w/ stone tool: palm fruit
TAF: Snail	Foraging w/ stone tool: snail
TAF: Unknown	Foraging w/ stone tool: unknown object

A.2 Supplemental results

A.2.1 Model 1: Comparing adult female:adult male ratio between location types on Jicarón

Table A.3: Posterior mean model estimates of model comparing sex ratio across location types on Jicarón, a Bayesian logistic mixed model. Model's explanatory power is moderate ($R^2 = 0.20$, 95% CI [0.19, 0.22]). All estimated effects are on logit scale. Random cameras are the reference category (the intercept).

	Estimate	***CI_95_low***	***CI_95_high***
Group-Level Effects			
Camera location	0.37	0.25	0.53
Population-Level Effects			
Intercept	0.26	0.02	0.50
Location type: Anvil	-0.97	-1.60	-0.38
Location type: Streambed	-0.75	-1.11	-0.39
Distance to coast	0.05	-0.07	0.17
Interaction Anvil x Distcoast	0.96	-0.18	2.13
Interaction Streambed x Distcoast	0.23	-0.24	0.66

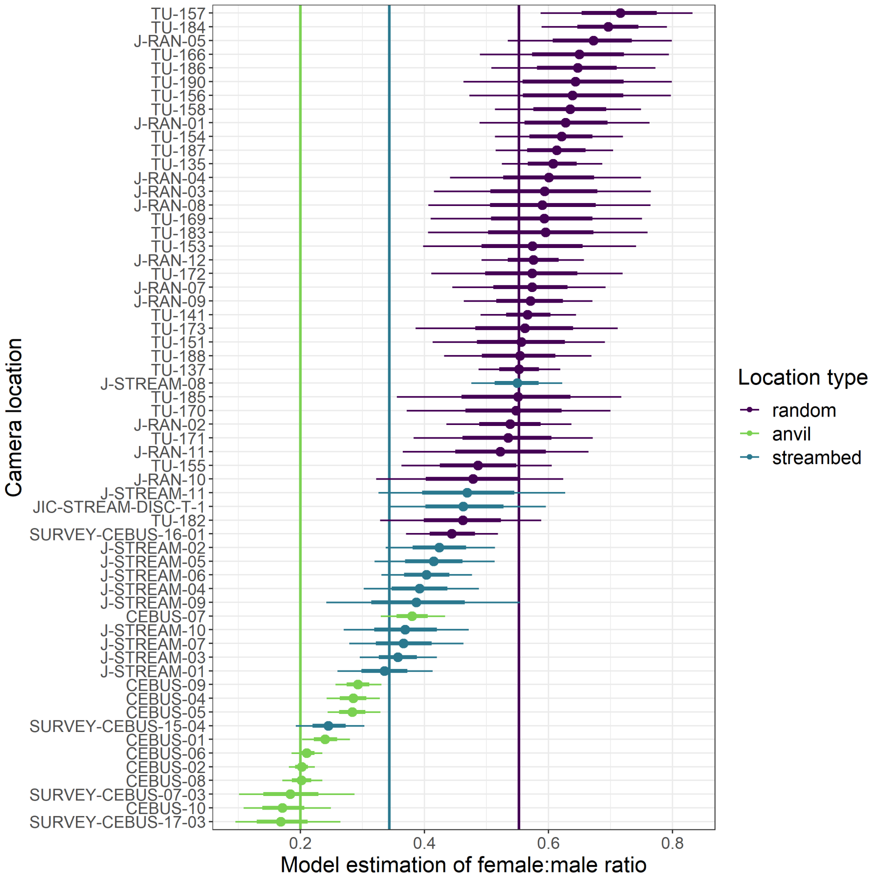

Figure A.1: Posterior mean estimates of the female:male ratio per camera location on Jicarón. Vertical lines indicate mean estimates per location type (purple for random, green for anvil, blue for streambed). Thick horizontal lines represent 95% credible intervals.

A.2.2 Model 1b: Estimating adult female:adult male ratio on Coiba

Table A.4: Posterior mean model estimates of model estimating sex ratio on streambed cameras on Coiba, a Bayesian logistic mixed model. Model's explanatory power is moderate ($R^2 = 0.39$, 95% CI [0.34, 0.43]). All estimated effects are on logit scale.

	Estimate	*CI_95_low*	*CI_95_high*
Group-Level Effects			
Camera location	0.57	0.02	1.89
Population-Level Effects			
Intercept	1.18	0.43	1.70

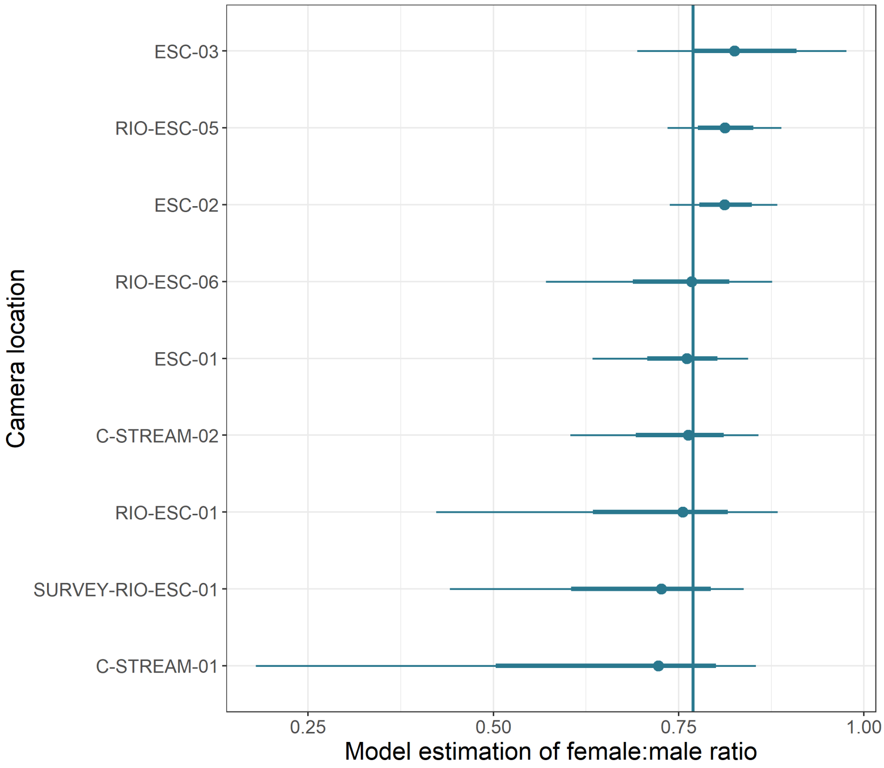

Figure A.2: Posterior mean estimates of the female:male ratio per camera location on Coiba. Vertical line indicates the mean estimate. Thick horizontal lines represent 95% credible intervals.

A.2.3 Model 2: Comparing adult female with infants:adult females without infants ratio between location types on Jicarón

Table A.5: Posterior mean model estimates of model comparing ratio of females with infants:females without infants across location types on Jicarón, a Bayesian logistic mixed model. Model's explanatory power is weak ($R^2 = 0.13$, 95% CI [0.10, 0.16]). All estimated effects are on logit scale. Random cameras are the reference category (the intercept).

	Estimate	***CI_95_low***	***CI_95_high***
Group-Level Effects			
Camera location	0.48	0.29	0.70
Month	0.35	0.18	0.63
Population-Level Effects			
Intercept	-1.34	-1.76	-0.93
Location type: Anvil	0.16	-0.59	0.44
Location type: Streambed	-0.16	-0.90	0.86
Distance to coast	-0.08	-0.25	0.09
Interaction Anvil x Distcoast	-0.52	-1.89	0.97
Interaction Streambed x Distcoast	0.75	0.12	1.36

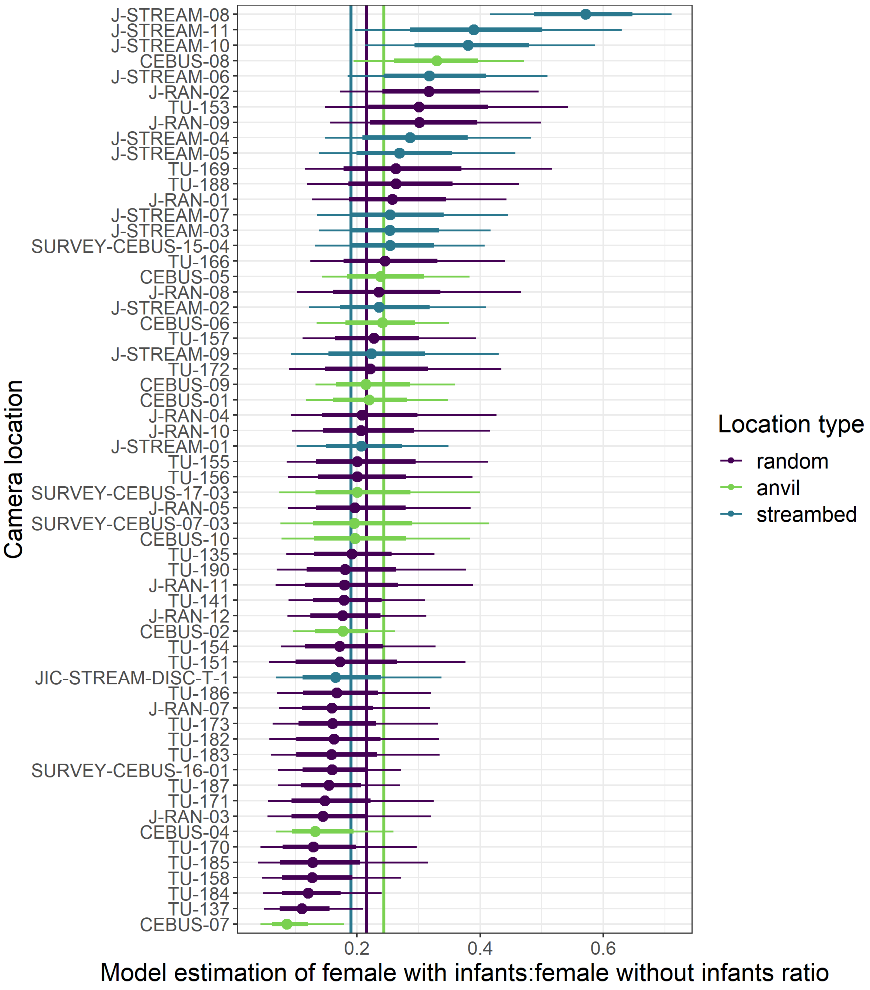

Figure A.3: Posterior mean estimates of female with infants:female without infants ratio per camera location on Jicarón. Vertical lines indicate mean estimates per location type (purple for random, green for anvil, blue for streambed). Thick horizontal lines represent 95% credible intervals.

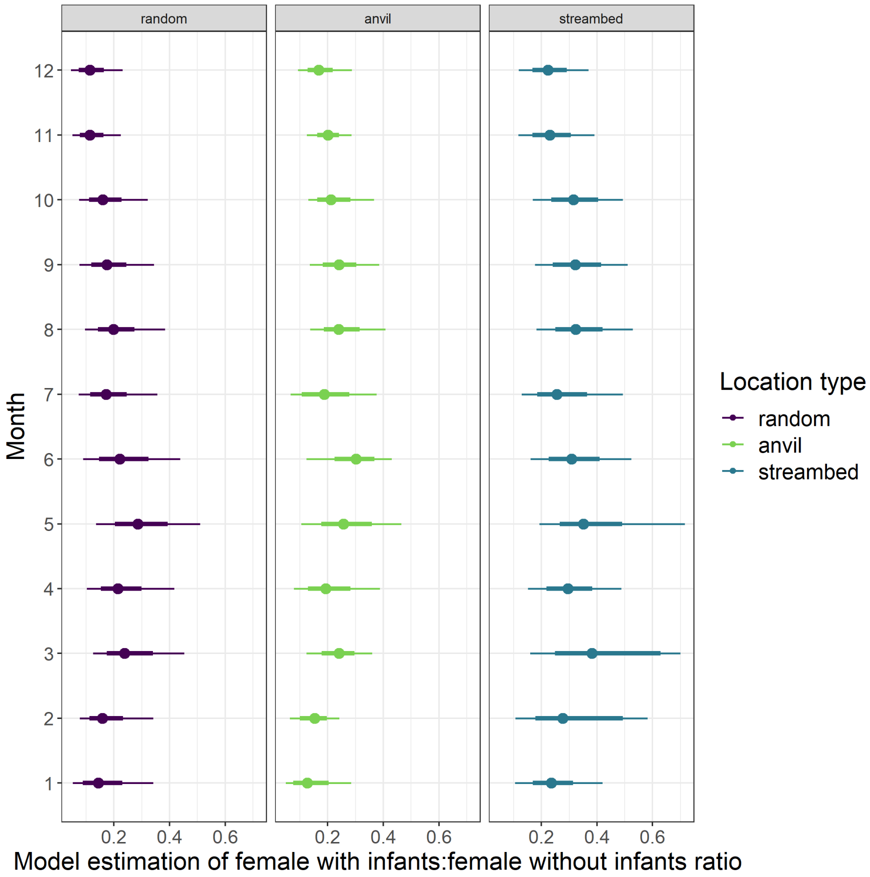

Figure A.4: Posterior mean estimates of female with infants:female without infants ratio per month and per location type on Jicarón. Thick horizontal lines represent 95% credible intervals.

A.2.4 Model 2b: Comparing adult female with infants:adult females without infants ratio at streambed cameras on Coiba

Table A.6: Posterior mean model estimates of model comparing ratio of females with infants:females without infants across location types on Coiba, a Bayesian logistic mixed model. Model's explanatory power is moderate ($R^2 = 0.38$, 95% CI [0.25, 0.48]). All estimated effects are on logit scale.

	Estimate	***CI_95_low***	***CI_95_high***
Group-Level Effects			
Camera location	2.60	1.23	4.94
Population-Level Effects			
Intercept	-2.47	-4.67	-0.55

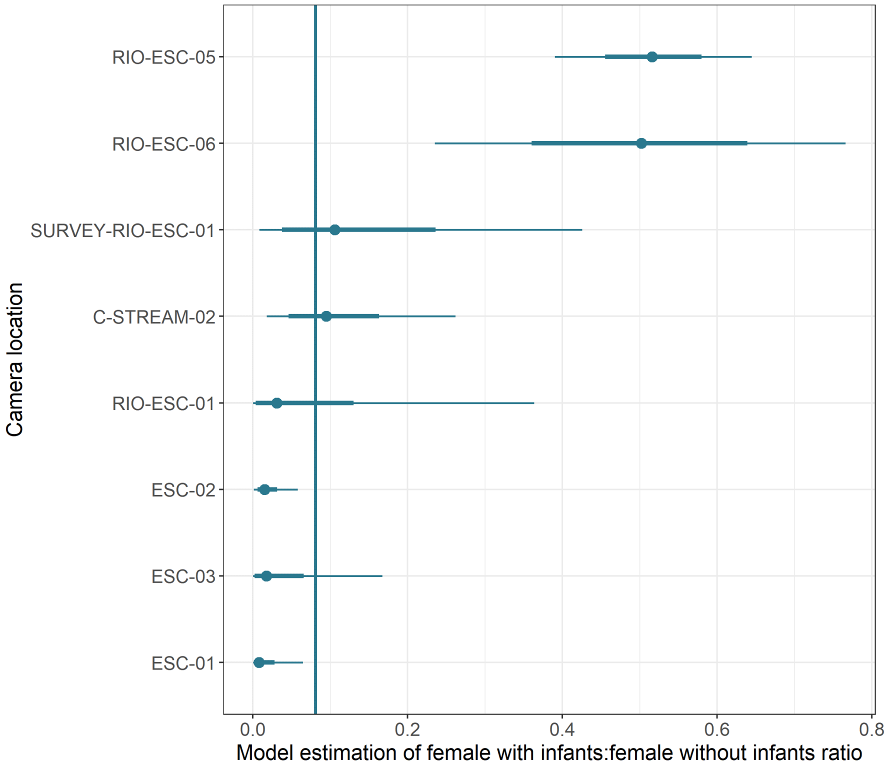

Figure A.5: Posterior mean estimates of female with infants:female without infants ratio per camera location on Coiba. Vertical line indicates the mean estimate. Thicker horizontal lines represent 95% credible intervals.

Appendix B

Supplementary information for 'Development and social dynamics of stone tool use in white-faced capuchins'

B.1 Electronic supplements

Video ethogram: https://keeper.mpdl.mpg.de/d/0c1b9853f3f342d8b3da/

Video B.1: https://youtu.be/tvuClVgwLRQ

B.2 Behavioral ethograms

B.2.1 Detailed coding of tool use sequences

Table B.1: Behavioral ethogram of all behaviors coded for every tool use sequence.

Behavior	Modifiers	Modifier Options	Definition
pound			*The capuchin hits the item with the hammerstone successfully, code pound at (approx.) the moment the hammerstone hits the item.*
	pound type	1. Crouching 2. Standing 3. Jumping	We differentiate between 3 pound types. 1. "crouching" pound, if the legs of the capuchins are at a 90-degree angle. 2. "standing" pound, if the legs are extended beyond 90 degrees (and often the body is elongated too). 3. "jumping" pound, if both feet leave the ground.
	position	1. 1 foot 2. 1 hand 3. tail support Multiple selection possible	Modifiers describing the position of the capuchin. The default is 2 footed (both feet on the ground) and 2 handed (both hands on the hammerstone). Only code tail support if you can see the capuchin clearly using their tail (i.e., gripping something with it or putting weight on it).
	hammer	1. Overhead	Modifier to indicate that the hammer was held above the capuchin's head during the hit, so whether any part is higher than their head at pound peak.
reposition			*When the capuchin repositions the item on the anvil (so anytime they touch/move the item in the sequence) or clearly changes their grip on the hammerstone. Code every time it occurs, but not every movement (e.g. if they grab the item and move it 3 times rapidly, code reposition once).* ***Note****: don't code the first time placing/adjusting item or gripping hammerstone at sequence start.*
	object type	1. hammer 2. item 3. peel	Whether it is the hammer or item that is repositioned. The third option is that they "peel" the item by holding it in their hand and manipulating it with hands or teeth (often tearing pieces off). **Note**: don't code peel when they do it at the end and eat the item straight after without more pounds.
misstrike			*When capuchins do not hit the item as intended, or something else goes wrong. You can often use audio cues to hear if they strike the item or the anvil.* ***Note****: if capuchin does hit the item successfully but also has a misstrike (e.g. item flies off) then code both the pound and the misstrike.*

	mistake type	1. item flies off 2. drop hammerstone 3. hammer break 4. anvil break 5. other	Specify what occurred, either no hit at all (the default), the item flies off the anvil, the hammerstone falls out of their grip, the hammer breaks or the anvil breaks. If not in this list then select other and add a comment to the behavior. **Important**: also add a comment if you see a capuchin injure themselves or others with the hammer.
hammer switch			*When a capuchin grabs another hammerstone during the sequence and continues with it.*
	hammer location	1. On anvil 2. Off anvil within reach 3. Off anvil walk 4. Carry in (c)	The location of the hammerstone they switch to.
	hammer ID	Enter the hammerstone ID as a comment, or if it's not marked/ unidentifiable: 7. Unmarked 8. Unknown	Enter the ID of the hammerstone switched to as a comment, which can be one of the marked hammerstones or in the case of an unmarked hammerstone code "unmarked" but describe it.
anvil switch			*When individuals switch from one anvil to another that are both within view of the camera, within a sequence. So they continue to process the same item at a different anvil.*
	anvil material	1. wood 2. stone	The material of the anvil that they switched to.

Table B.2: Overview of sequence-level variables coded for every tool use sequence.

Variable	Modifiers	Modifier Options	Definition
sequence start			*Start of tool use sequence, defined as the moment when the capuchin first places the item on the anvil. If the item is already on the anvil at the start of video, the start of the sequence equals the start of the video.* ***Note****: if capuchins are processing items on another anvil than the experimental anvil (e.g. a branch) make a comment saying "wooden anvil"*
	item type	1. Sea almond green (includes yellow) 2. Sea almond brown 3. Sea almond red 4. Sea almond unknown 5. Halloween crab 6. Hermit crab 7. Coconut 8. Fruit (add comment if known) 9. Other (add comment) 10. Unknown	Code which item is being processed
sequence end			*The end of the tool use sequence, defined as the moment the capuchin starts consuming the item (if opened) or otherwise when they let go off the hammerstone with no further strikes on the item.*
	outcome	1. Opened 2. Relocated 3. Abandoned 4. Continued	Add modifier to specify how the sequence ended. If the capuchin is eating the item, code it as "opened". The other options are the capuchin taking the item elsewhere ("relocating"), or "abandoning" it. "Continued" is an indicator that the sequence is not yet finished when the video ends. In case the video ends and you don't know what happened to the item (i.e., it's not recorded), keep seqend at "none" and add a comment saying it was unknown/missed. **Note**: if they open the item but do not eat it, then code "abandoned" with a comment saying "opened but not eaten".
	scrounging	1. scrounging 2. no scrounging	Code this behavior if any scrounging (other individuals eating parts of the item opened by the tool user) occurred during or after the sequence. **Important**: only code "no scrounging" if other individuals were present but there was no scrounging. If no other capuchins are visible, then choose "none".

	displacement	1. No displacement 2. Anvil displacement 3. Hammer displacement 4. Full displacement of both hammer and anvil	At the end of the sequence, did any displacement occur? If so, was the capuchin displaced just from the anvil or hammer or both? If displacement occurred, make a comment with the ID or age/sex of the displacing and displaced individuals. E.g.: “LAR displaces JOE” or “Subadult male displaces juvenile” **Important**: only code no displacement if other individuals were present but there was no displacement. If no other capuchins are visible, then leave it blank at “none”. **Note**: only code displacement once. For example, if a juvenile is using tools and gets displaced, then code displacement for the juvenile’s tool use sequence, but not for the sequence then started by the displacer.
	social attention	1. no social attention 2. social attention	At the end of the sequence, did any other individuals pay attention to processing by the tool-user? Attention means peering at the tool-user while they are processing (does not have to include scrounging). **Important**: if there was no opportunity for social attention (i.e., no other individuals around) then leave it blank at “none” and do not code "no social attention".
hammer stone			*To collect information about the hammerstones*
	hammer location start	1. In hand 2. On anvil 3. Off anvil within reach 4. Off anvil walk 5. Carry in	The location of the hammerstone first used for the tool use sequence relative to the experimental anvil. Code the location where the hammerstone is at the beginning of the sequence. “In hand” means the capuchin is already holding it when the video starts, while “on anvil” means it is lying on the anvil and off anvil can be either "within reach" (within 1 body length of the anvil) or at a "walking distance" (>1 body length). Lastly the hammerstone can be "carried in" from out of view.
	hammer location end	1. on anvil 2. off anvil within reach 3. off anvil out of reach 4. carry out	Code the hammerstone location again at the end of the sequence. Now the location can only be on the anvil, off anvil within reach (within 1 body length of the anvil), off anvil at a further distance or carry out if they take it.
	hammer ID	Enter the hammerstone ID as a comment, or if it’s not marked/unidentifiable: 7. Unmarked 8. Unknown	Comment the ID of the hammerstone first used for the sequence, which can be one of the marked hammerstones or in the case of an unmarked hammerstone code “unmarked” but describe its appearance in the comments.

B.2.2 Coding of sequences with capuchins present

Table B.3: Ethogram of behaviors coded per sequence with other capuchins present.

Behavior	Modifiers	Modifier Options	Definition
Present			*Code once for each non-tool-using individual present during the tool use sequence. Make sure to assign age-sex class and possibly ID.* ***Note:*** *always code for every capuchin, also if individual also scrounges or does something else in sequence*
Social attention			*Sustained (>3 sec) attention to the tool user while they are on the anvil from a close distance (<2 meters). Only code once for each individual who does it.*
Displace			*Displace the tool user from the anvil. Code once for each individual who does it.*
Scrounge			*Scrounging is eating the items opened by the tool user during the sequence*
	Toleration	1. Tolerated 2. Afterwards	Scrounging can be tolerated (occurring during the tool use, with the tool user still present and allowing it) or it can happen after the tool user has left the anvil. **Note:** In the rare occasion that scrounging occurs despite aggression from the tool user, make a comment with "stealing".
Avoid			*Move away from the tool user*
	Aggression	1. Aggression 2. No aggression	Whether the individual who avoids the tool user receives aggression from the tool user before moving away

B.3 Supplemental results

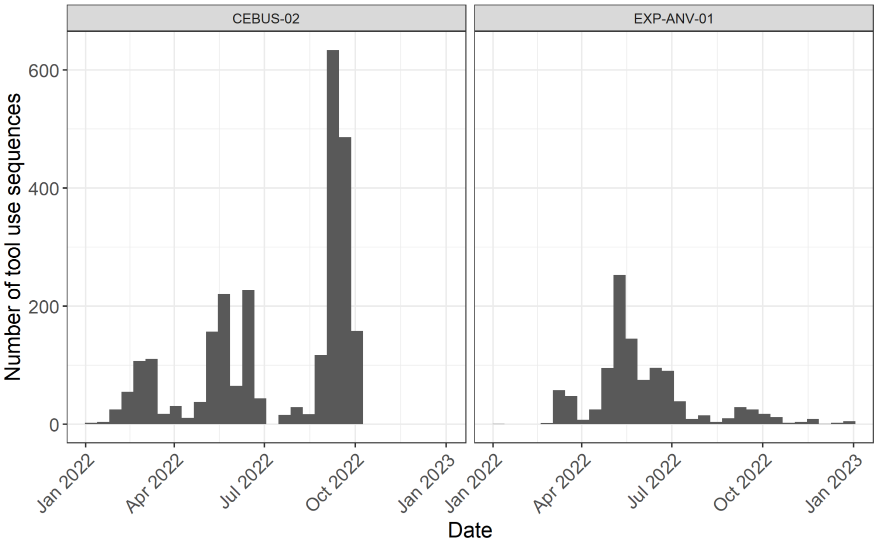

Figure B.1: Number of tool use sequences observed per experimental anvil. At CEBUS-02, cameras ran 2022-01-10 until 2022-06-29 and 2022-07-16 until 2022-09-30. At EXP-ANV-01, cameras ran 2022-01-10 until 2022-07-16 and 2022-07-17 until 2023-01-01.

B.3.1 Tool using proficiency

Models estimating tool use efficiency

Table B.4: Posterior mean model estimates of Model e1, a Gamma GLMM (Bayes $R^2 = 0.23$) examining factors influencing duration of tool use sequences. All estimated effects are on the log scale. The reference categories (the intercept) are juveniles (*age*), brown sea almonds (*item*), and stone (*anviltype*).

	Estimate	*Est. Error*	*CI_95_low*	*CI_95_high*
Multilevel Hyperparameters				
subjectID (11 levels)	0.31	0.11	0.16	0.58
Regression Coefficients				
Intercept	2.96	0.15	2.66	3.24
Age (Subadult)	-0.68	0.23	-1.17	-0.23
Age (Adult)	-0.54	0.24	-0.99	-0.04
item (green sea almond)	0.28	0.03	0.23	0.33
item (red sea almond)	0.40	0.06	0.27	0.52
item (unknown sea almond)	0.06	0.03	0.01	0.10
anviltype (wood)	0.02	0.02	-0.03	0.06
Further Parameters				
shape	4.02	0.11	3.82	4.23

Table B.5: Posterior mean model estimates of Model e2, a Poisson GLMM (Bayes $R^2 = 0.13$) examining factors influencing number of pounds needed to open an item. All estimated effects are on the log scale. The reference categories (the intercept) are juveniles (*age*), brown sea almonds (*item*), and stone (*anviltype*).

	Estimate	*Est. Error*	*CI_95_low*	*CI_95_high*
Multilevel Hyperparameters				
subjectID (11 levels)	0.17	0.07	0.08	0.35
Regression Coefficients				
Intercept	1.65	0.09	1.48	1.84
Age (Subadult)	-0.36	0.13	-0.64	-0.10
Age (Adult)	-0.31	0.15	-0.62	-0.03
item (green sea almond)	0.23	0.03	0.18	0.28
item (red sea almond)	0.27	0.06	0.14	0.39
item (unknown sea almond)	0.06	0.03	0.01	0.11
anviltype (wood)	-0.09	0.02	-0.14	-0.05

Table B.6: Posterior mean model estimates of Model e2b, a Poisson GLMM (Bayes $R^2 = 0.68$) examining factors affecting the rate of pounding in tool use sequences. All estimated effects are on the log scale. The reference categories (the intercept) are juveniles (*age*), brown sea almonds (*item*), and stone (*anviltype*).

	Estimate	*Est. Error*	*CI_95_low*	*CI_95_high*
Multilevel Hyperparameters				
subjectID (11 levels)	0.14	0.06	0.07	0.28
Regression Coefficients				
Intercept	-1.31	0.08	-1.47	-1.15
Age (Subadult)	0.30	0.13	0.06	0.54
Age (Adult)	0.29	0.13	0.01	0.52
item (green sea almond)	-0.05	0.03	-0.10	0.00
item (red sea almond)	-0.11	0.06	-0.24	-0.00
item (unknown sea almond)	0.00	0.03	-0.05	0.05
anviltype (wood)	-0.11	0.02	-0.15	-0.07

Models examining repositioning and peeling during tool use

Table B.7: Posterior mean model estimates of Model e3a, a Poisson GLMM (Bayes $R^2 = 0.17$), examining factors influencing number of repositions during tool use sequences. All estimated effects are on the log scale. The reference categories (the intercept) are juveniles (*age*), brown sea almonds (*item*), and stone (*anviltype*).

	Estimate	*Est. Error*	*CI_95_low*	*CI_95_high*
Multilevel Hyperparameters				
subjectID (11 levels)	0.53	0.19	0.27	1.00
Regression Coefficients				
Intercept	0.10	0.25	-0.44	0.59
Age (Subadult)	-1.21	0.40	-1.91	-0.33
Age (Adult)	-1.24	0.42	-2.03	-0.34
item (green sea almond)	0.18	0.08	0.02	0.34
item (red sea almond)	0.08	0.20	-0.32	0.46
item (unknown sea almond)	-0.03	0.08	-0.18	0.12
anviltype (wood)	0.04	0.06	-0.08	0.16

Table B.8: Posterior mean model estimates of Model e3b, a Poisson GLMM (Bayes $R^2 = 0.12$) examining factors influencing number of peeling of an item during tool use sequences. All estimated effects are on the log scale. The reference categories (the intercept) are juveniles (*age*), brown sea almonds (*item*), and stone (*anviltype*).

	Estimate	*Est. Error*	*CI_95_low*	*CI_95_high*
Multilevel Hyperparameters				
subjectID (11 levels)	0.48	0.16	0.27	0.88
Regression Coefficients				
Intercept	-0.84	0.24	-1.32	-0.39
Age (Subadult)	-0.90	0.36	-1.59	-0.15
Age (Adult)	-0.89	0.39	-1.60	-0.07
item (green sea almond)	0.39	0.10	0.19	0.59
item (red sea almond)	0.35	0.22	-0.11	0.77
item (unknown sea almond)	0.33	0.09	0.15	0.52
anviltype (wood)	0.20	0.08	0.05	0.35

Models examining mistakes during tool use

Table B.9: Posterior mean model estimates of Model e4a, a zero-inflated Poisson GLMM (Bayes $R^2 = 0.16$) examining factors influencing number of misstrikes in a tool use sequence. All estimated effects are on the log scale. The reference categories (the intercept) are juveniles (*age*), brown sea almonds (*item*), and stone (*anviltype*).

	Estimate	*Est. Error*	*CI_95_low*	*CI_95_high*
Multilevel Hyperparameters				
subjectID (11 levels)	1.72	0.51	0.95	2.92
Regression Coefficients				
Intercept	-1.97	0.73	-3.52	-0.68
Age (Subadult)	-1.21	0.88	-2.84	0.62
Age (Adult)	-0.79	0.85	-2.45	0.92
item (green sea almond)	-0.87	0.49	-1.92	0.03
item (red sea almond)	0.10	0.64	-1.27	1.24
item (unknown sea almond)	-0.15	0.28	-0.73	0.39
anviltype (wood)	-0.42	0.23	-0.88	0.05
Further Parameters				
zi	0.49	0.10	0.28	0.65

Table B.10: Posterior mean model estimates of Model e4b, a zero-inflated Poisson GLMM (Bayes $R^2 = 0.10$) examining factors influencing number of item flying in a tool use sequence. All estimated effects are on the log scale. The reference categories (the intercept) are juveniles (*age*), brown sea almonds (*item*), and stone (*anviltype*).

	Estimate	*Est. Error*	*CI_95_low*	*CI_95_high*
Multilevel Hyperparameters				
subjectID (11 levels)	0.21	0.18	0.01	0.69
Regression Coefficients				
Intercept	-1.14	0.27	-1.70	-0.66
Age (Subadult)	-1.46	0.29	-1.96	-0.83
Age (Adult)	-1.61	0.34	-2.24	-0.92
item (green sea almond)	1.25	0.19	0.87	1.63
item (red sea almond)	0.90	0.40	0.10	1.65
item (unknown sea almond)	0.15	0.24	-0.34	0.62
anviltype (wood)	-1.23	0.18	-1.58	-0.88
Further Parameters				
zi	0.43	0.11	0.19	0.61

B.3.2 Tool using development

Table B.11: Posterior mean model estimates of Model dev1, a Poisson GLM (Bayes $R^2 = 0.18$) examining individual development of tool use proficiency over time. All estimated effects are on the log scale.

	Estimate	*Est. Error*	*CI_95_low*	*CI_95_high*
Intercept	-9.84	19.79	-48.53	28.99
log(time)	0.55	0.93	-1.28	2.37
subjectID (PEA)	0.01	1.00	-1.93	1.96
subjectID (BAL)	0.00	0.97	-1.85	1.91
subjectID (TER)	-0.02	1.01	-2.02	1.96
subjectID (MIC)	-0.03	0.96	-1.92	1.90
subjectID (LAR)	-0.01	1.02	-1.98	1.98
subjectID (SPT)	-0.01	0.98	-1.97	1.90
subjectID (TOM)	-0.01	1.00	-1.93	1.94
subjectID (SMG)	0.01	1.00	-1.97	1.94
log(time) * subjectID (PEA)	-0.02	0.05	-0.11	0.07
log(time) * subjectID (BAL)	-0.02	0.05	-0.11	0.07
log(time)* subjectID (TER)	0.00	0.05	-0.09	0.10
log(time) * subjectID (MIC)	-0.03	0.05	-0.12	0.06
log(time) * subjectID (LAR)	-0.03	0.05	-0.13	0.06
log(time) * subjectID (SPT)	-0.03	0.05	-0.12	0.06
log(time) * subjectID (TOM)	-0.03	0.05	-0.12	0.07
log(time) * subjectID (SMG)	-0.03	0.05	-0.12	0.06

Models examining social attention during tool use

Table B.12: Posterior mean model estimates of Model socatt1, a Bernoulli GLMM (Bayes $R^2 = 0.26$) examining factors influencing the likelihood of an individual paying social attention to a tool use sequence. all estimated effects are on the logit scale. The reference categories (the intercept) are juveniles (*tooluser_ age*), juveniles(*observer_ agesex*), and CEBUS-02 (*location*).

	Estimate	*Est. Error*	*CI_ 95_ low*	*CI_ 95_ high*
Multilevel Hyperparameters				
sequenceID (844 levels)	0.72	0.27	0.13	1.22
Regression Coefficients				
Intercept	-4.81	0.30	-5.43	-4.25
Tool user (Subadult)	1.16	0.24	0.70	1.64
Tool user (Adult)	1.01	0.34	0.34	1.67
Observer (Subadult male)	-1.37	0.29	-1.95	-0.82
Observer (Adult male)	-2.29	0.49	-3.33	-1.38
Observer (Adult female)	-1.95	0.46	-2.89	-1.10
location (EXP-ANV-01)	0.94	0.22	0.52	1.37
Capuchins present	-0.38	0.09	-0.55	-0.22
Capuchins scrounging	1.32	0.18	0.99	1.70

Table B.13: Posterior mean model estimates of Model socatt1b, a Bernoulli GLMM (Bayes $R^2 = 0.08$) examining factors influencing the likelihood of an individual paying social attention to a tool use sequence. all estimated effects are on the logit scale. The reference categories (the intercept) are juveniles (*tooluser_ age*), juveniles(*observer_ agesex*), and CEBUS-02 (*location*).

	Estimate	*Est. Error*	*CI_ 95_ low*	*CI_ 95_ high*
Multilevel Hyperparameters				
tooluserID (10 levels)	0.16	0.15	0.01	0.54
Regression Coefficients				
Intercept	-4.08	0.33	-4.74	-3.47
Tool user (Subadult)	0.94	0.29	0.38	1.54
Tool user (Adult)	0.57	0.37	-0.16	1.32
Observer (Subadult male)	-1.23	0.26	-1.76	-0.76
Observer (Adult male)	-2.24	0.49	-3.29	-1.32
Observer (Adult female)	-1.76	0.43	-2.66	-0.97
Number of pounds	-0.09	0.04	-0.17	-0.00
Number of mistakes	-0.01	0.21	-0.45	0.40

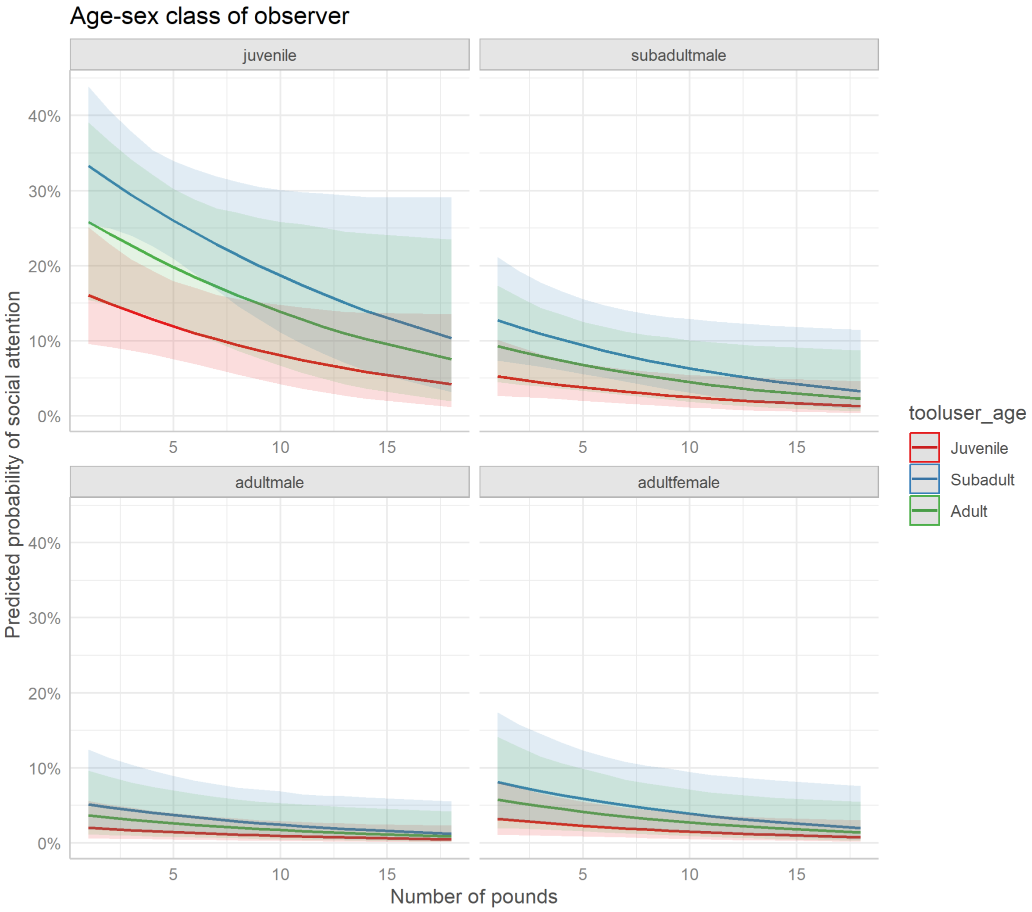

Figure B.2: Predicted probabilities from model socatt1b of probabilities of social attention occurring, depending on the number of pounds in the sequence. Each facet represents an observer age-sex class, and the color of the line the age of the tool user.

Appendix C

Supplementary information for 'Coupling of coastal activity with tidal cycles is stronger in tool-using capuchins'

C.1 Electronic supplements

Video S1: https://www.youtube.com/watch?v=Qwued08S3Xs

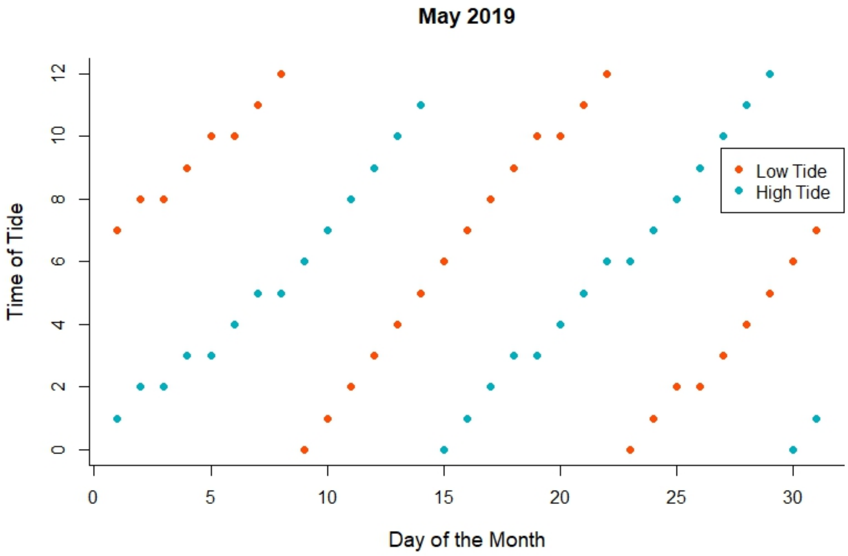

Figure C.1: Timing of tides at Jicarón in one month (May 2019)

Table C.1: Overview of still (S) and video (V) camera's deployed for tool-using group, distinguishing between anvil cameras, non-anvil cameras, and grid cameras.

Identical to Table A.1

Table C.2: Overview of still (S) and video (V) camera's deployed for non-tool-using groups, distinguishing between non-grid cameras (which capture multiple non-tool-using groups) and grid cameras (capturing a single non-tool-using group).

Location	***R1 Mar-Jul 2017***	***R2 Jul-Dec 2017***	***R3 Dec 2017-Mar 2018***	***R4 Mar-Jul 2018***	***R5 Jul-Dec 2018***	***R6 until Dec 2018-Mar 2019***	***R11 Dec 2021-Jul 2022***	***R12 May 2022-Jan 2023***
Non-grid cameras (capturing multiple groups)						no cameras		
SURVEY-CEBUS-01-01	S							
SURVEY-CEBUS-01-02				S				
SURVEY-CEBUS-02-01	V							
SURVEY-CEBUS-02-02	S							
SURVEY-CEBUS-03-01	V							
SURVEY-CEBUS-03-02	S							
SURVEY-CEBUS-03-03		V						
SURVEY-CEBUS-03-04			S					
SURVEY-CEBUS-04-01	S							
SURVEY-CEBUS-05-01	S							
SURVEY-CEBUS-05-02					S			
SURVEY-CEBUS-06-01	V							
SURVEY-CEBUS-09-01	S							
SURVEY-CEBUS-09-02	S							
SURVEY-CEBUS-10-01	S							
SURVEY-CEBUS-18-01		S						
SURVEY-CEBUS-22-01			S					
SURVEY-CEBUS-23-01			S					
Grid cameras (capturing one group)						no cameras		
NTU-55								S
NTU-69								S
NTU-70								S
NTU-71								S
NTU-72								S
NTU-85								S
NTU-86								S
NTU-87								S
NTU-88								S
NTU-101								S
NTU-102								S
NTU-103								S
NTU-104								S
NTU-117								S
NTU-118								S
NTU-119								S
NTU-120								S
NTU-132								S
NTU-133								S
NTU-134								S
NTU-135								S
NTU-136								S
NTU-152								S
NTU-153								S
NTU-169								S

C.2 Additional model results

C.2.1 Model MT_1: Comparing tidal patterns of tool-using group and non-tool-using groups

Table C.3: Posterior mean model estimates of Model MT_1, a Poisson GAM (Bayes $R^2 = 0.10$). All estimated population-level effects are on the logit scale. Non-tool-using groups are the reference category (the intercept).

	Estimate	*CI_95_low*	*CI_95_high*
Smooth terms			
Tidetime-Distance_1	0.29	0.01	0.91
Tidetime-Distance_2	0.98	0.03	3.53
Tidetime-Distance_3	0.48	0.01	1.68
Tidetime-Distance_4	0.41	0.02	1.24
Tidetime-Distance non-tool-users_1	0.41	0.01	2.61
Tidetime-Distance non-tool-users_2	0.76	0.02	2.61
Tidetime-Distance non-tool-users_3	5.36	0.51	8.79
Tidetime-Distance tool-users_1	0.16	0.01	0.46
Tidetime-Distance tool-users_2	1.43	0.05	3.84
Tidetime-Distance tool-users_3	0.29	0.01	1.02
Camera location	0.20	0.17	0.24
Population-Level Effects			
Intercept	0.50	0.35	0.64
Tool-users: Yes	-0.03	-0.19	0.17
Tensor product of Tidetime-Distance	0.03	-0.02	0.08

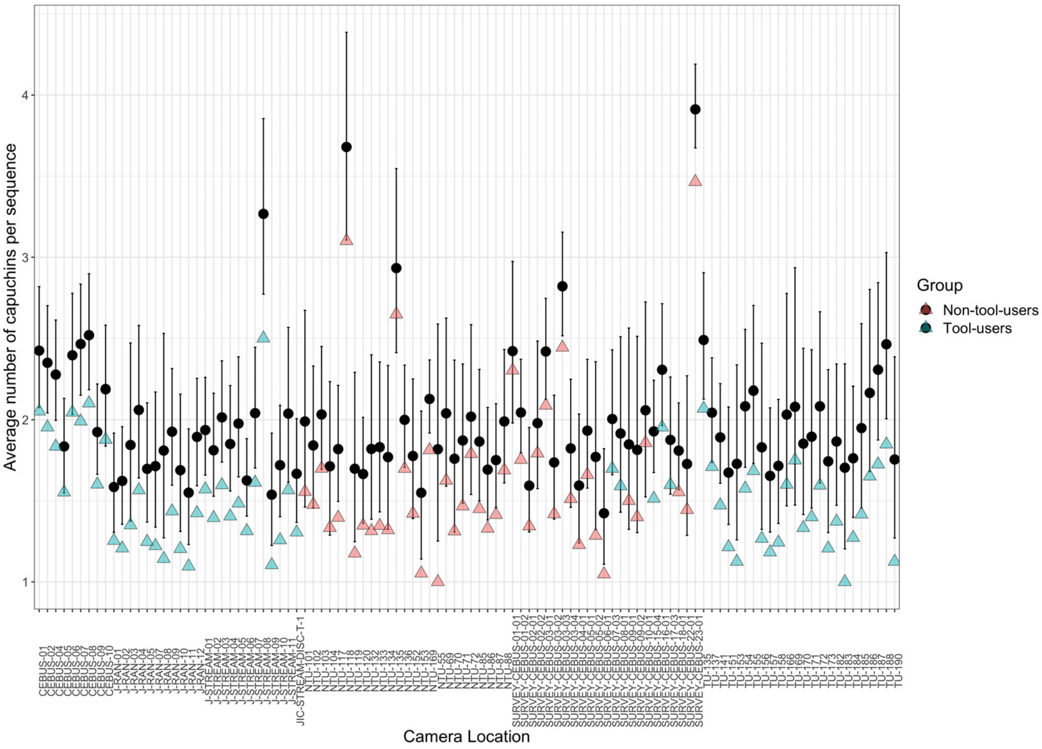

Figure C.2: Model MT_1's posterior mean estimates of the average number of capuchins per camera location represented by black circles. Bars indicate the 95% credible interval. Triangles represent the real average. Blue indicates tool-using and red non-tool-using groups.

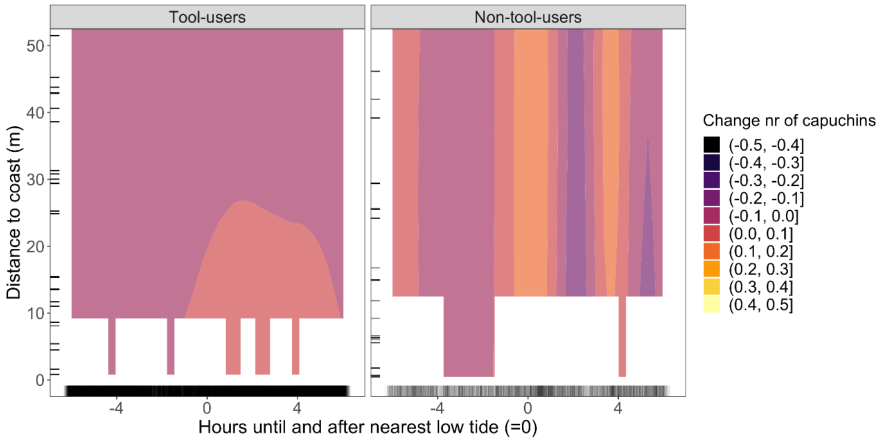

Figure C.3: Zoomed in view of Figure 3.1 to 0-50 meters from the coast. 2D heatmap showing capuchin activity (color) at various distances to the coast (y-axis) and hours until and after nearest low tide (x-axis), for the a) tool-using group and b) non-tool-using groups separately. More color-saturated areas indicate where > 89% of the posterior distribution of the derivative of the tensor smooth interaction lies on one side of 0.

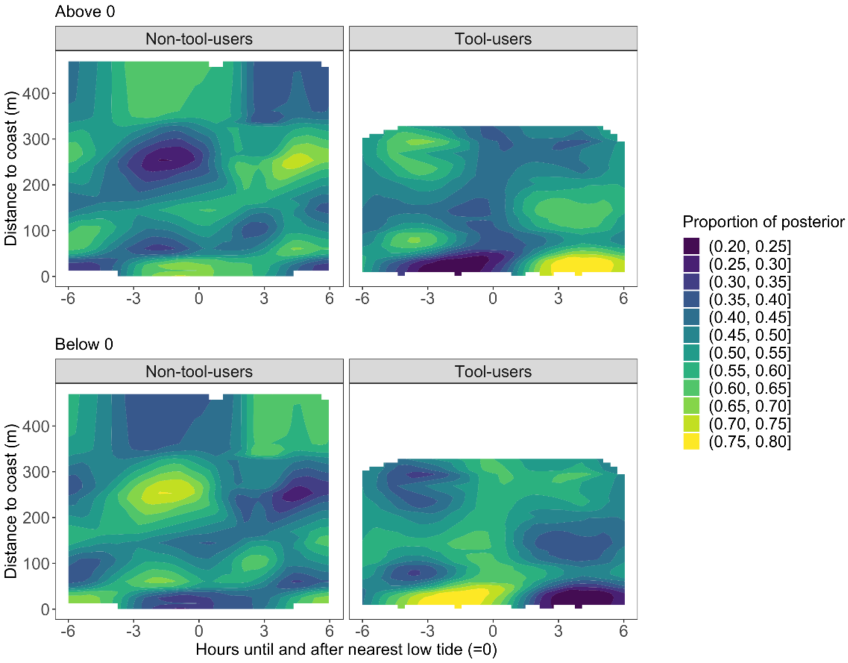

Figure C.4: 2D heatmap showing for Model MT_1 what proportion of the posterior of the derivative lies above or below 0 as calculated in Equation 3.1. Lighter colors indicate a larger proportion of the posterior with a reliable non-linear change.

C.2.2 Model MT_2: Tool-using group: comparing tidal patterns in wet vs. dry seasons

Table C.4: Posterior mean model estimates of Model MT_2, a Poisson GAM (Bayes $R^2 = 0.04$). All estimated population-level effects are on the logit scale. Dry season is the reference category (the intercept).

	Estimate	*CI_95_low*	*CI_95_high*
Smooth terms			
Tidetime-Distance_1	0.26	0.01	0.82
Tidetime-Distance_2	1.32	0.03	4.92
Tidetime-Distance_3	0.42	0.02	1.40
Tidetime-Distance_4	0.32	0.01	1.14
Tidetime-Distance dry season_1	0.14	0.01	0.41
Tidetime-Distance dry season_2	0.72	0.02	2.52
Tidetime-Distance dry season_3	0.38	0.01	1.18
Tidetime-Distance wet season_1	0.37	0.07	0.76
Tidetime-Distance wet season_2	1.12	0.05	3.01
Tidetime-Distance wet season_3	0.35	0.01	1.14
Camera location	0.16	0.13	0.21
Population-Level Effects			
Intercept	0.43	0.26	0.58
Season: Wet	0.06	-0.03	0.16
Tensor product of Tidetime-Distance	0.04	-0.0.01	0.09

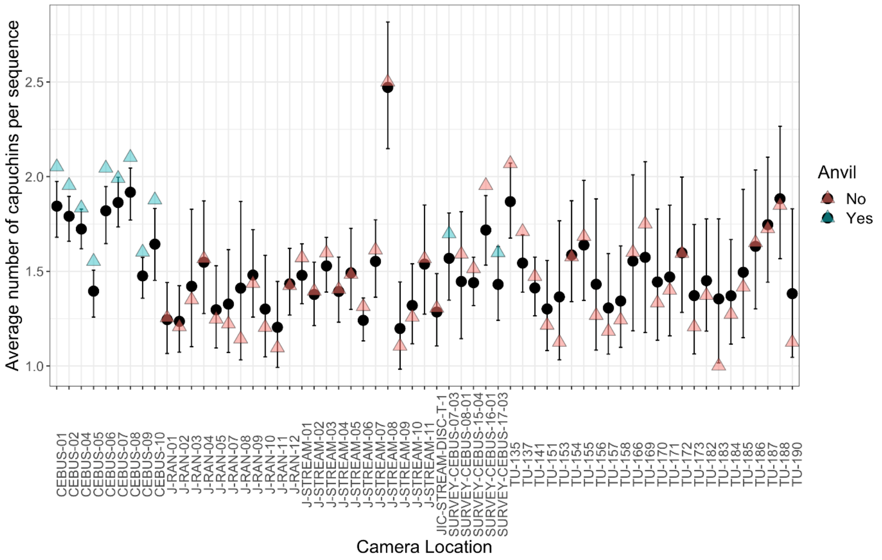

Figure C.5: Model MT_2's posterior mean estimates of the average number of capuchins per camera location represented by black circles. Bars indicate the 95% credible interval. Triangles represent the real average. Blue indicates cameras placed targeted on tool use anvils and red cameras not placed on a targeted tool use location.

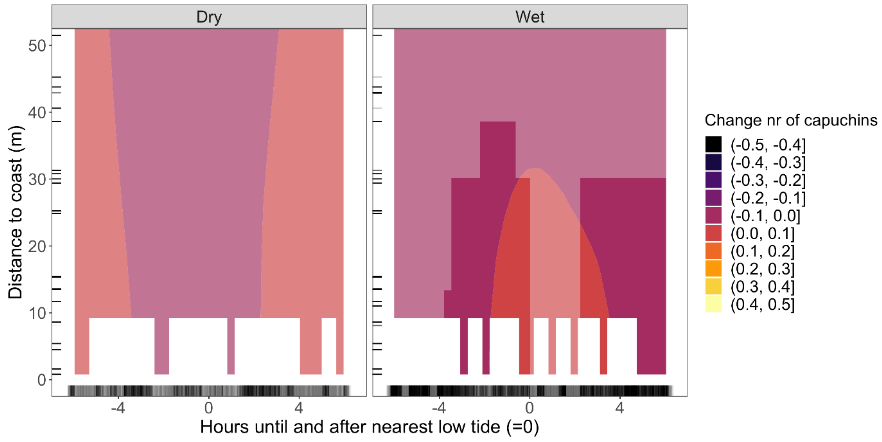

Figure C.6: Zoomed in view of Figure 3.2 to 0-50 meters from the coast. 2D heatmap showing capuchin activity (color) of the tool-using group at various distances to the coast (y-axis) and hours until and after nearest low tide (x-axis), for the a) dry and b) wet season separately. More color-saturated areas indicate where $> 89\%$ of the posterior distribution of the derivative of the tensor smooth interaction lies on one side of 0.

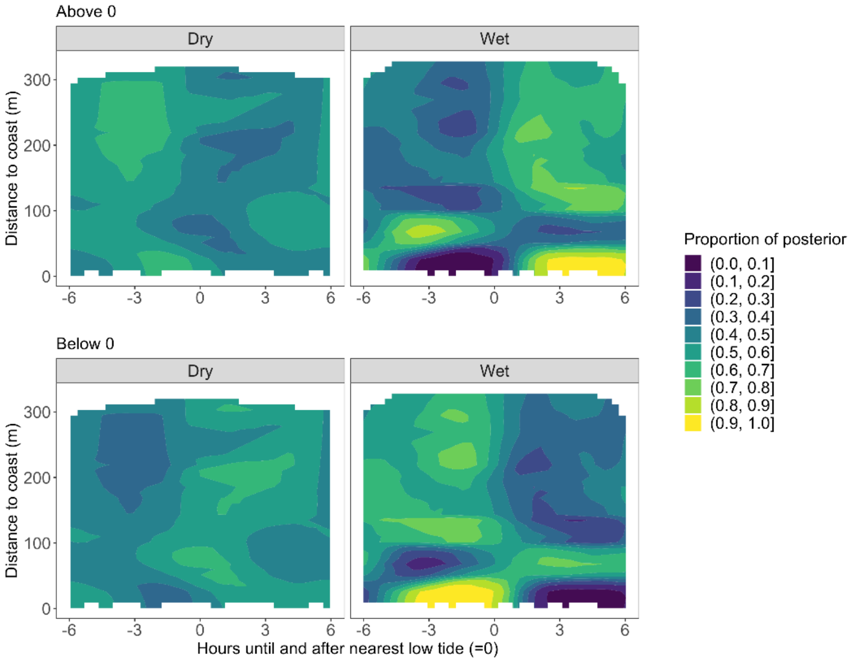

Figure C.7: 2D heatmap showing for Model MT_2 what proportion of the posterior of the derivative lies above or below 0 as calculated in Equation 3.1. Lighter colors indicate a larger proportion of the posterior with a reliable non-linear change.

C.2.3 Model MT_3: Non-tool-using groups: comparing tidal patterns in wet vs. dry season

Table C.5: Posterior mean model estimates of Model MT_3, a Poisson GAM (Bayes $R^2 = 0.24$). All estimated population-level effects are on the logit scale. Dry season is the reference category (the intercept).

	Estimate	*CI_95_low*	*CI_95_high*
Smooth terms			
Tidetime-Distance_1	0.434	0.01	1.14
Tidetime-Distance_2	0.95	0.02	3.47
Tidetime-Distance_3	0.67	0.02	2.36
Tidetime-Distance_4	0.37	0.01	1.36
Tidetime-Distance dry season_1	1.78	0.02	5.26
Tidetime-Distance dry season_2	0.87	0.02	3.12
Tidetime-Distance dry season_3	6.18	0.08	12.57
Tidetime-Distance wet season_1	0.16	0.01	0.52
Tidetime-Distance wet season_2	0.75	0.02	2.50
Tidetime-Distance wet season_3	0.49	0.01	1.69
Camera location	0.25	0.19	0.32
Population-Level Effects			
Intercept	0.49	0.33	0.65
Season: Wet	-0.03	-0.16	0.12
Tensor product of Tidetime-Distance	-0.04	-0.14	0.06

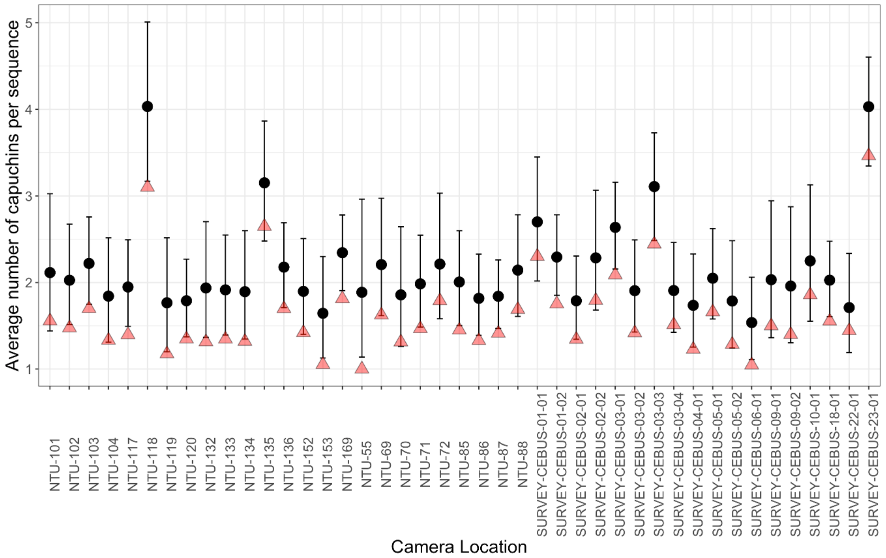

Figure C.8: Model MT_3's posterior mean estimates of the average number of capuchins per camera location represented by black circles. Bars indicate the 95% credible interval. Triangles represent the real average. Blue indicates cameras placed targeted on tool use anvils and red cameras not placed on a targeted tool use location.

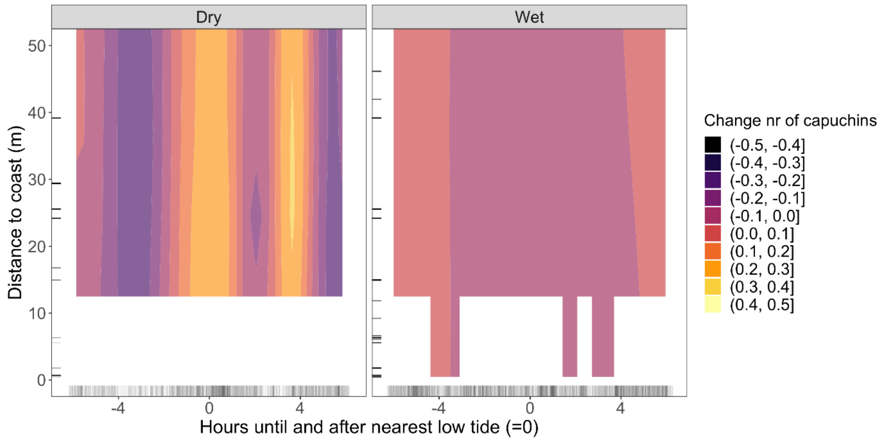

Figure C.9: Zoomed in view of Figure 3.3 to 0-50 meters from the coast. 2D heatmap showing capuchin activity (color) of the non-tool-using groups at various distances to the coast (y-axis) and hours until and after nearest low tide (x-axis), for the a) dry and b) wet season separately. More color-saturated areas indicate where > 89% of the posterior distribution of the derivative of the tensor smooth interaction lies on one side of 0.

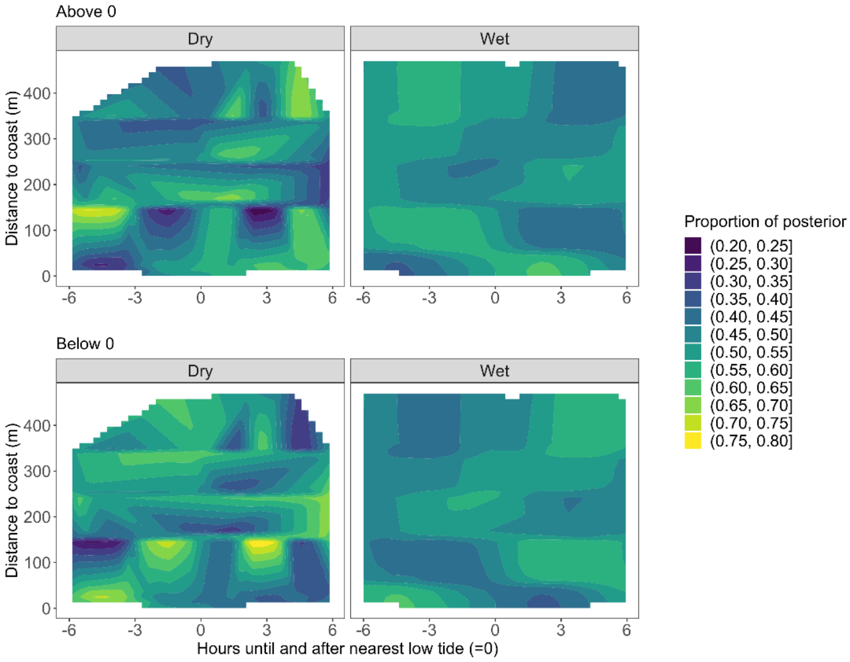

Figure C.10: 2D heatmap showing for Model MT_3 what proportion of the posterior of the derivative lies above or below 0 as calculated in Equation 3.1. Lighter colors indicate a larger proportion of the posterior with a reliable non-linear change.

C.2.4 Model MD_1: Tool-using group: comparing hourly activity in wet vs. dry season

Table C.6: Posterior mean model estimates of Model MD_1, a Poisson GAM (Bayes $R^2 = 0.05$). All estimated population-level effects are on the logit scale. Dry season is the reference category (the intercept).

	Estimate	*CI_95_low*	*CI_95_high*
Smooth terms			
Hour-Distance_1	0.93	0.03	3.36
Hour-Distance_2	1.01	0.03	3.75
Hour-Distance_3	1.00	0.03	3.60
Hour-Distance_4	0.95	0.03	3.44
Hour-Distance_5	0.93	0.02	3.36
Hour-Distance dry season_1	0.85	0.09	1.67
Hour-Distance dry season_2	0.95	0.02	3.18
Hour-Distance dry season_3	1.44	0.07	3.38
Hour-Distance wet season_1	0.93	0.21	1.63
Hour-Distance wet season_2	0.90	0.02	3.01
Hour-Distance wet season_3	1.04	0.02	3.28
Camera location	0.15	0.12	0.20
Population-Level Effects			
Intercept	0.47	0.23	0.71
Season: Wet	0.02	-0.22	0.25
Tensor product of Hour-Distance_1	-0.03	-0.12	0.06
Tensor product of Hour-Distance_2	0.02	-0.09	0.13
Tensor product of Hour-Distance_3	0.00	-0.04	0.05

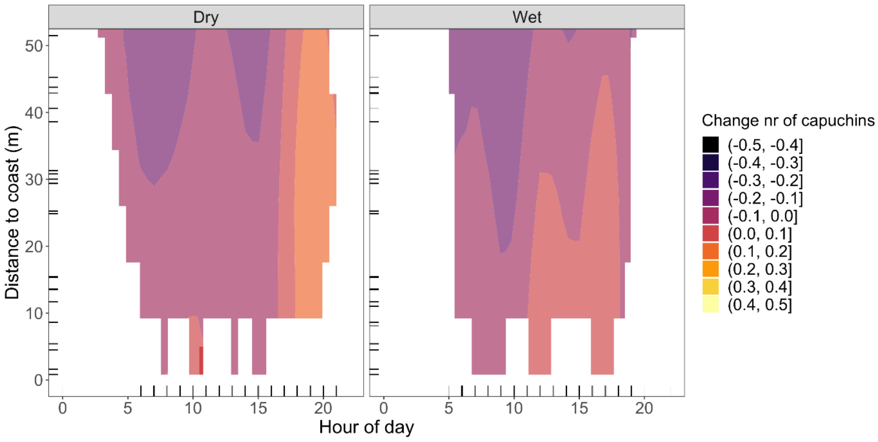

Figure C.11: Zoomed in view of Figure 3.4 to 0-50 meters from the coast. 2D heatmap showing capuchin activity (color) of the tool-using group at various distances to the coast (y-axis) and hours of the day (x-axis), for the a) dry and b) wet season separately. More color-saturated areas indicate where $> 89\%$ of the posterior distribution of the derivative of the tensor smooth interaction lies on one side of 0.

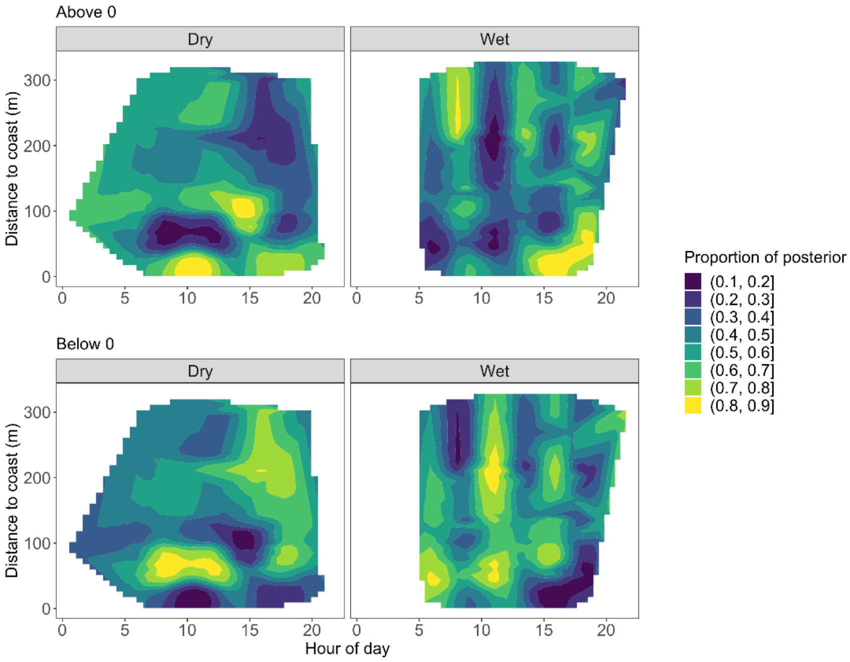

Figure C.12: 2D heatmap showing for Model MD_1 what proportion of the posterior of the derivative lies above or below 0 as calculated in Equation 3.1. Lighter colors indicate a larger proportion of the posterior with a reliable non-linear change.

C.2.5 Model MD_2: Non-tool-using groups: comparing hourly activity in wet vs. dry season

Table C.7: Posterior mean model estimates of Model MD_2, a Poisson GAM (Bayes $R^2 = 0.22$). All estimated population-level effects are on the logit scale. Dry season is the reference category (the intercept).

	Estimate	*CI_95_low*	*CI_95_high*
Smooth terms			
Hour-Distance_1	1.10	0.02	3.98
Hour-Distance_2	0.99	0.03	3.55
Hour-Distance_3	0.95	0.02	3.39
Hour-Distance_4	1.02	0.03	3.72
Hour-Distance_5	1.04	0.02	3.82
Hour-Distance dry season_1	1.26	0.07	2.71
Hour-Distance dry season_2	0.87	0.02	3.13
Hour-Distance dry season_3	1.85	0.06	5.19
Hour-Distance wet season_1	0.62	0.04	1.38
Hour-Distance wet season_2	0.81	0.02	2.94
Hour-Distance wet season_3	0.72	0.07	2.17
Camera location	0.26	0.20	0.33
Population-Level Effects			
Intercept	0.61	0.35	0.89
Season: Wet	-0.10	-0.34	0.12
Tensor product of Hour-Distance_1	-0.06	-0.22	0.10
Tensor product of Hour-Distance_2	0.08	-0.04	0.21
Tensor product of Hour-Distance_3	-0.04	-0.13	0.04

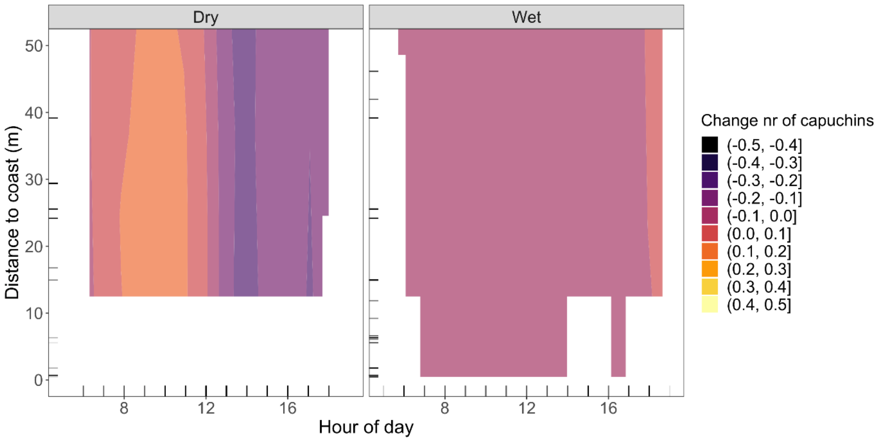

Figure C.13: Zoomed in view of Figure 3.5 to 0-50 meters from the coast. 2D heatmap showing capuchin activity (color) of the non-tool-using group at various distances to the coast (y-axis) and hours of the day (x-axis), for the a) dry and b) wet season separately. More color-saturated areas indicate where > 89% of the posterior distribution of the derivative of the tensor smooth interaction lies on one side of 0.

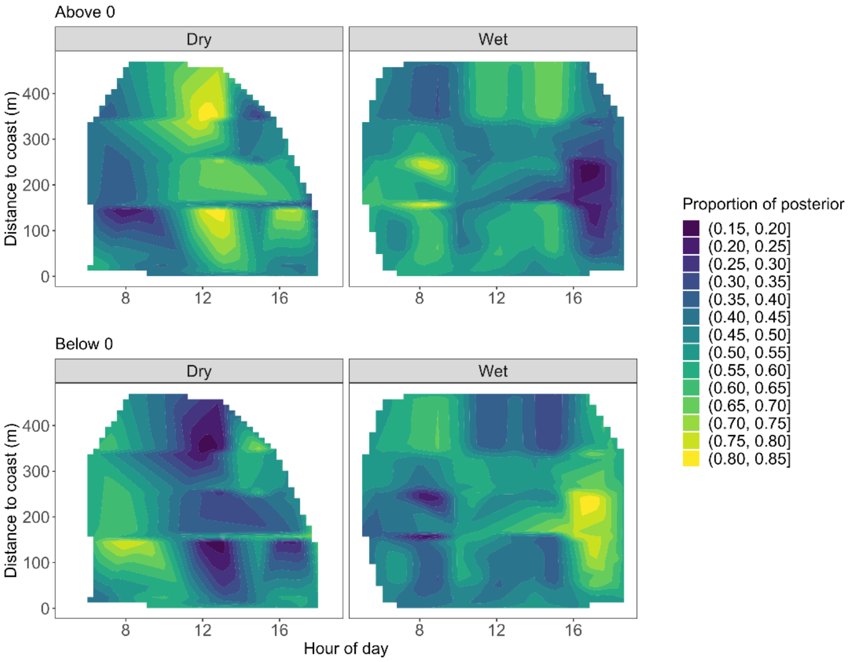

Figure C.14: 2D heatmap showing for Model MD_2 what proportion of the posterior of the derivative lies above or below 0 as calculated in Equation 3.1. Lighter colors indicate a larger proportion of the posterior with a reliable non-linear change.

C.3 Spanish abstract

Los mamíferos que explotan recursos costeros adversan cambios de disponibilidad y acceso a estos recursos debido a ciclos de la marea. Usar herramientas podría permitir forrajear más eficientemente y acceder recursos estructuralmente protegidos (e.g., moluscos y frutas). Para entender cómo el cambiante acceso a valiosos recursos modifica patrones comportamentales, y si el uso de herramientas facilita explotar recursos costeros más eficientemente, comparamos la relación entre ciclos mareales y patrones de actividad de grupos de monos carablanca que usan herramientas vs grupos que no en isla Jicarón, Panamá. Aunque solo un grupo de monos carablanca usa herramientas, todos los grupos costeros forrajean recursos intermareales. Usando >5 años de datos de cámaras trampa instaladas a diferentes distancias desde la costa, encontramos que estos monos aumentan su actividad durante periodos específicos de la marea, que esta relación difiere entre temporadas y entre grupos que no usan herramientas y el grupo que si usa. En contraste con grupos que no usan herramientas, los patrones de actividad del grupo que usa herramientas fueron más restringidos por la marea. Indicando que el uso de herramientas puede facilitar forrajear recursos más eficientemente. En conclusión, usar herramientas potencialmente permite que animales accedan nuevos nichos.

Appendix D

Supplementary information for ‘Rise and spread of a social tradition of interspecies abduction’

D.1 Supplemental methods

Interactive timeline: https://www.ab.mpg.de/671374/Capuchin-tool-use/interspecies-abduction-tradition

Video D1: https://youtu.be/s3Y3JWVvB9Q.

Table D.1: Overview of all cameras inspected for howler sightings by a single observer (ZG). Checked means all images were manually checked for howler infants, while coded means the deployment was formally coded as part of a larger project (multiple observers).

Camera location	**Deployment number**	**Deployed**	**Inspected**
Cameras on tool use anvils			
CEBUS-02-AUX (Alternative view of CEBUS-02	R11	2022-01-10 until 2022-07-16	Checked fully
	R12	2022-07-16 until 2023-01-09	Checked fully
	R13	2023-01-11 until 2023-05-27	Checked 2023-02-10 until 2023-02-26 and 2023-03-13 until 2023-05-29
CEBUS-02	R11	2022-01-10 until 2022-06-29	Checked fully
	R12	2022-07-16 until 2022-09-30	Checked fully
	R13	2023-01-11 until 2023-05-29	Checked 2023-02-10 until 2023-02-26 and 2023-03-13 until 2023-05-29
CEBUS-02-BU (Back up on CEBUS-02)	R13	2023-04-10 until 2023-07-07	Checked fully
CEBUS-04	R11	2022-01-09 until 2022-07-14	Checked fully

Table D.1: Overview of all cameras inspected for howler sightings by a single observer (ZG). Checked means all images were manually checked for howler infants, while coded means the deployment was formally coded as part of a larger project (multiple observers).

Camera location	**Deployment number**	**Deployed**	**Inspected**
	R12	2022-07-18 until 2023-01-09	Checked 2022-09-01 until 2022-09-20, 2022-11-01 until 2022-11-14, and 2022-12-01 until 2022-12-27
	R13	2023-01-09 until 2023-07-07	Checked 2023-02-10 until 2023-02-26, 2023-03-13 until 2023-03-31, and 2023-05-10 until 2023-05-17
CEBUS-05	R11	2022-01-10 until 2022-05-24	Checked fully
	R12	2022-07-18 until 2023-01-08	Checked 2022-09-01 until 2022-09-20, 2022-11-01 until 2022-11-14, and 2022-12-01 until 2022-12-27
	R13	2023-01-11 until 2023-07-19	Checked 2023-02-10 until 2023-02-26, 2023-03-13 until 2023-03-31, and 2023-05-10 until 2023-05-17
CEBUS-06	R11	2022-01-10 until 2022-07-15	Checked fully
	R12	2022-07-18 until 2023-01-08	Checked 2022-09-01 until 2022-09-20, 2022-11-01 until 2022-11-14, and 2022-12-01 until 2022-12-27
	R13	2023-01-19 until 2023-07-19	Checked 2023-02-10 until 2023-02-26, 2023-03-13 until 2023-03-31, and 2023-05-10 until 2023-05-17
CEBUS-07	R11	2022-01-09 until 2022-04-01	Checked fully
	R12	2022-07-18 until 2023-01-08	Checked 2022-09-01 until 2022-09-20, 2022-11-01 until 2022-11-14, and 2022-12-01 until 2022-12-27
	R13	2023-01-09 until 2023-03-20	Checked 2023-02-10 until 2023-02-26, 2023-03-13 until 2023-03-31
CEBUS-08	R11	2022-01-08 until 2022-03-20	Checked fully
	R12	2022-07-17 until 2023-01-08	Checked 2022-09-01 until 2022-09-20, 2022-11-01 until 2022-11-14, and 2022-12-01 until 2022-12-27
	R13	2023-01-10 until 2023-05-28	Checked 2023-02-10 until 2023-02-26, 2023-03-13 until 2023-03-31, and 2023-05-10 until 2023-05-17
CEBUS-09	R11	2022-01-09 until 2022-02-17	Checked fully
	R12	2022-07-17 until 2023-01-08	Checked 2022-09-01 until 2022-09-20, 2022-11-01 until 2022-11-14, and 2022-12-01 until 2022-12-27
	R13	2023-01-10 until 2023-02-22	Checked 2023-02-17 until 2023-02-19

Table D.1: Overview of all cameras inspected for howler sightings by a single observer (ZG). Checked means all images were manually checked for howler infants, while coded means the deployment was formally coded as part of a larger project (multiple observers).

Camera location	**Deployment number**	**Deployed**	**Inspected**
CEBUS-10	R11	2022-01-08 until 2022-07-15	Checked fully
	R12	2022-07-18 until 2023-01-08	Checked 2022-09-01 until 2022-09-20, 2022-11-01 until 2022-11-14, and 2022-12-01 until 2022-12-27
	R13	2023-01-12 until 2023-07-19	Checked 2023-02-10 until 2023-02-26, 2023-03-18 until 2023-03-31, and 2023-05-10 until 2023-05-17
CEBUS-11	R11	2022-01-09 until 2022-07-15	Checked fully
	R12	2022-07-18 until 2022-11-10	Checked 2022-09-01 until 2022-09-20, 2022-11-01 until 2022-11-14, and 2022-12-01 until 2022-12-27
	R13	2023-01-12 until 2023-03-09	Checked fully
EXP-ANV-01	R11	2022-01-10 until 2022-07-17	Coded fully
	R12	2022-07-18 until 2023-01-02	Checked fully
	R13	2023-01-11 until 2023-07-07	Checked fully
EXP-ANV-02 (alternative angle EXP-ANV-01)	R11	2022-01-10 until 2022-07-17	Coded fully
	R12	2022-07-18 until 2023-01-11	Checked fully
	R13	2023-01-11 until 2023-05-13	Checked fully
Cameras in streambeds			
J-STREAM-01	R11	2022-01-06 until 2022-07-19	Coded fully
J-STREAM-02	R11	2022-01-05 until 2022-05-14	Coded fully
J-STREAM-03	R11	2022-01-05 until 2022-04-18	Coded fully
J-STREAM-04	R11	2022-01-05 until 2022-07-14	Coded fully
J-STREAM-05	R11	2022-01-05 until 2022-05-14	Coded fully
J-STREAM-06	R11	2022-01-06 until 2022-07-17	Coded fully
J-STREAM-07	R11	2022-01-06 until 2022-05-04	Coded fully
J-STREAM-08	R11	2022-01-06 until 2022-07-14	Coded fully
J-STREAM-09	R11	2022-01-05 until 2022-05-14	Coded fully
J-STREAM-10	R11	2022-01-05 until 2022-07-15	Coded fully
J-STREAM-11	R11	2022-01-05 until 2022-05-13	Coded fully
J-STREAM-12*	R11		

Table D.1: Overview of all cameras inspected for howler sightings by a single observer (ZG). Checked means all images were manually checked for howler infants, while coded means the deployment was formally coded as part of a larger project (multiple observers).

Camera location	**Deployment number**	**Deployed**	**Inspected**
Cameras at random locations 15 m from a streambed camera			
J-RAN-01	R11	2022-01-09 until 2022-06-22	Coded fully
J-RAN-02	R11	2022-01-05 until 2022-07-16	Coded fully
J-RAN-03	R11	2022-01-05 until 2022-07-16	Coded fully
J-RAN-04	R11	2022-01-09 until 2022-06-28	Coded fully
J-RAN-05	R11	2022-01-06 until 2022-07-17	Coded fully
J-RAN-06*	R11		
J-RAN-07	R11	2022-01-06 until 2022-03-21	Coded fully
J-RAN-08	R11	2022-01-06 until 2022-07-18	Coded fully
J-RAN-09	R11	2022-01-09 until 2022-06-28	Coded fully
J-RAN-10	R11	2022-01-09 until 2022-05-08	Coded fully
J-RAN-11	R11	2022-01-10 until 2022-05-05	Coded fully
J-RAN-12	R11	2022-01-08 until 2022-06-19	Coded fully
Cameras placed as part of 100 m spaced grid			
TU-135	R12	2022-05-15 until 2023-01-09	Coded fully
TU-137	R12	2022-05-15 until 2023-01-10	Coded fully
TU-141	R12	2022-05-14 until 2023-01-09	Coded fully
TU-151	R12	2022-05-16 until 2023-01-09	Coded fully
TU-152	R12	2022-05-15 until 2022-05-21	Coded fully
TU-153	R12	2022-07-16 until 2022-08-29	Coded fully
TU-154	R12	2022-05-15 until 2022-05-21	Coded fully
TU-155	R12	2022-07-15 until 2023-01-10	Coded fully
TU-156	R12	2022-05-13 until 2022-08-19	Coded fully
TU-157	R12	2022-05-14 until 2023-01-10	Coded fully
TU-158	R12	2022-05-14 until 2023-01-10	Coded fully
TU-166	R12	2022-05-16 until 2022-10-30	Coded fully
TU-168	R12	2022-07-14 until 2022-08-14	Coded fully
TU-170	R12	2022-07-16 until 2022-10-14	Coded fully
TU-171	R12	2022-07-15 until 2023-01-10	Coded fully

Table D.1: Overview of all cameras inspected for howler sightings by a single observer (ZG). Checked means all images were manually checked for howler infants, while coded means the deployment was formally coded as part of a larger project (multiple observers).

Camera location	**Deployment number**	**Deployed**		**Inspected**
TU-172	R12	2022-05-13 2023-01-10	until	Coded fully
TU-173	R12	2022-05-13 2023-01-05	until	Coded fully
TU-182	R12	2022-05-16 2023-01-27	until	Coded fully
TU-183	R12	2022-07-14 2022-08-27	until	Coded fully
TU-184	R12	2022-07-16 2023-01-27	until	Coded fully
TU-185	R12	2022-07-16 2023-01-28	until	Coded fully
TU-186	R12	2022-07-15 2022-10-10	until	Coded fully
TU-187	R12	2022-07-15 2022-11-18	until	Coded fully
TU-188	R12	2022-05-13 2023-01-10	until	Coded fully
TU-190	R12	2022-05-13 2023-01-11	until	Coded fully

D.2 Detailed description of events

D.2.1 Howler 1 (Jan 26, 2022 - Feb 3, 2022)

The first sighting of a howler infant occurred on Jan 26, 2022, at 06:47, when we observe three capuchins (all immatures) traveling through an anvil site. One of the capuchins, an unidentified juvenile male, carries Howler 1 ventrally on his chest. A subadult male traveling right behind the juvenile male is recognizable as Joker (the carrier of this howler infant on later dates). Howler 1 appears to be between 2-3 weeks of age and in good physical condition. The next day, on Jan 27, 2022, there are two sightings of Howler 1 at 07:07 and 16:18, in both cases an unidentifiable juvenile male is carrying the howler ventrally and traveling (seemingly) alone.

Three days later, on Jan 30, 2022, we see Joker with Howler 1 at 07:09 at two different camera locations close to each other. In the first sighting, Joker is consuming a hermit crab at a tool-anvil while carrying Howler 1 ventrally. Howler 1 clings to him and seems alert. In the second sighting, Joker travels past carrying Howler 1 ventrally. Four days later, on Feb 3, 2022, at 14:22, we see Howler 1 for the last time. Joker is carrying the howler dorsally during aggressive social interactions with capuchins that are out of view of the camera trap. An adult male sits next to Joker, and Joker headflags—a common behavior to recruit partners in coalitionary aggression [330] —towards the adult male, then vocally threatens an off-screen capuchin. After Joker's vocal threats, Howler 1 produces an unusually high-pitched vocalization, which resembles a howler lost-call (Figure D.1).

After the last sighting of Howler 1, we twice observe Joker on camera traps without it. The first clear sighting of Joker is 10 days after the last observation of the howler, on Feb 13, 2022, and the second is on Mar 3, 2022.

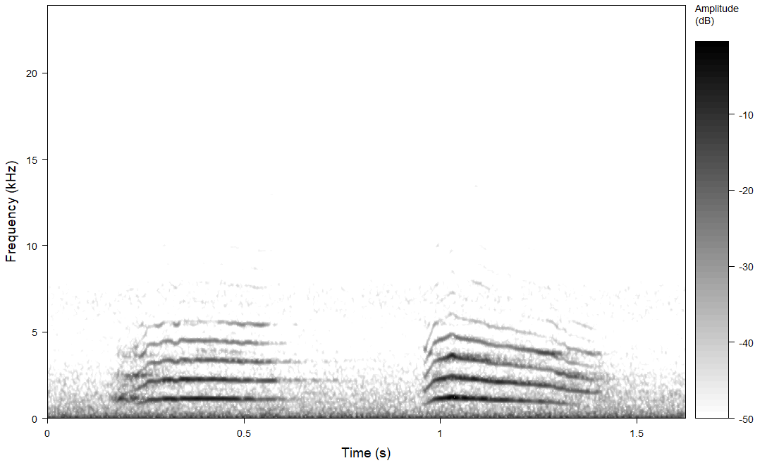

Figure D.1: Spectrogram of high-pitched lost-call from howler infant. Spectrogram was made using the package `seewave` in `R` and the following settings: Hamming window, 75% overlap, 48 kHz sampling frequency

D.2.2 Howler 2 (Apr 7, 2022 - Apr 13, 2022)

We see Howler 2 for the first time in the evening of Apr 7, 2022, at 17:19, 64 days after the last sighting of Howler 1. Four capuchins travel past a camera on an anvil, including a subadult male (whose appearance is consistent with Joker but who cannot be identified with certainty), who is carrying Howler 2 dorsally. Howler 2 is bigger than Howler 1 (estimated 3-4 weeks old), and appears more alert and looking around. In a series of videos between 17:35-18:00, we see more than six capuchins, including Joker, foraging and using tools at an anvil site. Joker does not use tools to access sea almond endocarp, but rather consumes the fleshy mesocarp without tools while carrying the howler dorsally. Howler 2 frequently lost-calls while on Joker's back, as the howler climbs around and looks into the canopy, and vocalizes at another capuchin when the capuchin shows interest in Joker's food. Ten minutes later, from 18:12-18:33, we observe another series of sequences of at least 10 capuchins consuming coconuts and foraging at another anvil site. Joker, with Howler 2 dorsally, also consumes some coconut, and rests on the ground. At 18:33, an adult male and adult female threaten Joker, who redirects the aggression off-screen and then leaves with Howler 2 riding dorsally. Howler 2 can be heard lost-calling constantly throughout this entire period, including in some videos off-screen.

Howler 2 is last sighted six days later on Apr 13, 2022. On this day at 16:59, we see a subadult male, who is likely Joker, traveling with Howler 2 dorsally. At 17:03, six capuchins are seen foraging and traveling at a camera in a streambed. Joker is among them, easily identifiable and carrying Howler 2 dorsally, who is attentive. At 18:02 Howler 2 is seen for the final time at a camera near the coast, where Joker along with at least four other capuchins, forage on the beach. Howler 2 is carried dorsally, and is attentive and vocalizing (lost-calling).

D.2.3 Howler 3 (Apr 10, 2022)

On Apr 10, 2022, at 17:09, we see Joker seemingly alone foraging in a stream. Howler 2 is nowhere to be seen in the view of the camera (despite being sighted again three days later on 2022-04-13). Then another subadult male capuchin (identifiable as Terry, a carrier of later howler infants) and a juvenile capuchin (Balthasar, also a carrier of later howler infants) appear, along with Howler 3, who was likely carried in by either Terry or Balthasar. Howler 3 is small (2-3 weeks old), and is subsequently pulled on by both Joker and Terry, and is observed being dragged through the stream face-down. It appears to be deceased, although this is challenging to confirm this with still images alone. After some pulling, Joker picks up Howler 3 in one hand and carries it out of frame.

D.2.4 Howler 4 (May 1, 2022 - May 4, 2022)

Howler 4 is first seen on May 1, 2022, 19 days after the sighting of Howler 3. At 16:37, we see two capuchins foraging in a stream, one subadult male, who looks consistent with Joker but cannot clearly be identified, is carrying a small howler dorsally. On May 2, 2022, there were two sightings, one with a party of four capuchins at 12:11 and one with two capuchins at 14:09, in both cases, capuchins are traveling and we see Joker (clearly identifiable) carrying Howler 4 dorsally.

On May 3, 2022, a series of videos from a camera on an experimental anvil between 18:04 and 18:19 show Joker eating sea almond exocarp without tools while keeping Howler 4 lying at his feet. Whenever Joker moves, he carries Howler 4 in his hand, and the infant itself is largely immobile aside from sporadic small movements. Joker allows food to drop onto Howler 4's body and generally does not interact with it. At least three other capuchins are present, two adult males mostly using tools at the anvil and a juvenile foraging. All other capuchins come to inspect Howler 4 at various moments, but only briefly touch it or peer at it. At 18:19, Joker leaves without Howler 4. A still camera with a different angle on the anvil programmed to record time-lapse photos every 12-hour shows the howler still lying next to the anvil, where Joker left it, at midnight on May 3, 2022.

The next trigger at this site is the next morning, May 4, 2022, at 07:37, when a juvenile capuchin goes over to Howler 4. It pulls on it, bites it and drags it around by its tail. The juvenile appears nervous and curious, and inspects the howler often. The howler is alive at this time but rarely moves. An adult male uses tools on the anvil and sporadically inspects Howler 4, but the infant is mostly left lying alone until 09:13 when Joker returns. Joker inspects and picks up Howler 4 and embraces the howler ventrally. After that, he forages on anvil debris and consumes sea almonds while leaving Howler 4 lying at his feet, and a subadult male (Terry) and adult male consume sea almonds with tools on the anvil. At 09:42, Joker leaves the frame carrying Howler 4 ventrally. The next day, May 5, at 17:35, Joker is seen carrying the (presumably dead) Howler 4 in one hand, which is the last sighting of this infant howler. We observe Joker traveling past a camera on July

18, 2022, at 16:00, also without any howler infants present.

D.2.5 Howler 5 (Sep 7, 2022 - Sep 14, 2022) & Howler 6 (Sep 8, 2022 - Sep 12, 2022)

The next time we see a howler infant on our camera traps is on Sep 7, 2022, approximately four months (127 days) after the last sighting of Howler 4. The series of sightings that follows is markedly different from what we observed before: not only are there multiple carriers that switch rapidly, but there are also two howler infants present in the capuchin group at the same time. Two of the new carriers, namely a juvenile male named Balthasar, and a subadult male named Terry, were already observed in the vicinity of the previous howler infants. Balthasar was seen in the same observation as Howler 2 (Apr 7, 2022, at 17:56) and Howler 3 (the dead howler in the streambed). Terry was the other individual, alongside Joker, pulling on Howler 3, and was also observed alongside Howler 4 (May 4, 2022, at 09:19).

Two howler infants present simultaneously
The first sighting of Howler 5 (3-4 weeks old) is between 17:52 and 18:37 at two camera traps facing anvils close to each other. A large group of capuchins (at least 11 individuals of all age-sex classes) is seen foraging on and around the anvils. Initially, we only hear Howler 5 lost calling, and adult howlers calling back with contact calls from the canopy. When Howler 5 comes into view, it is dorsal on a juvenile male, Balthasar, who uses tools at the anvil with the howler infant on his back. At 18:08, a juvenile capuchin tries to approach Balthasar and inspect Howler 5, but Balthasar turns away from it and prevents interaction. At 18:21, what sounds like an adult female howler can be heard responding to the lost-calling infant howler with an unusual, distressed-sounding, vocalization which most resembles a wail [331] or screech [332]. The vocalizing back and forth between Howler 5 and the adult howler continues until 18:37, and while some capuchins present appear vigilant towards the canopy, we see and hear no signs of aggression or indication that the adult howlers come to the ground. On Sep 7, 2022, we hear two howler infants lost-calling at different distances from the camera, suggesting that Howler 6 may already have been stolen as well, although this infant is only seen on camera for the first time the following day.

The next morning at 06:46, we observe Balthasar traveling with Howler 5 dorsal. Howler 6 appears for the first time 30 minutes later, on a streambed camera at 07:19. A subadult male, identified as Mick, carries Howler 6 dorsally. Howler 6 appears to be in poor condition, and looks smaller than Howler 5 (1-2 weeks old) and potentially wet. On the afternoon of this day, Howler 6 is seen several times, at 15:35, 17:32, and 18:11, now carried by another subadult male (Terry). In all instances, Terry is using tools at an anvil while Howler 6 is ventral and appears weak. During the tool use, Terry keeps nudging the howler infant's head to the side with his elbow as he brings the hammerstone down, but Howler 6 does not appear to respond to this. In one observation at 15:40, Howler 6 is seen trying to nurse, and Terry nips at it, seemingly annoyed. Who is carrying Howler 5 this afternoon is unclear, as we observe Balthasar without a howler infant throughout the day (at 07:52, 15:38, 16:30, and 17:18).

However, on Sep 9, 2022, Balthasar is carrying Howler 5 again, and they are observed four times between 14:19 and 14:39, and again at 17:01. In the majority of the sightings, Balthasar is using tools with Howler 5 dorsal and alert on his back. At 14:33, Howler 5 even climbs off Balthasar and runs out of view of the camera while vocalizing. Balthasar runs after the howler infant and retrieves it. The next morning (Sep 10, 2022), Howler 5 is being carried by Mick, and is seen dorsal and lost-calling while Mick travels and uses tools (at 07:47, 08:26, 08:31, and 08:46). In the afternoon, at 16:54, Balthasar is observed foraging with a howler infant ventral, which cannot clearly be identified as either Howler 5 or Howler 6.

Two days later, on Sep 11, 2022, we mostly observe Howler 5. In the morning (09:04, between 09:15-09:55, 10:32), Balthasar is carrying the howler dorsally and ventrally while using tools. We observe Howler 5 climbing off Balthasar several times, and (attempting to) consume anvil debris, which it appears to chew. While Howler 5 is ventral on Balthasar, it attempts to nurse. In response, Balthasar nips the howler infant several times, and then bites it on the head eliciting a distressed squeal from the infant. Around 11:45 and 15:29, we observe an unidentifiable subadult male carrying a howler infant dorsally, who also cannot be reliably identified as either Howler 5 or Howler 6. Additionally, at 15:15, we hear several adult male howler roars at the same anvil where Howler 5 was first observed.

Only a single howler infant remaining in the capuchin group
The next day, Sep 12, 2022, we know with certainty that one of the howler infants has died, which appears to be Howler 6. At a tool-anvil site, a brown static object suddenly appears at the top of the streambed in the background of a video at 10:25. At 12:09, a juvenile capuchin approaches the object and pushes it with its hand, after which it rolls down the hill into the streambed. While it is rolling, a tail can be observed, and it appears to be totally rigid, suggesting it is a howler infant that was likely already dead for several hours. Only twenty minutes later, at 12:29, Balthasar is seen at another camera carrying Howler 5 dorsally, who is in good health and alert. Balthasar uses tools with Howler 5 dorsal at 12:39, until the howler climbs off and starts eating anvil debris. At 12:44, Balthasar leaves and abandons Howler 5 at the anvil, who lost calls at him as he is walking away. Immediately after, Terry comes running up to the anvil and embraces Howler 5 ventrally. Howler 5 vocalizes in response, and moves to cling dorsally as Terry starts using tools. Three hours later, at 15:44, Howler 5 has switched carriers again and is now dorsal on Mick, who uses tools and displaces Balthasar from the anvil. In the afternoon, at 17:38, we again hear adult howlers vocalizing at the same anvil as the day prior, including an unusual vocalization which sounds like a high-pitched howl, likely originating from an adult female howler as females do not howl as much as, or at the same pitch as males in this species.

Howler 5 is still seen several times (at 08:11, 09:16 and 09:17) on the following day, when we also hear more adult howler roars at 07:58. In all instances the infant is carried by Terry (both ventrally and dorsally). In the last sighting, Terry is using tools with Howler 5 dorsal, and it falls off during the tool use. Terry looks over at the howler, which appears to be weaker now than in previous sightings, but does not assist it, and it climbs up on Terry's back on its own. The very last sighting of Howler 5 is the next day, Sep 14, 2022, and here it appears to already be dead. At 06:37, Terry is using tools at an anvil, and carries Howler 5 into frame in his hand. Howler 5 lies next to the anvil motionless, and several times Terry (accidentally) hits the side of the howler infant's head with the hammerstone, with no response.

D.2.6 Howler 7 (Nov 7, 2022 - Nov 8, 2022)

The next howler infant sighting comes 55 days later, on Nov 7, 2022. However, four days prior, on Nov 3, 2022, we see an adult male howler traveling on the ground at a camera in the vegetation in the tool-using group's range. Then on Nov 7, 2022, at 13:25, we see a subadult male (either Mick or Terry) traveling with Howler 7 half-dorsal, half-ventral. Howler 7 is rather small (2-4 weeks old), and does not appear to be in the best physical condition. At 15:49, Howler 7 has switched carriers and is dorsal on Balthasar, while at 16:35, it is again observed both dorsal and ventral on a subadult male (either Mick or Terry).

In general, we have fewer sightings of howler infants later in the year because fewer of our cameras are running (as they ran out of memory or battery). The last sighting of Howler 7 is one day later, at 16:10, in a large group of 9 capuchins at an anvil site. The capuchins are eating coconut and foraging, and two juveniles inspect Howler 7, who is hanging on the arm of Joker (the innovator of the tradition and carrier of the first four howler infants). Howler 7 appears to be in poor condition: its fur is patchy and it seems emaciated. It is not seen after this observation, although on Nov 30, 2022, we see another howler adult traveling on the ground at 16:35, this time an adult female, potentially carrying a small infant ventrally.

D.2.7 Howler 8 (Dec 9, 2022 - Dec 10, 2022)

We observe another howler infant 32 days later, on Dec 9, 2022, at 10:47. An unidentifiable subadult male capuchin carries Howler 8 dorsally, who appears to be 2-3 weeks old. Howler 8 is seen many times on the next day. In the morning, at 06:35 and 07:33, it is carried dorsally by a subadult male which we cannot clearly identify. However, at 11:42, we are certain that Mick is carrying Howler 8 dorsally while traveling. By the next sighting of Howler 8 at 15:24, it has switched carriers and is now on a juvenile male called Zim, who we had not observed carrying howler infants before. At 15:57, Zim is eating a coconut with Howler 8 dorsal, but appears uncomfortable with the howler infant on its back. Zim repeatedly grabs at Howler 8, and nips in its direction. Howler 8 also climbs off and appears to consume some coconut. In the last sightings of Howler 8, at 17:35 and 17:53, Terry is now the carrier and forages with the howler infant riding dorsally.

On Dec 15, 2022, at 13:46, we observe a juvenile howler traveling by itself on the ground at one of our cameras in the vegetation. The howler is older than any of the infants we saw carried by the capuchins, and thus unlikely to be Howler 8 or 9. The next capuchin sighting at this specific camera is 1.5 hours later.

D.2.8 Howler 9 (Dec 16, 2022 - Dec 19, 2022)

On Dec 16, 2022, one day after the lone juvenile howler was seen traveling on the ground, and 6 days after the last sighting of Howler 8, we observe Howler 9 for the first time. At 14:58, Terry is seen foraging in the streambed, and at 15:47, using tools at an anvil, with Howler 9 dorsal. Howler 9 is alert and appears to be 2-4 weeks old. We observe Howler 9 again on Dec 17, 2022 (dorsal on an unidentifiable subadult male), and on Dec 18, 2022 (carried dorsally by Zim, the juvenile carrier of Howler 8). On Dec 19, 2022, Howler 9 is observed dorsal on Mick at 07:24, and dorsal on Terry at 14:27, which is the last observation we have of this infant.

D.2.9 Howler 10 (Feb 17, 2023 - Feb 19, 2023)

We observe Howler 10 for the first time on Feb 17, 2023, 60 days after the last sighting of Howler 9. At 18:48, the howler infant of approximately 3-4 weeks of age is seen carried dorsally by Terry, with Joker also traveling with the two. The following day at 09:53, Balthasar is carrying Howler 10, with Mick also present, and at 17:17, Howler 10 has switched back to Terry. Terry is using tools, and the howler infant, seemingly weakened, slides off during tool use but also climbs back on.

On Feb 19, 2023, early in the morning at 06:47, the whole group of capuchins appears, foraging in a streambed near an anvil. Howler 10 is dorsal on Terry, who is eating at the anvil without using tools, and the infant continuously lost-calls and looks into the canopy. At least one adult howler is present, as we hear responses to the lost-calls and contact calls of the infant, and the capuchins also repeatedly look into the canopy after the adult howler howls. Until 07:26, we hear the infant howler calling continuously and the adult howler responding nearby, while the capuchins forage.

At 07:26, Howler 10 comes into view of the camera on another carrier, Zim, and climbs off him. Howler 10 runs off and seems to climb into the trees slightly out of view, likely attempting to return to the adult howlers above. Mick, who was sitting close-by at the anvil, intervenes and grabs the howler infant by its tail. He throws it onto the anvil and threatens it, nipping at it and pushing it down onto the ground. The howler infant vocalizes in distress, and then nearly all present capuchins start vocally threatening up into the canopy, we assume at the adult howler(s) present there. When Mick turns his attention elsewhere, the howler infant runs out of view, but is followed by Zim, who seemingly picks him up again (inferred from the change in vocalizations of the infant, who makes distraught noises). At 07:28, the capuchins are mostly calm again, and Howler 10 comes into view carried dorsally by Balthasar.

At 07:40, at the same camera, we observe Balthasar with Howler 10 foraging on anvil debris. The capuchins are still alert, looking into the canopy, and the infant is lost-calling and also attentive upwards. An adult female capuchin then threatens Balthasar with the howler infant. At 08:00, still at the same site, we now see Howler 10 on Zim, who is also eating anvil debris when the howler infant climbs off him. Zim gently grabs the howler and follows him out of frame. Prior to this, an adult female, likely the same one as 20 minutes prior, threatens Zim with the howler infant.

Our last sightings of Howler 10 are from the evening of Feb 19, at 17:24-17:33 and 18:08. In all cases, Balthasar is carrying the howler infant dorsally, and in one observation, the howler again appears to be weakened and sliding off its carrier.

D.2.10 Howler 11 (Mar 20, 2023 - Mar 21, 2023)

29 days after the last sighting of Howler 10, on Mar 20, 2023, Howler 11 is first seen on our cameras. First seen at 14:44 being carried by Terry, Howler 11 is by far the youngest howler infant we observed being carried. It is less than a week old, potentially only 1-2 days old, as it still has a silver coloring and its eyes are mostly closed. It is clinging to Terry ventrally/dorsally as Terry uses tools. At some point, Terry threatens something off-screen, which could be another capuchin or perhaps a howler. Howler 11 does not vocalize or move much.

The next day, the last sightings of Howler 11 occur at 15:37 and 15:52-16:02. In all cases, Terry is carrying the infant, and using tools at anvil sites. In some observations Howler 11 is ventral on Terry, and upside down, so with its head hanging down between Terry's legs as he uses tools or travels.

Appendix E

Supplementary information for ‘Habitual tool use on monopolizable resources affects group cohesion’

Animation of capuchin sightings:
https://keeper.mpdl.mpg.de/d/ad41ce04639143589f79/

E.1 Supplemental methods

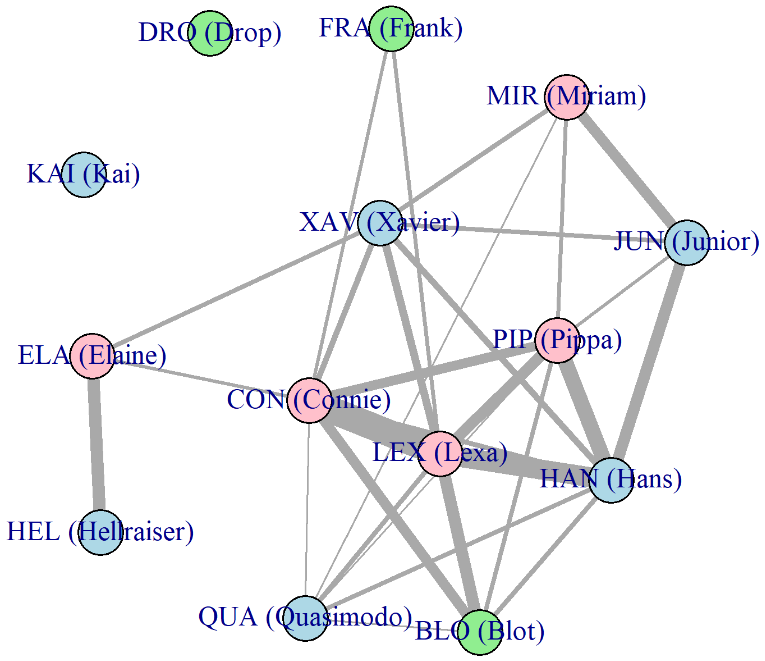

Figure E.1: Social network of the non-tool-using group. Each node is an individual, and node color reflects the age-sex category (pink for adult females, blue for adult males, green for subadults and juveniles). If a line connects two individuals, they were observed in the same sequence, the thickness of the line reflects the frequency of individuals co-occurring.

E.2 Supplemental results

E.2.1 Models estimating party size

Table E.1: Posterior mean model estimates of Model sps_bm1a, a hurdle Poisson GLMM (Bayes $R^2 = 0.06$) comparing mean party size between the tool-using and non-tool-using group. The link for the non-zero component of the model (mu) is log, and for the zero component (hu) logit.

	Estimate	*Est. Error*	*CI_95_low*	*CI_95_high*
Multilevel Hyperparameters				
locationfactor (levels: 49)				
sd(mu_Intercept)	0.39	0.06	0.28	0.53
sd(hu_Intercept)	0.51	0.08	0.37	0.68
Regression Coefficients				
mu_Intercept	0.31	0.10	0.09	0.49
hu_Intercept	0.91	0.13	0.67	1.16
mu_gridtypeTU	-0.26	0.15	-0.54	0.03
hu_gridtypeTU	0.09	0.17	-0.25	0.43

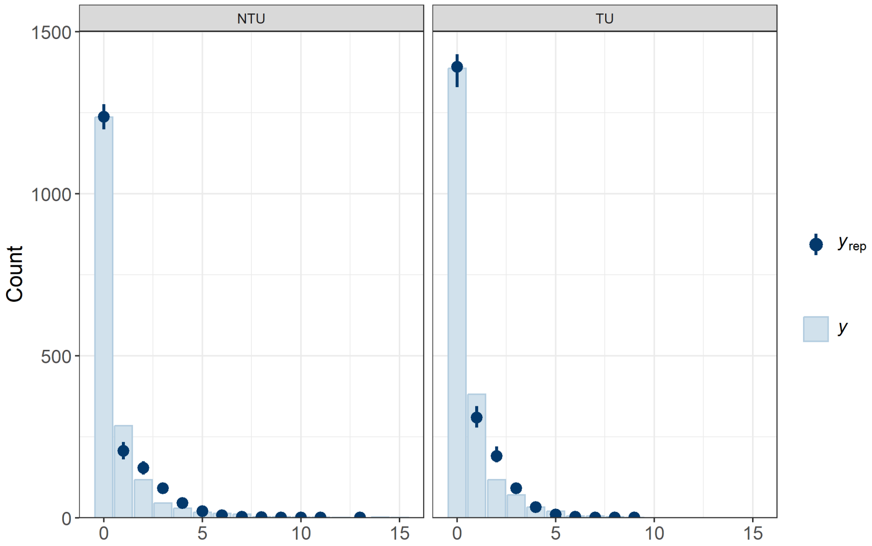

Figure E.2: Posterior distribution from model sps_bm1a, comparing the mean social party size between the non-tool-using (NTU) and tool-using (TU) group. The light blue bars reflect the estimated frequencies of each social party size, with the dark blue error bars reflecting the variation in estimates of a 100 samples from the posterior.

Table E.2: Posterior mean model estimates of Model ps_bm1b, a hurdle Gamma GLMM (Bayes $R^2 = 0.24$) comparing standard deviation in party size between the tool-using and non-tool-using group. The link for the non-zero component of the model (mu) is log, and for the shape and zero component (hu) identity.

	Estimate	*Est. Error*	*CI_95_low*	*CI_95_high*
Multilevel Hyperparameters				
locationfactor (levels: 48)				
sd(Intercept)	0.21	0.05	0.12	0.32
Regression Coefficients				
Intercept	-8.17	0.13	-8.43	-7.91
gridtypeTU	-0.17	0.10	-0.38	0.04
Further Distributional Parameters				
shape	1.86	0.11	1.65	2.09
hu	0.41	0.02	0.38	0.44

Table E.3: Posterior mean model estimates of Model sps_gam1, a hurdle Poisson GAM (Bayes $R^2 = 0.06$) comparing the fluctuation in social party size depending on the hour of day between the tool-using and non-tool-using group. The link for the non-zero component of the model (mu) is log, and for the zero component (hu) logit.

	Estimate	*Est. Error*	*CI_95_low*	*CI_95_high*
Smoothing Spline Hyperparameters				
sds(shourgridtypeNTU_1)	0.84	0.68	0.03	2.50
sds(shourgridtypeTU_1)	0.42	0.43	0.01	1.61
sds(slocationfactor_1)	0.39	0.06	0.28	0.53
sds(hu_slocationfactor_1)	0.51	0.08	0.37	0.67
Regression Coefficients				
Intercept	0.30	0.11	0.09	0.51
hu_Intercept	0.91	0.13	0.66	1.16
gridtypeTU	-0.27	0.15	-0.56	0.02
hu_gridtypeTU	0.10	0.17	-0.24	0.46
shour:gridtypeNTU_1	0.25	0.82	-1.42	1.93
shour:gridtypeTU_1	0.39	0.66	-1.09	1.64

E.2.2 Models estimating party composition

Table E.4: Posterior mean model estimates of Model pc_bm1, a hurdle Poisson GLMM (Bayes $R^2 = 0.04$) comparing the number of adult females in a party between the tool-using and non-tool-using group. All estimates are on the log scale.

	Estimate	*Est. Error*	*CI_95_low*	*CI_95_high*
Multilevel Hyperparameters				
locationfactor (levels: 49)				
sd(Intercept)	0.29	0.05	0.20	0.40
Regression Coefficients				
Intercept	-1.04	0.08	-1.20	-0.88
gridtypeTU	-0.24	0.12	-0.46	-0.01
nAM	0.09	0.06	-0.04	0.21
gridtypeTU:nAM	-0.29	0.12	-0.53	-0.06
Further Parameters				
zi	0.01	0.01	0.00	0.05

Table E.5: Posterior mean model estimates of Model pc_bm2, a hurdle Poisson GLMM (Bayes $R^2 = 0.08$) comparing the number of adult males in a party between the tool-using and non-tool-using group. All estimates are on the log scale.

	Estimate	*Est. Error*	*CI_95_low*	*CI_95_high*
Multilevel Hyperparameters				
locationfactor (levels: 49)				
sd(Intercept)	0.36	0.06	0.26	0.50
Regression Coefficients				
Intercept	-1.16	0.09	-1.35	-0.98
gridtypeTU	-0.49	0.14	-0.77	-0.23
nAF	0.06	0.06	-0.05	0.16
gridtypeTU:nAF	-0.28	0.12	-0.52	-0.05
Further Parameters				
zi	0.01	0.01	0.00	0.03

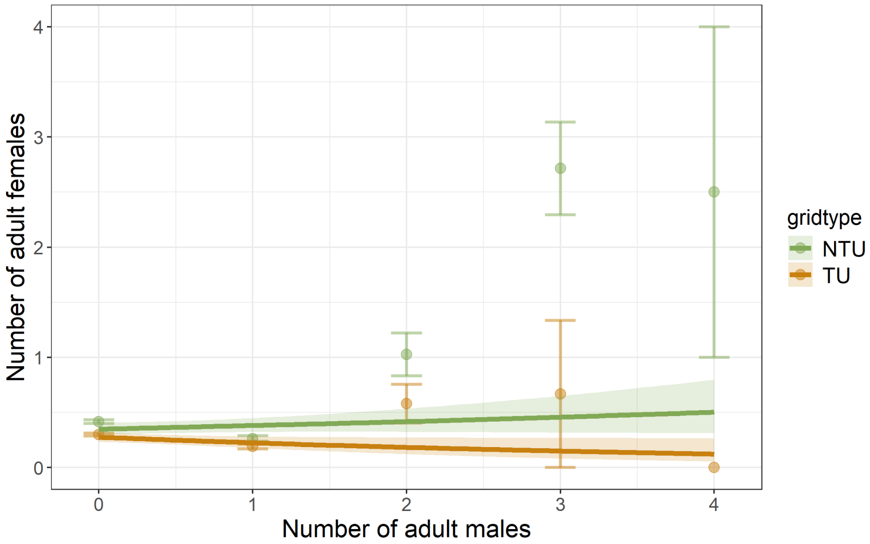

Figure E.3: Model estimates from zero-inflated Poisson GLMM of relationship between number of adult females and number of adult males occurring together in a sequence for tool-using group (orange) and non-tool-using group (green). The bold line reflects the model estimates, with the shaded area representing the 95% confidence interval. Points reflects the means from the real data, with whiskers representing their 95% confidence intervals.

E.2.3 Models estimating spatial cohesion

Table E.6: Posterior mean model estimates of models gp_tu and gp_ntu, Gaussian process regressions estimating the covariance of party size and distance between camera traps. All estimates are on the log scale.

Model gp_tu (tool-using group)					**Model gp_ntu (non-tool-using group)**				
	Mean	*Sd*	*5.5%*	*94.5%*		*Mean*	*Sd*	*5.5%*	*94.5%*
Camera locations (indexed)					*Camera locations (indexed)*				
cam[1]	-1.55	0.52	-2.34	-0.71	cam[1]	-0.04	0.16	-0.29	0.21
cam[2]	-1.73	0.52	-2.52	-0.89	cam[2]	-0.07	0.12	-0.27	0.13
cam[3]	-1.88	0.52	-2.67	-1.05	cam[3]	0.02	0.10	-0.14	0.17
cam[4]	-1.98	0.53	-2.77	-1.12	cam[4]	-0.12	0.15	-0.37	0.11
cam[5]	-1.92	0.53	-2.73	-1.06	cam[5]	-0.13	0.08	-0.26	-0.01
cam[6]	-1.82	0.53	-2.63	-0.98	cam[6]	0.62	0.08	0.49	0.74
cam[7]	-1.80	0.53	-2.60	-0.95	cam[7]	-0.16	0.17	-0.44	0.10
cam[8]	-1.92	0.53	-2.74	-1.06	cam[8]	-0.09	0.10	-0.26	0.07
cam[9]	-2.03	0.53	-2.84	-1.18	cam[9]	-0.18	0.11	-0.36	-0.01
cam[10]	-2.05	0.53	-2.86	-1.19	cam[10]	-0.15	0.12	-0.34	0.04
cam[11]	-1.91	0.54	-2.73	-1.05	cam[11]	-0.11	0.15	-0.35	0.12
cam[12]	-1.93	0.53	-2.73	-1.06	cam[12]	0.43	0.10	0.28	0.59
cam[13]	-1.90	0.53	-2.71	-1.05	cam[13]	0.04	0.09	-0.11	0.19
cam[14]	-1.88	0.53	-2.69	-1.03	cam[14]	-0.11	0.13	-0.31	0.10
cam[15]	-1.85	0.53	-2.66	-0.99	cam[15]	-0.24	0.17	-0.52	0.01
cam[16]	-1.99	0.53	-2.81	-1.12	cam[16]	0.11	0.07	0.00	0.23

cam[17]	-1.96	0.53	-2.78	-1.11	cam[17]	-0.11	0.21	-0.45	0.21
cam[18]	-2.05	0.53	-2.87	-1.20	cam[18]	0.01	0.12	-0.19	0.20
cam[19]	-2.01	0.52	-2.81	-1.16	cam[19]	-0.12	0.16	-0.39	0.13
cam[20]	-1.89	0.53	-2.70	-1.03	cam[20]	-0.01	0.12	-0.20	0.17
cam[21]	-1.80	0.53	-2.60	-0.95	cam[21]	0.06	0.15	-0.17	0.30
cam[22]	-1.72	0.52	-2.46	-0.89	cam[22]	-0.10	0.10	-0.26	0.06
cam[23]	-1.66	0.52	-2.46	-0.82	cam[23]	-0.16	0.11	-0.33	0.00
cam[24]	-1.97	0.53	-2.78	-1.11	cam[24]	-0.11	0.09	-0.26	0.04
					cam[25]	0.03	0.11	-0.15	0.22
Regression Coefficients					*Regression Coefficients*				
camera	2.26	0.52	1.42	3.05	camera	0.48	0.06	0.38	0.58
η^2	1.21	0.64	0.40	2.36	η^2	0.05	0.03	0.02	0.10
ρ^2	0.03	0.02	0.01	0.05	ρ^2	3.91	2.18	1.40	7.96

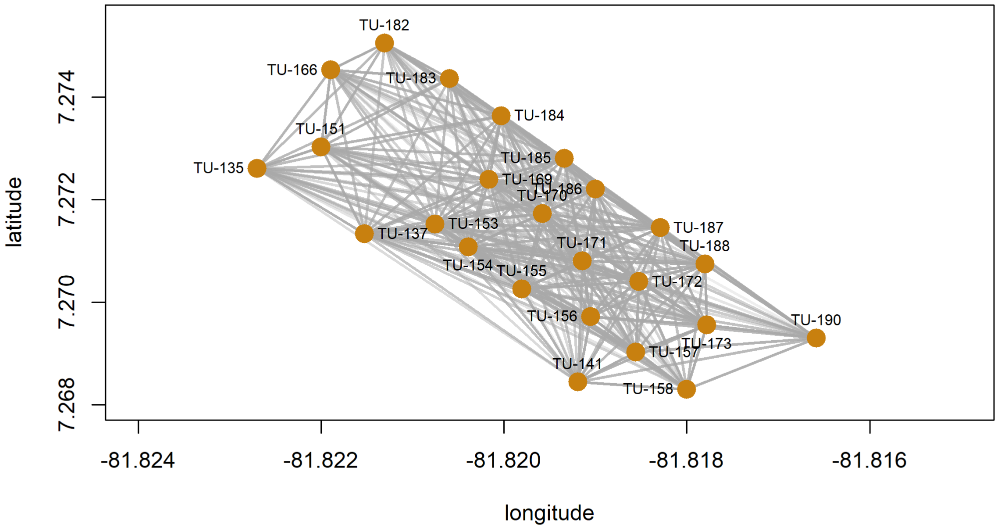

Figure E.4: Posterior correlations among cameras in geographic space for the tool-using group, estimated by model gp_tu.

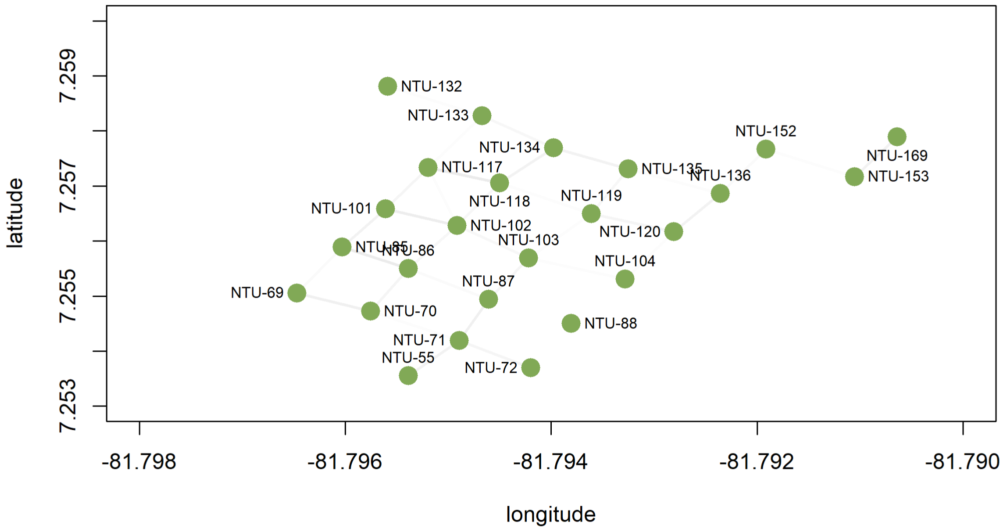

Figure E.5: Posterior correlations among cameras in geographic space for the non-tool-using group, estimated by model gp_ntu.

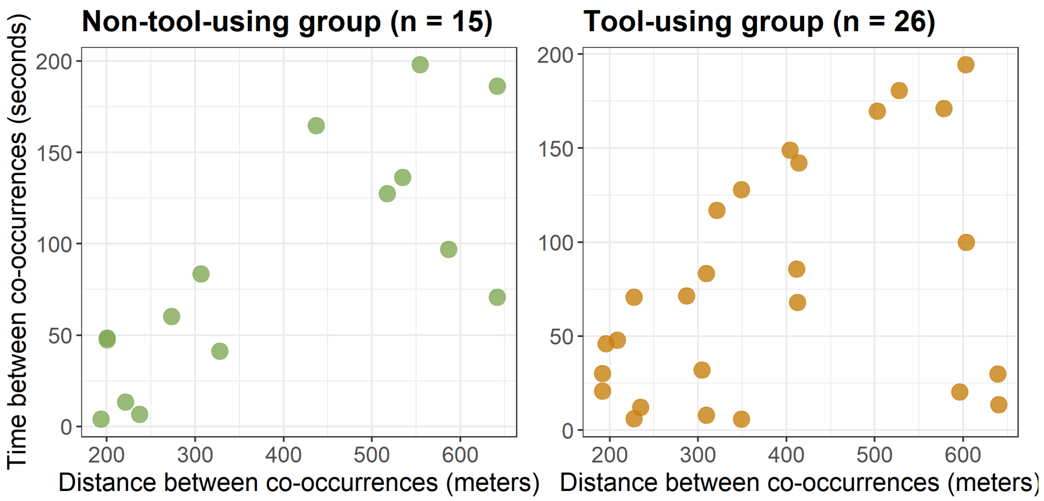

Figure E.6: Co-occurrences in the non-tool-using (left in green) and tool-using group (right in orange). Each dot represents the co-occurrence of two sightings. The x-axis reflects the distance in meters between the cameras where the co-occurring sightings were seen, the y-axis reflects the time in seconds between the co-occurring sightings.

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Zoë Goldsborough

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I'm an ambitious researcher with a strong passion for animal behavior, specifically social learning, welfare, and communication. I work hard for my goals and enjoy learning new things in my spare time.

WORK EXPERIENCE

2020-2025 **University of Konstanz & MPI AB, Konstanz, Germany**
IMPRS Doctoral Student
Supervisors: Prof. Dr. Meg C. Crofoot & Dr. Brendan J. Barrett
I studied social learning and tool use in white-faced capuchin monkeys in Panamá using camera traps. I was a member of the CASCB PhD Swarm, and also one of three IMPRS Doctoral Student Representatives from 2021-2022, as well as the PhDnet External PhD Representative in 2023.
Parental leave from December 2023-August 2024

2020 **Utrecht University, Utrecht, the Netherlands**
Research Assistant
I coordinated and executed the experiments at the chimpanzee colony at Royal Burgers' Zoo, the Netherlands, for a project on prosocial behavior. This included training chimpanzees individually, testing pairs in a cooperative task observations, and data coding.

2019 **MSc. Minor Research Project at Chimfunshi,Zambia**
Researcher & Research Assistant
Supervisors: Dr. E.J.C. van Leeuwen & Dr. A.M. Schel
As part of my Master's degree, I spent 5 months in Zambia studying the initiation of a social custom, the grooming handclasp in semi-wild chimpanzees. I also assisted in the data collection of a PhD student studying empathy. This entailed focal follows, ad lib recordings of agonistic interactions, and experimental work.

2018 **MSc. Major Research Project at Burgers' Zoo, the Netherlands**
Supervisors: Dr. C.E. Webb & Prof. Dr. E.H.M. Sterck
I conducted behavioral observations on captive chimpanzees, to investigate whether individual differences exist in the expression of abnormal behavior.

2017-2019 **StudentsPlus Tutoring, the Netherlands**
Tutoring of primary and high school students on topics such as English and Biology, providing a personalized approach and guidance.

2017 **Bsc. Honour's Thesis at Dierenpark Amersfoort, the Netherlands**
Supervisors: Dr. I.A. Flameling & Dr. M.J.H.M. Duchateau
Through behavioral observations of two zoo-housed tigers, I explored whether visitor presence affected their behavior.

2016-2018 **Stichting AAP, Almere, the Netherlands**
Voluntary Animal Caretaker, Mammal Department
I took care of the animals in the mammal department, including shifting animals, preparing and distributing food, and designing enrichment.

EDUCATION

2019 **Workshop ‘Social Network Analyses’, MPI for Ornithology**

2017-2019 **Master’s Degree in Behavioral Ecology, Utrecht University**
Grade: 8.7/10.0 (Cum laude)
Master’s Thesis: A Phylogeny of Social Learning: Assessing Recent Literature on Stimulus and Local Enhancement, supervised by Dr. E. O’Sullivan & Dr. M.J.H.M. Duchateau

2016 **Summer School ‘Observing Primate Behavior’, Utrecht University**
I completed a three-week summer school on primate behavior and wrote a report on self-scratching rates and rank in long-tailed macaques.

2014-2017 **Honor’s Bachelor Degree in Environmental & Neuro-Sciences, University College Roosevelt**
GPA: 3.9/4.0 (Summa cum laude)
Individual Research Project: Review of CRISPR-Cas9 technique

GRANTS AND FELLOWSHIPS

2021 **CASCB Small Project Grant (9996 EUR)**
Together with my PhD supervisor Dr. Brendan J. Barrett to fund the deployment of camera traps to study capuchin tool use.

2019 **Animal Behavior Society Student Research Grant (600 USD)**
For my research proposal on the role of communication in the initiation of the grooming handclasp in semi-wild chimpanzees.

2018 **U/SELECT Honor’s Society Grant (2500 EUR)**
I was selected as one of the 12 members of U/SELECT, the Honor’s program of the Graduate School of Life Sciences of Utrecht University. This program represents the top 1% of the graduate school, and all members are awarded a grant to support their research.

INVITED TALKS & EVENTS

2024 **Animal Welfare Day, Max Planck Institute of Animal Behavior**
I co-organized the first Animal Welfare Day at the MPI-AB and hosted a discussion session on ethical and welfare considerations of non-invasive methods to study animals.

2023 **Neuro-Diversity Days, Max Planck Institute of Animal Behavior & University of Konstanz**
I co-organized the first Neuro-Diversity Days, consisting of lectures and interactive workshops to generate awareness of neurodiversity.

2021 **Guest Lecture on Doing a PhD in Animal Behavior, University College Roosevelt**
I gave an invited guest lecture at UCR’s Future Week as well as in an undergraduate course in Biology on my research and career path and pursuing a career in animal behavior.

2019 **Guest Lecture on Thanatology, Harvard University**
In February, I gave an invited guest lecture on thanatology, the study of death responses, in primates for the undergraduate course Primate Social Behavior.

CONFERENCE TALKS AND POSTERS

2025 **Presentation at Culture Conference 2025, Utrecht, the Netherlands**
In February, I presented at the Culture Conference with an oral talk on my PhD chapter describing the rise and spread of a social tradition of interspecies abduction, for which I won the prize for Best Student Talk.

2023 **Presentation at Behavior Conference 2023, Bielefeld, Germany**
In August, I held a talk about research from my PhD considering how habitual tool use affects group cohesion in white-faced capuchins.

2022 **Presentation at joint EFP-GfP Conference 2022, Arnhem**
I held a talk about my PhD research on tool use and tidal cycles in white-faced capuchins for which I was awarded the prize for 3rd Best Student Talk.

2021 **Recorded Talk at Cultural Evolution Society (CES) 2021**
In June, I presented a pre-recorded talk and live Q and A on my research on the initiation of handclasp grooming by chimpanzees.

Poster Presentation at Virtual ASAB Easter Meeting
I presented a poster on my research on the initiation of handclasp grooming by chimpanzees.

2018 **Presentation at Benelux Congress of Zoology, Royal Belgian Zoological Society**
I presented a poster and held a talk about my research on individual differences in abnormal behavior in chimpanzees at this three-day congress.

2018 **Poster Presentation at 3rd Symposium of NVD (Dutch Association of Zoos**
In May, I presented a poster on my Bachelor's Honor's Thesis on the effect of visitor density and tigers, which was awarded with the prize for best poster.

AWARDS

2025 **Award for Best Student Talk at Culture Conference 2025, Utrecht, the Netherlands**

2022 **Prize for 3rd Best Student Talk at joint EFP-GfP Conference 2022, Arnhem**

2020 **Primates 2020 Social Impact Award**
Awarded to the article "Do chimpanzees (*Pan troglodytes*) console a bereaved mother" for having the highest social impact (based on Altmetric scores and full-text downloads) of all papers published in *Primates* in the last half of 2019 and first half of 2020

2018 **Poster Prize at 3rd Scientific Symposium of NVD, Dutch Association of Zoos**

SUPERVISION & TEACHING

2024 *Co-supervisor* for Master Thesis "Neophobia and Tool Use in Island-living Capuchin Monkeys (*Cebus capucinus imitator*)" by Lucia Bruscagnin at **University of Konstanz, Konstanz, Germany**

2023	*Training multiple student assistants* on coding protocols for annotating videos of capuchin tool use behavior at **Max Planck Institute of Animal Behavior, Konstanz, Germany**
2021	*Second examiner and supervisor* for Bachelor Thesis “A Review of Ecological and Social Factors Driving Tool Use by Animals on Islands” by Anna Sherlock at **University College Roosevelt, Middelburg, the Netherlands**
2019	*Teacher's Assistant* at **Utrecht University, Utrecht, the Netherlands** I gave lectures and monitored a mini research assignment as a teaching assistant in an undergraduate course on animal behavior.
2018	*Program Designer & Psychology Teacher* at **Summer School Junior Utrecht University, Utrecht, the Netherlands** I designed a psychology program for primary school students and gave lectures to 80 students at a time during a three week summer school.

REVIEWING

2025	**PloS One**
2024	**Animal Behavior & Cognition**
2023	**Journal of Comparative Psychology; Animals; Behavior**
2022	**Peer Community in Registered Reports; Applied Animal Behavior Science**
2021	**Mind & Language** (Collaborative Peer Review)

PUBLICATIONS

Brooker, J. S., **Goldsborough, Z.,** van Leeuwen, E. J. C., Kordon, S., Webb, C. E., & Clay, Z. (*in prep*). Reassuring body contact promotes social tolerance in bonobos and chimpanzees.

Goldsborough, Z., Crofoot, M., Jacobson, O., Corewyn, L., del Rosario-Vargas, E., León, J., and Barrett, B. J. (2025). The Rise and Spread of a Social Tradition of Interspecies Abduction. *Current Biology,* 35, R1-R3. doi: 10.1016/j.cub.2025.03.056

Fox-Rosales, L. A., Monteza-Moreno, C. M., Barret, B. J., **Goldsborough, Z.,** Jansen, P. A., McLean, K., & Crofoot, M. C. (2024). Niche expansion of capuchin monkeys to forest floor on guild-reduced islands increases interspecific spatio-temporal overlap. *Biotropica*, 56(3), e13315. doi: 10.1111/btp.13315

Goldsborough, Z., Crofoot, M. C. & Barrett, B. J. (2024). Male-biased stone tool use by wild white-faced capuchins (*Cebus capucinus imitator*). *American Journal of Primatology*, 86(4), e23594. doi: 10.1002/ajp.23594

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Van Leeuwen. J.C., **Goldsborough, Z.** (2023). What animal cultures may beget: Comment on "Blind alleys and fruitful pathways in the comparative study of cultural cognition" by Andrew Whiten, *Physics of Life Reviews*, 44, 99-101. doi: 10.1016/j.plrev.2022.12.010

Goldsborough, Z., Sterck, E. H. M., de Waal, F. B. M., & Webb, C. E. (2022). Individual Variation in Chimpanzee Repertoires of Abnormal Behavior, *Animal Welfare*, 31(1), 125-135. doi: 10.7120/09627286.31.1.011

Goldsborough, Z., Webb, C. E., de Waal, F. B., & van Leeuwen, E. J. (2021). Zoo-housed female chimpanzee adopts local female-specific tradition upon immigrating into a new group, *Behavior*, 158(6), 547-564. doi: 10.1163/1568539X-bja10075

Goldsborough, Z., van Leeuwen, E.J.C., Kolff, K.W.T., de Waal, F.B.M. & C.E. Webb (2019), 'Do chimpanzees (*Pan troglodytes*) console a bereaved mother?', *Primates* 61: 93-102. doi: 10.1007/s10329-019-00752-x

Goldsborough, Z. (2017), 'The Effect of Visitor Density on the Behavior of Two Siberian Tigers (*Panthera tigris altaica*) Housed in a Zoo Enclosure: A Case Study', Reinvention: an International Journal of Undergraduate Research, BLASTER 2017, Special Issue

Goldsborough, Z. (2016), 'The Question of Cetacean Culture', Ad Astra, University College Roosevelt Undergraduate Journal, Issue 11

SCIENTIFIC COMMUNICATION

2024	**The Atlantic** (American Magazine). *Do Animals Know That They Will Die?* **RedaktionsNetzwerk Deutschland** (German News). *Katzen, Elefanten, Elstern: Wie auch Tiere traurern* **N+1** (Russian Newspaper). Самки белолицых капуцинов с острова Хикарон отказались использовать инструменты.
2021	**DeMorgen** (Belgian Newspaper). *Chimpansee kopieert gek loopje om erbij te horen* **Volkskrant** (Dutch Newspaper). *Chimpansee kopieert maf loopje om erbij te horen* **KidsWeek** (Dutch Children's Newspaper). *Chimpansees apen elkaar na om erbij te horen* **Radio1 BE** (Belgian National Radio Station). *Interview on article about chimpanzee copying local custom.* **National Geographic.** *Why chimpanzee moms are so much like our own* **ZieZoo** (Magazine of Royal Burgers' Zoo). *Zijn na-apers onder chimpansees succesvollere nieuwkomers?* **El Español** (Spanish Newspaper). *¿Qué piensan los animales de la muerte?: por qué el duelo no es exclusivo de los seres humanos*
2019	**NRC** (Dutch Newspaper). *Chimpansees troosten moeder van doodgeboren aapje* **DeMorgen** (Belgian Newspaper). *Chimpansees troosten moeder na miskraam*

SKILLS

Languages: English (fluent), Dutch (fluent), German (proficient)
IT Skills: SPSS, R, Excel, Word, PowerPoint, ELAN, BORIS
Interests: Writing, literature, hiking, film, statistics, nature

Appendix 1 to § 6 General Provisions of Doctoral Regulations

Affirmation in Lieu of Oath

1. The doctoral thesis on the topic

stone tool use by white-faced capuchin monkeys

is entirely my own work.

2. ☒ I have used only the sources and aids indicated, and have not received assistance from unauthorized third parties. In particular, texts or ideas that were obtained from other works have been identified as such.

3. ☒ My work does not copy or paraphrase any text passages or other content generated by an AI tool.

   ☐ If I have used text-generating AI tools as **aids**, I understand that I am solely responsible for the accuracy of the content of the AI-generated text passages and other AI-generated content, as well as for referencing other people's wording and ideas in accordance with the principles of good scientific practice. I have used AI tools as described below.

(If necessary, please use additional insertion sheets!)

4. ☐ The work or parts of the work ~~have already been~~/have never been [1] submitted to an institute of higher education in Germany or abroad as part of an examination or qualification procedure.

Title of the work:

Institution of higher education; year:

Type of examination or qualifications procedure:

5. ☒ I hereby affirm that the above statements are true and correct.
6. ☒ I am aware of the significance of the affirmation in lieu of oath and the consequences under the penal code of giving an incorrect or incomplete affirmation in lieu of oath.

I hereby affirm that I have stated the truth to the best of my knowledge and have concealed nothing.

Konstanz, 24.04.2025

place and date
(signature)

[1] **Delete as appropriate. If the work has already been submitted, complete the fields indicating the title of the submitted work, the institute of higher education, the year in which it was submitted, and the type of examination or qualification procedure**