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Behavioral Flexibility and Cognitive Performance in Macaques

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Behavioral Flexibility and Cognitive Performance in Macaques

By

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Dedications & Acknowledgements

Mom

The first person I'd like to dedicate this written labor of love to is my late mother, Jane. As long as I can remember, my mother has been my best friend and biggest cheerleader. As a kid she encouraged me to embrace my individuality with quirky style choices and lengthy literary writings and poems expressing my trials and tribulations. I grew up as an only child, with my mother and I as a thick team of thieves against the world. Although shy and observant at first, when it was just me and Mom, or a small group of friends, I'd stand on my milk crate soapbox to happily tell my story to anyone who cared to hear. Mom was always front and center, listening intently and cheering me on.

As I got older, the cheering never faded. I could always count on Mom to attend a flute recital or softball game (often raucously cheering in the stands), in her fashionably late style. Throughout my upbringing she incessantly reminded me of my unique beauty, character and intelligence. Me getting high marks throughout school had her beaming with pride and boasting across town. She eagerly encouraged me to go away to college and take advantage of all opportunities of interest that became available. Despite all my world adventures that came afterwards and took me to faraway (and sometimes dangerous) places, she always pushed me to "enjoy the experience" and "get out of dodge". In hindsight, I greatly respect this as I know it must have been hard to watch her only child repeatedly fly off into the "great unknown" to study monkeys and see the world.

In addition to blindly supporting all my passion-driven decisions to study science in far flung places, Mom also taught me some very valuable life skills that have contributed to my success and are worth mentioning here in brief. First, she taught me to keep my wits about me - always assume you're in a New York City subway at 2AM and know where your exits are. She also taught me essential professional skills such as how to iron a suit, starch a shirt and shine my shoes. From her days as a legal assistant in NYC, she passed on her ability for high attention to detail and flawless copyediting that I emulate to this day. However, when she wasn't diligently working, she also taught me how to let loose and cut a rug on the dancefloor, with classic moves like the cha-cha and the mashed potato. Finally, she taught me that the best things in life require risks. She was a firm believer in manifestation, and the ability to accomplish anything you set your mind to, and I have used this practice for years to accomplish my goals. Visualizing and following the breadcrumbs through the open doors of opportunity leading to those outcomes is by far the most important strategy she has taught me in my lifetime, and I am forever grateful. Thanks Mom, for all your support and love that shaped the person I am today and will forever be into the future.

Dad

Although my father is a man of few words, I'd like to take some time here to acknowledge his immense influence on me in reaching this milestone in my scientific career and life at large. Undoubtedly where my scientific curiosities blossomed, my father always gently nudged me towards learning about the natural world around me. It was he who gifted chemistry science kits and proposed home-made physics experiments and even got me science-related games for our Windows 95 home office computer. Although my mother grew up in the city, my father was more of a country boy, and helped to foster my deep appreciation for the outdoors that continues to grow to this day. Some of my earliest memories include my father carrying me to the top of some of the highest peaks in the Catskill Mountains on his back before I could hardly walk. As I got older, we would camp overnight in lean-tos and stargaze as he told me about the chemistry and physics of how these balls of light came to be. With the arrival of freezing temperatures on the mountaintop, he would remind me of how fickle water is as it drastically changes its behavior and transforms into snow. He taught me to value quality gear and bundle up to enjoy the cold weather and icy or wet East-Coast ski conditions. This outdoor experience undoubtedly served me well as I went on to conduct fieldwork in remote locations across the world.

As I grew up, my father motivated me to strive for educational prowess by incentivizing achieving the highest honors at school. He also taught me some of the toughest albeit useful lessons regarding self-discipline and strong work ethic. He'd remind me that if you keep trying and practicing, that you can do anything. He has always been, and likely will always be the moral compass by which I judge my actions. I deeply respect him and am honored to be his daughter. Thanks for always supporting me Dad, even when I wanted to run off to the jungle and you feared I might never return and finish graduate school.

Victor

I could write pages and pages about how great Victor Santiago Jr. is, but for the purposes of finishing up this thesis in a timely fashion, I will keep it short and sweet. Not only has Vic been there throughout the many ups and downs of this dissertation journey, but he has remained undoubtedly supportive. Despite the many times I left for months on end to chase my dreams of studying monkeys in the jungle or foreign cities, he has always had my back and welcomed me home with open arms. Whenever I was crunching for grant deadlines, exams or big presentations he always supported me by giving me space to get my best work done and kept me nourished (and hydrated) at times when I was so engrossed in my task that I could barely come up for air. The little surprise notes of encouragement and conversations over tea when I would take a break from writing my thesis are some of my most cherished memories. At times when I was stressed or working a little too hard, Vic would remind me to take a break and be good to myself. Thanks for reminding me to slow down when I would get wound too tight. Finally, Victor is an incredibly talented and innovative engineer. Without his expertise, the construction of the puzzle boxes for my experiments would have been undoubtedly inferior, and I thank him immensely for his consultation. I look forward to collaborating in the future, both in life and love. Thanks Vic, for being my best friend, and I look forward to all the new chapters we'll open together in the future.

McCowan Lab

When I joined the McCowan Laboratory for Welfare and Conservation in late 2015, I packed up all my earthly possessions and drove across the country to start my first "real job". I traveled 3,000 miles to the California National Primate Research Center (CNPRC) in Davis, California where I met my new co-workers, some of whom have become cherished life-long friends (#iykyk). I am particularly grateful for those in the lab who helped mentor me during my first year as a research assistant as I prepared for graduate school applications and assessed my fit here at UC Davis, including Darcy Hannibal, Jessica Vandeleest, Brianne Beisner, Krishna Balasubramaniam, Stefano Kaburu and Pascal Marty. I am also incredibly grateful to countless staff members, animal care technicians and behavior staff, and research staff at the CNPRC whom I have worked with and learned from over the years. Above all else, I'd like to thank and acknowledge the fearless leader of our lab, Brenda McCowan. Thank you, Brenda, for all your support and encouragement over the years, it has been a true pleasure working with you. I couldn't have asked for a better major professor, and I look forward to continuing our work in the future.

Animal Behavior Graduate Group & Davis Family

Prior to applying to the Animal Behavior Graduate Group, I was intimately aware of the program and had lofty dreams of perhaps studying in California one day. When the opportunity came to fruition to apply under Dr. Brenda McCowan, I was ecstatic. I distinctly remember during interviews some faculty expressing disbelief after I had revealed that I hadn't applied to any other programs or schools. I was all in, UC Davis or bust. Since joining the Animal Behavior Graduate Group, I have grown incredibly as a scientist and become a deeper thinker due to the interdisciplinary and collaborative nature of our community. Not only are the students and faculty approachable, inclusive and supportive but many of them are top candidates in their field and work with innovative cutting-edge technologies or methods. In addition to all the amazing friends I have met through the ABGG and affiliate programs, I am particularly grateful for all of my academic mentors, including members of my academic qualifying and dissertation committees: Justine Smith, Sarah Benson-Amram, Damien Caillaud, Karen Bales and Andrew Sih. Thank you for shaping my research questions and challenging me to be a better scientist.

Abstract

Cognitive ecology investigates how interactions with the environment shape the cognitive abilities of organisms. Studies on humans have emphasized that cognition is selected for under specific environmental conditions to extract information efficiently. More recently this approach has been applied to animals and focuses on how variation within the environment shapes the evolution of cognitive systems. Animals may use certain behavioral styles or cognitive traits to adapt to the amount of variability and predictability in their environment. Variation in resources and environmental complexity are two major factors that drive the diversity of cognitive adaptations seen across animals, as these are often beneficial for specific conditions or allow for adjusting to novel or changing conditions. For example, animals who experience displacement due to rapid urbanization may benefit from enhanced cognitive abilities and/or behavioral flexibility to adjust to those environmental changes quickly.

Combining cognitive and urban ecology is particularly interesting because animals often need to consider both predictable and unpredictable elements of human behavior to survive. While many animals can capitalize on the predictable elements of human behavior in the urban environment by avoiding direct interactions with humans, those who can capitalize on more unpredictable sources of variation, such as opportunistic provisioning, may gain an advantage in environments where this type of variation exists in substantial quantities. One way that animals may capitalize on these benefits is by exhibiting traits such as reduced neophobia, enhanced problem-solving abilities, and behavioral flexibility. These traits would allow them to access a wider variety of food resources available in urban spaces and may provide significant fitness advantages.

This dissertation explores several aspects of behavioral flexibility ranging from specific, technical quantifications of an individual's flexibility to solve foraging problems to more holistic or general strategies that individuals may adopt in foraging contexts. Combining experiments from the field and captivity, I explore how individuals innovate (i.e. solve a new problem or apply an old solution to a new problem) and whether they are flexible in their problem-solving behavior. For both the cognitive experiments and behavioral observations, I focused on two closely related species of macaques, rhesus

(*Macaca mulatta*) and long-tailed (*Macaca fascicularis*). By combining these approaches, I explore both the proximate mechanisms of behavioral flexibility through induced innovation as well as the natural manifestations of flexibility in female foraging behavior. Together, these projects quantify inter-individual differences in foraging behavior and extractive foraging abilities, as well as the role of individual traits in those abilities. Further, these studies provide important insights on the differences in foraging strategies for individuals living in complex and uncertain environments. These insights may be important for understanding the effects of rapid human-induced environmental change and how animals cope with those changes through behavioral diversity and problem-solving.

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I. Introduction

All organisms face similar daily challenges: find food, find mates, yet avoid predators and competition. Behavioral ecology is the study of how of organisms interact with each other within their environment to balance these challenges. Theoretical frameworks based upon ecological principles can allow scientists to make predictions about how organisms should behave. In most biological models, the organism's goal is to maximize benefits and minimize costs (optimal foraging model: Charnov, 1976; individual choice models: Stephens, 2008; Marshall et al., 2012). These costs may be associated with the level of risk in the environment. An organisms' level of risk-sensitivity or impulsive behavior can influence how individuals or populations interact with their environment (Dingemanse et al., 2010; Stephens, 1981). These models predict that individuals should prefer non-risky options if they can acquire enough energy to survive. However, individuals will become more risk-prone once they cannot obtain enough energy using risk-aversive strategies. These responses depend on the quality of information available to the organism as well as the sampling rate of individuals. Individuals must balance the costs and benefits of sampling with the level of predictability in environmental information (Dall et al., 2005), which will influence which cues animals attend to (vervet monkeys: Teichroeb & Chapman, 2013). If the environment is unpredictable, organisms should not rely on sampling because future information is likely unreliable. However, if the environment is predictable, then organisms should rely on sampling as it may provide advantages in future encounters (blue jays: McLinn & Stephens, 2006). These concepts have been useful to predict how species with different levels of risk sensitivity survive in different habitats, especially those that experience higher levels of human disturbance (Short & Petren, 2008; Rehage & Sih, 2004).

It has been proposed that these patterns of predictability may select for cognitively demanding, yet advantageous abilities, such as learning. The learning of associations between objects in the environment, for example, should be selected for if it provides a fitness advantage to individuals within their lifetime (Dunlap & Stephens, 2009). The recent integration of traditional foraging theories from behavioral ecology with cognitive science has resulted in the new field of cognitive ecology. Combining these perspectives has been useful in developing predictions about lifestyles that organisms who experience different levels of environmental predictability may adopt. For instance, species that live in predictable environments may be more risk-averse and more selective specialists for resources such as food or habitat. Similarly, those environmental conditions may select for animals that adopt a more residential lifestyle rather than a migratory one (Mettke-Hofman, 2014). However, organisms that live in variable environments may be more risk-prone, more generalists and better colonizers of novel environments. The adaptive flexibility hypothesis suggests that individuals at different stages of the invasion front colonizing new environments are likely to show variation in behavioral flexibility, where those at the edge of the front are more likely to show higher levels of flexibility (Wright et al., 2010). Others have suggested that the combination of flexibility and enhanced cognitive abilities are likely to be adaptive under these invasive conditions (Szabo, Damas-Moreira, Whiting, 2020). Overall, less predictable conditions may select for organisms to adopt certain traits such as tool-use or food-caching to survive unpredictable food shortages (Mettke-Hofman, 2014). Thus, predictability and uncertainty of environmental variables are two crucial components influencing how individuals should make foraging decisions.

In addition to environmental complexity, there have been several other proposed mechanisms to explain how cognition evolved. A main hypothesis is the ecological intelligence hypothesis, which states that food distribution and the difficulty of procurement has largely shaped cognitive abilities in organisms (Reviewed in Pravosudov & Roth, 2013; Rosati, 2017). For example, in primates terrestriality (Heldstab et al., 2016; Meulman et al., 2012) and seasonality (Melin et al., 2014) have been indicated as influential factors in the evolution of complex foraging extraction abilities. Alternatively, the social intelligence hypothesis proposes that cognitive traits have been shaped by group selection pressures and the ability to keep track of individual attributes (Whiten & Byrne, 1988; Whiten & van Schaik, 2007; Seyfarth & Cheney, 2015). Although many of the studies that explore mechanisms of cognition only address one of these hypotheses at a time, organisms need to cope simultaneously with ecological and social challenges, and cognition is likely selected for by some combination of the two (Cunningham & Janson, 2007).

However, cognition can also be constrained by phylogenetic traits such as body size or lifespan (van Schaik & Deaner, 2003). The cognitive buffer hypothesis states that organisms with shorter lifespans or time to maturation have fewer opportunities to build upon experience to solve complex problems, which may select against costly cognitive traits (Sol, 2009; van Schaik & Deaner, 2003). Thus, enhanced cognitive abilities can be adaptive for organisms depending on phylogenetic constraints as well as the physical or social constraints in their environment. Regardless of the mechanism, it has been shown that an individual's cognitive traits can influence parameters related to fitness proxies or outcomes, making it a useful variable to consider and quantify (body condition: Huebner, Fitchel & Kappeler, 2018; mating effort: Keagy et al., 2009, 2011; reproductive success: Cole et al., 2012; competitive ability: Cole and Quinn, 2012).

Models suggest that food unpredictability drives both generalism in dietary choices and social foraging (Overington, Dubois & Lefebvre, 2008). When food sources are unpredictable, generalism is favored so individuals can rely on a variety of food items instead of a select few. Similarly, social foraging is also favored under these conditions since living in social groups provides advantages such as increasing the likelihood to find food patches. However, group-living also imposes potential costs such as intraspecific competition. When individuals live in social groups, they must balance their individual energetic needs with the costs and benefits associated with social foraging. The producer/scrounger foraging model is an example where individuals must choose to either adopt the strategy of producer, where you actively go out and search for food, or you play scrounger and use social cues from producers to find food (Giraldeau & Dubois, 2008). Foragers who act as producers will gain an advantage to arriving at a food source first by receiving a finder's share (Bitetti & Janson, 2001). The evolutionary stable strategy (ESS) for this game is a mix of producers and scroungers, where the proportion of the two varies with increasing group size. While generalism is not affected much by group size, the tendency to act aggressively and group size are positively correlated. These individual asymmetries can be incorporated into game theoretic models, such as the hawk/dove game, where the hawk represents the aggressive phenotype and the dove represents the shy phenotype (brown capuchins: de Waal & Davis, 2003).

Although all social foragers must balance the predictability of resources with overall social foraging costs and benefits, sex differences in foraging strategies are common. These differences stem from sexual selection and the imbalance that exists between male and female reproductive investment, such as the production of gametes (Bateman, 1984). This theory posits that since males can produce many small gametes which are energetically cheap, they are mostly restricted by their access to fertile females. Alternatively, females produce relatively few large gametes which are energetically costly, causing them to be most restricted by access to food. Additionally, females often bear a large portion (if not all) of the responsibility of parental care, posing additional energetic costs which select for mechanisms of female mate choice (Queller, 1997). Furthermore, these energetic costs for females vary significantly across different phases of reproduction, with lactation posing the highest costs due to the production of milk and infant-carrying effort (Dufour & Sauther, 2002; Thompson, 2013).

Attributes such as social rank can determine an individual's amount of social interference when foraging, which in turn determines their energetic reserves. These dynamics can explain how individuals make choices about joining patches, where low-ranked individuals prefer patches without dominants present (Rands et al, 2006). This social interference poses energetic costs on individuals due to extended travel bouts in search of suitable food patches. These individual energetic costs can constrain overall group size, where larger groups will only travel to patches that can feed all their members sufficiently (Grove, 2011). Furthermore, an individual's likelihood to adopt a strategy of either producer or scrounger is based, at least in part, on individual energy reserves (Lendvai et al., 2004). Incorporating energy reserves or proxies for energy intake into models that explore decision making (Stephens, 2008) in foraging contexts are both relevant and lacking.

Thus far, the influence of stability and predictability on the behavior and cognitive traits of organisms has been discussed extensively in terms of natural environmental variation. However, habitat disturbances such as urbanization can alter known biological patterns or phenomena, as well as the stability and predictability of those systems. Wildlife may be influenced by human behaviors that are both predictable (reliable food subsidies: Oro et al., 2013) and unpredictable (persecution/trapping: Horrocks & Baulu, 1988; Williams et al., 2011). Thus, organisms that live in urban environments must cope with indirect alterations to naturally occurring environmental variation as well as the direct effects of human activities. In this way, urban ecosystems, unlike natural ecosystems, are driven both by biological and human social processes. While modern studies seek to combine these variables into an integrated framework addressing coupled human-natural systems (CNHS framework: Morzillo, de Beurs & Martin-Mikle, 2014), most urban ecology studies have focused on changes to natural biological phenomena, such as local temperature adjustments (urban heat island) and precipitation patterns (Battles & Kolbe, 2019; Han, Baik & Lee, 2014). These abiotic changes can then influence biotic factors, such as the rate of primary plant production (Buyantuyev & Wu, 2009), as well as the distribution of primary (lizards: Battles & Kolbe, 2019) and secondary consumers (coyotes & foxes: Moll et al., 2018). In fact, the level of urbanization has been shown to influence the distribution of both specialist and generalist species (birds: Devictor, Juillard & Jiguet, 2008). Environmental modifications induced by human activities have widespread and pervasive effects spanning from the individual up to the community level. For wildlife to live in areas with high human disturbance, they must employ strategies to cope with these altered conditions. One mechanism for organisms to cope with rapid environmental changes is through behavioral flexibility. Behavioral flexibility is defined as when an organism can adjust their behavior to match current environmental conditions. Since natural selection requires genetic changes over generations, behavioral flexibility can provide advantages by allowing organisms to respond to rapid environmental changes within their lifetime. Traits like behavioral flexibility are often selected for in organisms that experience high levels of unpredictability (woodpecker finches: Tebbich & Teschke, 2014). Some organisms need to deal with natural unpredictability, such as extreme weather patterns (eg. Madagascar cyclone season: Dunham, Erhart & Wright, 2011) while other organisms may need to also deal with unpredictability associated with urban environments and human behavior. In fact, organisms that live in urban environments may experience more environmental heterogeneity and/or more dynamic and rapidly changing disturbances compared to many natural systems (Donihue & Lambert, 2015).

Organisms who inhabit urban spaces must deal with both the social dynamics of their own group mates, as well as the social behavior of humans. These dynamics are arguably very different, since individuals interact with their groupmates repeatedly, while they may only interact with a particular human as little as a single encounter. However, it can be argued that foragers may need to make similar decisions concerning the risks and benefits of engaging with humans to acquire food (or joining a food patch at the risk of receiving aggression). However, under these circumstances' organisms may use different information or cues to make these decisions, since they may not know the individual attributes of humans, such as rank. For example, studies on interactions between humans and monkeys show that male monkeys are more likely to initiate interactions with women and children (often in attempts to acquire food), while male humans are more likely to initiate interactions with male macaques (often in retaliation or giving aggression) (Fuentes & Gamert, 2005). Locals and tourists alike enjoy feeding free-living monkeys, including long-tailed and rhesus macaques. In highly urban areas, these acts of provisioning can make up a large portion of the monkey's diet and can have profound effects on their behavior (Jaman & Huffman, 2013). Monkeys may opt to avoid direct human contact and instead feed on human refuse. By adopting this strategy, monkeys can acquire human foods without the potential risks of interacting with humans, such as receiving aggression or incurring injuries (Dickman, 2012). It has been shown that increased tourism can increase infant mortality. These risks can be attributed to increasing the levels of interspecific aggression at provisioning sites (Berman et al., 2007), and it can be argued that infants may incur potential risks of being near humans by receiving aggression or incurring injuries themselves. Thus, to meet the varying energetic demands that females face across their reproductive cycle, they may employ different strategies to acquire high energy human foods depending on the amount of risk posed to themselves and their dependent infants.

One way to measure behavioral flexibility is through cognitive performance. We can give animals puzzles to see how they solve them, to get a glimpse at how they figure it out. Induced innovation is an experimental technique to measure an animal's response to a novel problem. During this process we can measure aspects of behavior that may reflect behavioral flexibility, such as behavioral diversity while solving. Many scientists have shown the importance of this measure of exploratory diversity in how animals solve foraging problems in a variety of species (raccoons: Daniels et al., 2019; spotted hyenas: Benson-Amram & Holekamp, 2012; elephants: Jacobson et al., 2021; lions & snow leopards: O'Connor et al., 2022), albeit with mixed results as to the directionality of the effect. Some studies found that higher levels of exploratory diversity resulted in greater success of solving the puzzle (Daniels et al., 2019; Benson-Amram & Holekamp, 2012), while others found that lower levels of exploratory diversity led to higher success in solving (Jacobson et al., 2021) or no relationship at all (O'Connor et al., 2022). Clearly more research is warranted for comparative studies to ascertain the role of exploratory diversity in behavioral flexibility processes leading to innovation success.

Although gathering information on innovation tendencies may be informative for the study of behavioral flexibility, it does not measure flexibility directly. A more classic test used to measure behavioral flexibility is the reversal learning paradigm. In this paradigm, the animal learns an association between two stimuli, after which the association is removed, and the animal is tested on their ability to inhibit their previously learned successful response in search of a new solution. Individuals who incur fewer errors are considered more flexible. These behavioral tendencies to inhibit previously successful responses while exploring new objects likely facilitates their ability to solve a wider variety of foraging puzzles in the urban space to gain access to new sources of food.

Problem-solving abilities as well as the level of risk sensitivity of individuals have also been linked to variation in risk present in the urban environment (common mynas: Sol et al., 2011). Nowak et al. (2017) found that Samango monkeys (*Cercopithecus mitis*) would venture into riskier urban habitats in search of food during periods of low natural food availability. A follow-up study with the same population showed that individual responses to novel objects depended upon whether the items were found in the risky urban environment, or the safe forested environment (le Roux, Mathibane & Nowak, 2019). In other species, populations that have had more exposure to humans have in some instances shown complex cognitive abilities such as tool-use or enhanced problem-solving (Luncz et al., 2017; van de Waal & Bshary, 2010). One such study tested foraging extraction abilities in bonnet macaques (*Macaca radiata*) and found that urban groups are more likely to solve foraging extraction problems than rural groups (Mangalam et al., 2013). Another study found a significant influence of provisioning by humans on the frequency of 'sophisticated' solving techniques in bonnet macaques (Pal et al., 2022). However, in some cases human disturbance has been shown to have a negative effect on primate behavioral diversity and tool-use (long-tailed macaques: Gumert, Hamada & Malaivijitnond, 2013; chimpanzees: Kühl et al., 2019). Although the links between environmental predictability, cognitive abilities and the urban environment are only beginning to be investigated, it is evident that individuals who can employ different strategies, and exhibit flexibility, may confer significant fitness advantages. The following chapters explore the influences of the urban environment on foraging and problem-solving in wild macaques, as well as how individual traits influence flexibility and problem-solving in captive macaques.

II. Objectives & Research Questions

Using theoretical frameworks from behavioral and cognitive ecology, I investigated the role of individual variation in behavioral flexibility and cognitive performance in macaques. In Chapter 1, I analyzed observational data from a long-term dataset on two species of macaques (*Macaca mulatta* & *Macaca fascicularis*) to test for evidence of behavioral flexibility in an urban ecosystem. Specifically, I studied how females adjust their activity budgets and interactions with humans during stages of reproduction that face different energetic requirements and risks. In Chapter 2, I used field methods to conduct cognitive experiments on two free-ranging groups of long-tailed macaques (*Macaca fascicularis*) analyzed in Chapter 1. During these experiments, we induced innovation with several objects, including both familiar water bottles and a novel puzzle-box to test individuals' problem-solving abilities. In Chapter 3, we expanded these studies on innovation to testing captive rhesus macaques (*Macaca mulatta*) with a multi-solution box to measure their flexibility to inhibit previous responses using a modified reversal learning paradigm. In all chapters, I investigated the influence of individual traits on the outcomes of interest (behavior or cognitive performance). Altogether, my dissertation addresses the following research questions: **(Ch. 1)** How do females adjust their behaviors based on perceived costs or benefits in their environment? **(Ch. 2)** How do individual traits or within trial behaviors influence solving **(a)** familiar or **(b)** novel problems? **(Ch. 3)** How do individual traits or within trial behaviors influence solving multiple novel problems, and does inhibition of previous responses predict repeated innovation?

III. General Methods

i. Study Species

The genus *Macaca* is the most geographically widespread among all nonhuman primates, with the largest habitat and behavioral diversity within and across species. Macaques are distributed mainly throughout South and Southeast Asia, with one exception species residing on either side of the Strait of Gibraltar (Fooden, 1982). Based on genetic data, the genus *Macaca* can be ordered from ancestral to more recently evolved lineages, and categorized into three distinct groups: *silenus*, *sinica* and *fascicularis* (Hoelzer & Melnick, 1996). The traditional theory for the evolutionary distribution of macaque species was driven by interspecific competition for resources (Fooden, 1982). This theory has been recently reviewed and outlines how species-specific behavior or personality may influence the likelihood of a species to invade and persist in new areas or habitats (Capitanio & Mason, 2019).

However, additional theories have outlined how other variables such as climatic changes have influenced the dispersal behavior and distribution of macaques (Abegg & Thierry, 2002). These models posit that while some species are more ancestral and restricted in their ranges, such as the lion-tailed (*M. silenus*) and Sulawesi (*M. nigra*) macaques, species of more recent lineages such as long-tailed macaques (*M. fascicularis*) were able to disperse further during favorable glacial periods and widely expanded their ranges (Abegg & Thierry, 2002). This proposal was based upon the preference of the long-tailed macaque for riverine, edge habitats which may have facilitated dispersal via sea-rafting to other landmasses including many islands within the Indonesian archipelago. In fact, the fascicularis lineage which includes long-tailed macaques, has the most continuous distribution of all the lineages, from the moderately temperate climates of Japan (*M. fuscata*), Taiwan (*M. cyclopis*), and Afghanistan (*M. mulatta*) to the tropical habitats of Indonesia (*M. fascicularis*).

While macaque species' distributions have been largely attributed to socioecological variables, there are other phylogenetically constrained traits that group similarly behaved species within the genus (Thierry, Iwaniuk & Pellis, 2001). These 'social styles' of macaques allow species to be categorized by characteristics of their social behavior such as the steepness of the dominance hierarchy or levels of reciprocity (Petit, Abegg & Thierry, 1997). Most species can be placed among these four categories that grade species of macaques on a scale from egalitarian (Grades 3 & 4) to despotic (Grades 1 & 2). Egalitarian species are characterized by low hierarchy steepness, and high levels of reciprocity, while despotic species show the opposite, high steepness and low reciprocity.

Interestingly, some theories have even proposed that macaques' phylogenetic relationships fall short of explaining certain traits shared among macaque species, such as their ability to live near humans, describing certain species as "weed species" (Richard & Goldstein, 1989). Although this idea is not new, this area of research has been left relatively unstudied. More recently, primatologists have begun to stray from the traditional ideals that many behavioral ecologists hold, which is that "natural" behavior must only be assessed in "natural" or "undisturbed" environments. Instead, scientists have begun to embrace that by studying how animals live in both natural and disturbed habitats we can gain a better understanding of species-specific tendencies for living under novel conditions and dealing with environmental change. Recently, scientists have called for a systematic quantification of these effects on primates to understand these patterns and their implications for primate behavioral diversity (McKinney, 2015).

Despite all the theories that have been proposed to categorize macaques based on different characteristics, there are some traits that all macaques share. All macaque species live in multi-male, multi-female groups which are structured by a matrilineal society (Thierry, Singh & Kaumanns, 2004). Macaques are polygamous, but the level of mate-guarding and monopolization potential can vary by species (long-tailed macaques: Girard-Buttoz et al., 2014; assamese macaques: Schülke, Heistermann &

Ostner, 2014) and parameters such as group size (Nunn, 1999). Males are the primary dispersers, although some female dispersals have been rarely observed (Thierry, Singh & Kaumanns, 2004). The degree of sexual dimorphism across primates is determined, at least in part, by the availability of fertile females (Mitani, Gros-Louis, Richards, 1996). Although all macaque species show sexual dimorphism, the severity is relatively mild compared to other genera due to lower monopolization potential over fertile females (Plavcan, 2002). All macaques are omnivorous and generalists considering their wide range of food items in their diet (Fa & Lindburg, 1996). However, certain populations may specialize on certain foods if they are abundant locally. For example, an alternate common name for long-tailed macaques is "crab-eating macaques", since coastal populations are often found feeding on crustaceans and mollusks (Gumert & Malaivijitnond, 2012).

For the projects outlined in this dissertation, I will focus on two species of macaques: rhesus and long-tailed. I chose these species because they have two of the most widespread distributions of all extant non-human primates (Abegg & Thierry, 2002) and live under a variety of environmental conditions. Both species are well known urban adapters and motivated extractive foragers, making them great candidates for studies of urban ecology and behavioral flexibility. They both derive from the *fascicularis* lineage and are graded more despotic than other species (Grades 1 & 2) and thus should have similar behaviors. Rhesus macaques are found throughout Asia, with most of the population inhabiting India or China. Long-tailed macaques are found in southeast Asia including countries such as Malaysia, Thailand, Indonesia, and the Philippines (Figure 1). Portions of the rhesus macaque range experience freezing temperatures in the winter such as in the northern mountains of India, while in the more southern regions they can have warmer temperatures in the dry season. While the majority of rhesus habitat is landlocked, long-tailed macaques are instead restricted to highly coastal areas or islands, and as a result have been observed to use tools to feed on shellfish.

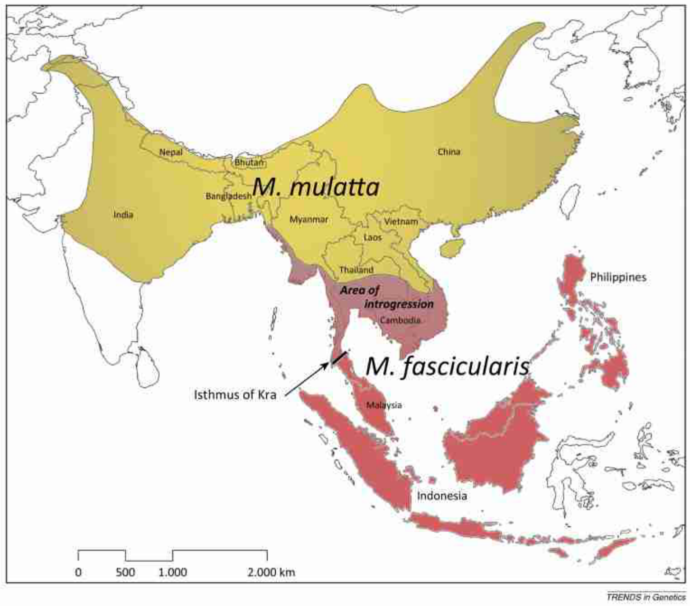


Figure 1. Natural distribution of rhesus (*Macaca mulatta*) and long-tailed (*Macaca fascicularis*) macaques (Haus et al., 2014).

ii. Study Sites & Long-term Dataset

The McCowan lab established several field sites in 2016 and studied multiple species of macaques abroad for several years (Northern India: Kaburu et al., 2019; Southern India: Balasubramaniam et al., 2020; Malaysia: Marty et al., 2019). For chapter 1, I use the long-term behavioral dataset collected at these field sites to explore questions regarding behavioral flexibility in urban macaques. These behavioral observations are then paired with cognitive assessments of innovation in chapter 2 with two groups from a single site in Malaysia. Each respective section provides more detail on what data were used per chapter from this long-term study.

This dataset is from a large behavioral study on urban macaque behavior that was conducted between 2016 - 2018. The project included two species, rhesus macaques (*Macaca mulatta*) in India and long-tailed macaques (*Macaca fascicularis*) in Malaysia. In each country the team set up two different sites that varied in the level of human interaction, with the aim of one site being described as “moderate” and the other as “high”. Within each site we studied several social groups of resident macaques. Teams collecting data in each location rotated observations evenly across sites to ensure similar levels of observation time per location and per group. The sites in India were both located in the city of Shimla

(31° 05′ N–077° 10′ E), where humans and macaques interact frequently at temple and shopping areas. Both sites in Shimla experience high levels of human disturbance. However, the nature of interactions was different at each site, where Jakhoo Temple experienced positive and negative interactions with macaques associated with the temple, while at Mall Road there were predominantly negative interactions with macaques associated with food stealing in the market areas. The sites in Malaysia included both an urban tourist park called Templar Park (3°17′58″N, 101°37′08″E) and a Buddhist temple called Batu Caves (3°14′14″N, 101°41′02″E). Templar Park is located just north of Kuala Lumpur in a forested area and is characterized as moderate in terms of human disturbance due to inconsistent waves of human attendance in large volumes, whereas Batu Caves is located within the city limits and is characterized as high disturbance with more consistent human attendance in high volumes. Both sites experience both positive and negative interactions between macaques and humans due to provisioning and stealing. However, the steep limestone cliffs and stairs leading to the temple at Batu Caves provides more opportunities for concentrated interactions, resulting in more negative interactions with humans including stealing and aggression.

In chapters 1 and 2, I used the long-term dataset to investigate how individual attributes may drive individual differences in behavior and problem-solving ability. Individual attributes for these chapters were either observed (i.e. Sex of the individual) or were calculated using the long-term dataset. General calculations for individual attributes from the long-term dataset are described in the respective chapters where they are used.

IV. Chapter 1: Behavioral Flexibility and Foraging Strategies

Introduction

One major question in behavioral ecology addresses how individuals make foraging decisions. Optimal foraging theory has provided a framework for scientists that considers both the risks and rewards of exploring the environment for food versus exploiting a given known food patch. It predicts that individuals should maximize their benefits when foraging (such as choosing high quality items) and minimize their costs of foraging (such as handling time). Although this framework provides a good starting place for understanding the optimal decision-making processes of foraging, it is often too simplistic and lacks many variables that may influence animal behavior. For example, in urban environments where wildlife must consider both natural and artificial processes, these foraging models seem to lack an entire layer of complexity. In urban spaces, wildlife need to be aware of both natural environmental shifts (such as seasonality affecting food availability) as well as acute temporal changes in human behavior (such as peak times of tourism) since direct interactions with humans can impose both rewards (such as acquiring preferred human foods) and risks (such as receiving aggression or incurring injuries from humans). Thus, we can use the optimal foraging model in combination with our current knowledge in urban ecology to make predictions about how wildlife may make foraging decisions in human dominated areas. Based on the literature we know that wildlife can interact with humans differentially based on their age/sex class (long-tailed macaques: Fuentes & Gamerl, 2005; Formosan macaques: Hsu, Kao & Agoramoorthy, 2008), some species can steal and barter with humans to receive specific food items (long-tailed macaques: Brotcorne et al., 2017), and some wildlife can even remember or interact differently with specific humans based on their prior experience (crows: Marzluff et al., 2010; horses: Proops et al., 2018) These studies provide evidence that wildlife can quickly adjust their behavior and even learn new strategies to exploit human food resources that allow them to thrive in urban areas. However, very little is known about the mechanisms that drive foraging flexibility in wildlife living in urban spaces.

Foraging decisions could also be heavily sex dependent due to competing goals or investment stemming from sexual selection theory. Due to the female's inherent larger investment in offspring (i.e. larger egg size, more infant care), there is an expectation that their behavior may be driven by schedules of offspring care to maximize female fitness. Alternatively, for males there is often a significantly smaller investment in offspring (i.e. smaller sperm size, less infant care), and as a result we expect that their behavior may be driven by different schedules than females. These differences in investment may also coincide with physiological changes reflecting different reproductive phases or strategies. For example, males often lose weight during breeding season when they are focused on acquiring a female mating partner (rhesus macaques: Bernstein et al., 1989; mouse lemurs: Wrogemann, Radespiel & Zimmermann, 2001). For females, physiological demands substantially vary across their reproductive cycle, where females experience the highest physiological strain during lactation when they are nursing an infant compared to when they are pregnant or cycling (Dufour & Sauther, 2002). Indeed, some females even experience lowered immune function and slower wound healing during times of high energetic need such as lactation (baboons: Archie et al., 2014). In fact, even the act of carrying infants can impose additional energetic costs on females during lactation periods when compared to male counterparts (Altmann & Samuels, 1992). The timing of physiological changes for males and females can depend on either the synchrony of group mating behavior or individual female cycling schedules (i.e. pregnant, lactating, or cycling). Additionally, the level of sexual dimorphism in a species can further influence differences in energetic needs across males and females (Key & Ross, 1999). In highly dimorphic species, the energetic requirements of females may be more equivalent to males due to an increase in male body size. However, species with low sexual dimorphism may result in females experiencing greater energetic requirements due to an increased energetic load due to pregnancy and lactation despite sharing similar body sizes as male counterparts. Thus, sex is an important consideration when predicting how individuals may make foraging decisions.

Most studies that investigate behavioral changes across the female reproductive phase focus on broad categories such as the entire lactation, pregnancy or cycling period. These reproductive phases are often calculated by using the average gestation or lactation time for the species from the literature or the sample population. Only a handful of studies break those phases into smaller categories such as the early or late states of lactation and pregnancy (Rangel Negrin et al., 2021; Touitou et al., 2021; Dunham & Rodriguez-Saona, 2018; Gould et al., 2011; Cano-Huertes et al., 2017). However, some studies report female behavior in even more specific time frames such as per month or per week (Maestripieri, 1999; Dias, Rangel-Negrin & Canales-Espinosa, 2011; Bardi et al., 2001). This variation in the definition of reproductive categories can make comparisons across studies challenging. Nevertheless, certain patterns have emerged in the current research on female behavioral changes across reproductive phases such as changes to activity budgets, feeding behavior, and overall energy balance. Across non-human primates, some species were found to be less active during lactation phases compared to either pregnancy or cycling phases (ring-tailed lemurs: Gould et al., 2011, mantled howlers: Rangel Negrin et al., 2021; black howlers: Dias, Rangel-Negrin & Canales-Espinosa, 2011), while others were found to be less active during lactation and pregnancy compared to cycling phases (spider monkeys: Ruvio, Stone & Fienup, 2017; white-faced capuchins: Rose, 1994).

Feeding behavior across primate species varies both in the amount of time dedicated to feeding across phases, as well as shifting the rate of feeding or selecting different food types across phases. Many species switch to feeding on more fruits and protein sources during lactation compared to during pregnancy or cycling phases when they may instead rely on a more fiber-rich diet (spider monkeys:

Ruvio, Stone & Fienup, 2017; mantled howlers: Rangel Negrin et al., 2021; Mexican howlers: Serio-Silva, Hernández-Salazar & Rico-Gray, 1999; Assamese macaques: Touitou et al., 2021). Despite switching to different food types across phases, females across species show a general pattern of feeding less during lactation compared to pregnancy or cycling periods (siamangs: Lappan, 2009; vervet monkeys: Harrison, 1983). In fact, some studies show that females fed less specifically during early lactation compared to later stages of lactation or other phases (assamese macaques: Touitou et al., 2021; black and white colobus: Dunham & Rodriguez-Saona, 2018; ring tailed lemurs: Gould et al., 2011). Some studies suggest that reducing both your foraging rate and switching food types across phases may allow females to maximize their foraging returns by choosing foods with lower handling times and/or higher nutritional qualities (white-faced capuchins: Rose, 1994; chimpanzees: Murray et al., 2009). Alternatively, even if females are not adjusting their overall foraging time, or switching to alternative food types, females may address their increased energetic needs during lactation by increasing their foraging intake rate, thus increasing their energy intake (white-faced capuchins: McCabe & Fedigan, 2007). Additionally, adjustments to foraging behavior may be a response to changes in food availability and interact with the physiological constraints of reproductive phases and behavior. For example, in mantled howlers feeding and resting behavior were influenced by an interaction between reproductive phase and food biomass, where cycling and gestating females spent more time feeding than lactating females when food availability is higher, and cycling females spent less time resting than gestating and lactating females when food was more available (Cano-Huertes et al., 2017). Although females may experience physiological constraints imposed by their reproductive cycle, they may be able to adjust their behavior to fit their energetic needs depending on the availability of food in the environment.

Both individual physical constraints on behavior as well as group-level interest in newborns entering the group can influence changes to social behavior across reproductive phases. For example, during the later stages of pregnancy females are experiencing some of their highest energetic burdens, and as a result are often observed withdrawing from social activities in their group (japanese macaques: Bardi et al., 2001; pig-tailed macaques: Maestripieri, 1999). This social isolation may persist into the early stages of lactation as the mother spends a large portion of her time attending to her highly dependent offspring and has less time to engage in interactions with conspecifics. However, an alternative pattern in may emerge given that the birth of infants can pique interest from other females in the group and result in a flurry of interactions surrounding new mothers, usually in pursuit of getting near the newest infant members (spider monkeys: Ruvio, Stone & Fienup, 2017). This interest in newly born infants can be driven by a female's reproductive condition, where either following an infant loss during lactation, or during the onset of pregnancy females show a higher infant interest potentially stemming from regulatory hormones (pig-tailed macaques: Maestripieri & Wallen, 1995).

Many studies control for additional environmental variables that may influence female foraging behavior but may not be of primary interest, such as seasonality or dominance rank. Seasonality is important to control for when measuring energetic requirements because it can influence food availability and thus constrain foraging behavior regardless of differing energetic requirements across reproductive phases (e.g. colobus monkeys feed less during the dry season compared to the wet season; Dunham & Rodriguez-Saona, 2018). Consistent seasonal constraints on feeding behavior are likely to select for strictly seasonal reproductive strategies where females can meet their energetic requirements of lactation when food availability is highest and most predictable. Additionally, for species that have strict dominance hierarchies, rank can greatly determine an individual's priority of access to preferred items or food resources. Considering the steep dominance hierarchies of macaques, rank is an important control variable for understanding changes in behavior across reproductive phases, particularly those regarding feeding behavior.

Among all the studies investigating behavioral shifts across female reproductive phases, very few look at the influence humans have on these behaviors in an urban environment. Only a few studies have investigated the effect of provisioning on behavior across female reproductive phases. In these studies, females who were provisioned more often showed higher levels of urinary C-peptide, which is a measure of pancreatic function and energetic correlates, compared to times when they did not receive food hand-outs from humans (chacma baboons: Fürtbauer, 2020). Additionally, the nature of the provisioning interaction could influence an animal's response, or propensity to participate in the provisioning event. For example, a provisioning event where food is distributed over a large area may pose a lower threat to individual participation than an event where food is highly concentrated in a smaller area, due to the relationship between monopolization of food resources and competition in animal social groups. Thus, provisioning on a more acute scale, where humans are handing out foods directly to individual animals may make those individuals targets for aggression, particularly if they are lower in the dominance rank order, resulting in differing costs and benefits for individuals within the urban environment (Marty et al., 2019). Despite the obvious benefits of receiving food handouts from humans, there are also some potential costs that animals may be considering when making foraging decisions. For example, sometimes direct interactions with humans can result in negative interactions for wildlife such as receiving aggression and/or being the target of weapons (i.e. slingshot, rocks, sticks). Females may be particularly vulnerable to these costs during the early stages of lactation, when their infants are highly dependent and vulnerable to predation threats. Females may adjust their behavior in areas where they experience these threats imposed to their young infants. In urban areas, humans may pose predator-like threats as they often capture wild primates to be sold into the pet trade or consumed as bushmeat. Infants can either be targeted for these purposes because they are easier to handle, or they can be orphaned as a by-product of their mother being captured or killed. Thus, females may adjust their behaviors such to avoid risky interactions with humans during times when their infants are most vulnerable to predation. In fact, female vervet monkeys have been shown to interact with humans less during early lactation compared to other reproductive phases due to potential exposure to infant risk (Saj et al., 1999).

Objective:

Our study is an important extension of a traditional question of how females can flexibly adjust their behavior across reproductive phases, however, it is innovative in that we apply this framework to the more novel urban environment with rhesus and long-tailed macaques as study subjects. To investigate potential drivers of flexibility, we collected behavioral observations on two closely related species of macaques living in different climatic environments as well as at different intensities of human interaction. We chose rhesus and long-tailed macaques because they can be found in a variety of different environments and have shown high levels of foraging flexibility when faced with different environmental challenges (long-tailed macaques use tools in palm oil plantations: Luncz et al., 2017; long-tailed macaques use tools for coastal shellfish: Malaivijitnond et al., 2007; rhesus macaques open coconuts: Comins et al., 2011). In this analysis, we focus on the foraging decisions and overall behavioral patterns of females because their reproductive cycle provides a framework to investigate decision-making during phases in which females face different types of risks or challenges. We compare males to females to explore whether they experience similar behavioral changes (indicating a universal environmental variable they are responding to) or different behavioral changes (indicating sex-dependent behaviors). We hypothesize that infant risk will drive behavioral changes in urban female macaques with the expectation that those with younger, more vulnerable infants will reduce their interactions with humans compared to other time periods. Alternatively, the higher energetic demands of lactation could override infant risk, in which case we might expect an increase in human interactions to gain access to highly preferred human handouts.

Methods

Study Site and Subjects

Data were collected on a total of seven groups of macaques from July 2016 to February of 2018. These groups included two species of macaques, the rhesus macaque (*Macaca mulatta*) and the long-tailed macaque (*Macaca fascicularis*). Observations for rhesus macaque groups were conducted in the city of Shimla (31° 05′ N–077° 10′ E) at two sites separated by 1.5 km distance: Mall Road and Jakhoo. Mall Road is a busy road that runs through the city of Shimla and contains both residential and commercial buildings. Jakhoo is a Hindu temple situated on the highest peak of Shimla and is surrounded by a forested area. Data were collected from three groups, one from Mall Road, and two from Jakhoo (Table 1). Although both Mall Road and Jakhoo experience high volumes of human visitors, the interactions between humans and macaques are different across these two sites. On Mall Road, humans will often avoid macaques or express aggression towards them. However, in Jakhoo, a higher diversity of interactions between macaques and humans is observed surrounding the temple, including humans feeding the macaques, macaques stealing items from humans, and humans expressing aggression towards macaques.

Observations for long-tailed macaque groups were conducted in and around the city of Kuala Lumpur at two sites separated by 10 km distance: Batu Caves (3°14′14″N, 101°41′02″E) and Templar Park (3°17′58″N, 101°37′08″E). Batu Caves is comprised of a Hindu temple situated at the top of steep limestone formations and is a major attraction for tourists visiting the city. Templar Park is a recreational park in the rainforest north of Kuala Lumpur where people come to enjoy the area for hiking, picnicking, or swimming near a series of waterfalls. Data were collected from four groups, two from Batu Caves and two from Templar Park (Table 1). Although both sites experienced high volumes of human visitors at times, their attendance patterns could differ due in part to proximity to the city center and activities available. For example, Batu Caves had high volumes of humans visiting consistently (sometimes daily) to visit the temple grounds. On the other hand, Templar Park was often lightly attended during weekdays, but would fill up on weekends, holidays, and for special occasions for people to picnic and swim.

Species	**Location**	**Group**	**# of Females**	**# of Males**	**Obs. time (h)**
Rhesus macaque *Macaca mulatta* (Shimla, India)	Jakhoo	Ripped Ear	28	13	212.58
	Jakhoo	Hook	18	9	83.53
	Mall	Mall	17	7	203.41
Long-tailed macaque *Macaca fascicularis* (Kuala Lumpur, Malaysia)	Templar Park	Entrance	30	11	202.66
	Templar Park	Hulk	12	7	113.82
	Batu Caves	Pirate	19	6	127.42
	Batu Caves	Lip	19	15	15.09

Table 1: Demography of all study groups per species with total number of adult females, adult males, and observation time in hours.

Behavioral Data Collection

Behavioral data were collected by two teams led by S. Kaburu and P. Marty in India and Malaysia respectively, for a total of nine observers. Interobserver reliability was assessed by Cohen’s kappa as greater than 0.85 (Martin & Bateson, 1993). Observers collected behavioral data on all adults through focal animal sampling (Altmann, 1974) five days per week between 9:00 a.m. and 5:00 p.m. Focal samples were collected on each individual two times per week, balancing across morning and afternoon sessions. The order of focal animals was predetermined using a randomized list of individuals. Focal animal samples were of 10-minute durations where we collected continuous recordings of interactions with conspecifics as well as interactions with humans. Human-monkey interactions were defined as any behavior initiated by a focal individual towards a human, or by a human towards a focal monkey where they express a subsequent reaction (for a complete ethogram of macaque and human behaviors, see Kaburu et al., 2019, S1). Interactions between humans and macaques included displacements, aggression, provisioning, or neutral interactions such as approaches without displacements or humans taking photos. Conspecific interactions included dominance interactions, aggression, submission, affiliation, and grooming between monkeys. We also conducted scans at 2-minute intervals to collect information on the activity of the focal animal, their proximity to conspecifics and whether they were observed on a human or natural surface. Natural surfaces included non-manicured grasses, trees, rocks or rivers. Anthropogenic surfaces included anything that had been modified by humans, including mowed lawns, artificial structures, pavement, or artificially diverted rivers. When individuals were feeding on a scan, we also noted whether they were feeding on human or natural foods. Natural foods included local fruits or foliage from a nearby forested area. Anthropogenic (i.e. human) foods included anything that had been processed or provided by a human, including processed foods such as chips, cookies, and breads. Occasionally, humans would provision the monkeys with prepared foods or raw produce that was past its peak prime. A total of 958.58 focal hours were included in this analysis (Rhesus macaques: Males (211.39 hours), Females (288.39 hours); Long tailed macaques: Males (149.06), Females (309.97)).

Demographic data were collected daily on each group to document changing group dynamics such as the birth of new infants and the death or disappearance of individuals from the group. Individual injuries or health concerns were also noted, such as whether a female was observed to be cycling (ex. bleeding) or suspected to be pregnant (ex. late stage visible).

To calculate dominance ranks, we used dyadic interactions from the focal samples and supplemented with ad libitum sampling since dominance interactions were sparse. We recorded all displacements, submissions and agonistic dyadic interactions from a winner-loser matrix using the package 'Perc' in R (v4.0.4; R Core Team, 2021; Fujii et al., 2015). Hierarchies were calculated separately for males and females and ordinal ranks were scaled to account for differences in group size. This resulted in a rank matrix ranging between 0 and 1, where low values indicated low ranked individuals and high values indicated high ranked individuals.

Calculating Female Reproductive Phases

To calculate female reproductive phases, we used the demographic data on infant births to estimate durations of pregnancy and lactation. The average gestation period for both rhesus and long-tailed macaques is 165 days (Ardito, 1976), or roughly 5.5 months. Similarly, the average weaning period for both rhesus and long-tailed macaques is roughly 7 months (Reitsema, Patrick & Muir, 2016, Werner et al., 1980; Dang et al., 1992). To keep comparisons across phases consistent, we calculated the pregnancy phase and lactation phases to be six months long each. Since these phases are thought to have differences in energetic need and/or infant risk we split the pregnancy and lactation phases into early and late phases of three months each. This resulted in our final set of phases for comparison comprising of early pregnancy (hereafter EP), late pregnancy (LL), early lactation (EL), and late lactation (LL). To contextualize how often females interact with humans when they are not pregnant or lactating, we also calculated two control ("cycling") phases of the same three-month duration that flank the beginning of pregnancy and the end of lactation (PRE and POST respectively).

Calculating Seasonality

To assess the interdependency of female reproductive phases and other general time-based changes, seasonal categories were defined and compared to a female's reproductive phase. Broad seasonal categories were assigned based on the overall temperature and rainfall for a period of several months (ranging from 2-4 months per season). Seasons assigned were monsoon, post-monsoon, winter and summer (S2). Monsoon season is characterized by heavy rainfall on nearly a daily basis. Post-monsoon season is a period most characteristic of autumn, with low amounts of rainfall and a cooler temperature. Winter has cold temperatures often resulting in snowfall rather than rainfall, while summer has higher temperatures with low amounts of rainfall. Importantly, winter temperatures are only experienced by one of the species studied here, rhesus macaques. This is because of the high-altitude location of the study site, which experiences colder temperatures and snowfall rather than rainfall. Potentially due to this radical shift in climatic conditions across the year, rhesus macaques experience a more seasonal pattern in breeding and birthing, whereas long-tailed macaques who live in a lower altitude tropical climate experience breeding and birthing behavior more evenly across the entire year (Table 2, Figure 3). After testing for collinearity, it became clear that reproductive phase and season are moderately correlated ($\chi^2 = 79.51$, $p = 0.0004$, Cramer's V = 0.3; Figure 2). This is somewhat expected given that reproductive phases for some females can occur during specific times of year, which may or may not coincide with the onset of climatic season.

	Rhesus m.	*Long-tailed m.*
January	Post-Monsoon	Winter*
February	Post-Monsoon	Winter*
March	Monsoon	Summer
April	Monsoon	Summer
May	Summer	Summer
June	Summer	Monsoon
July	Summer	Monsoon
August	Summer	Monsoon
September	Monsoon	Monsoon
October	Monsoon	Post-Monsoon*
November	Monsoon	Post-Monsoon*
December	Post-Monsoon	Post-Monsoon*

Table 2. Seasonal cutoffs for both species included in this study, rhesus and long-tailed macaques. An asterisk indicates the annual breeding season for rhesus macaques.

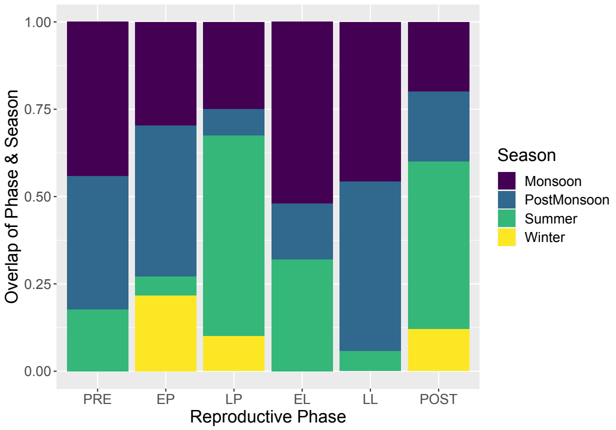


Figure 2. Proportional graph of reproductive phase and overlap with climatic seasons. Reproductive phases included pregnancy (EP, LP), lactation (EL, LL), and cycling phases (PRE, POST).

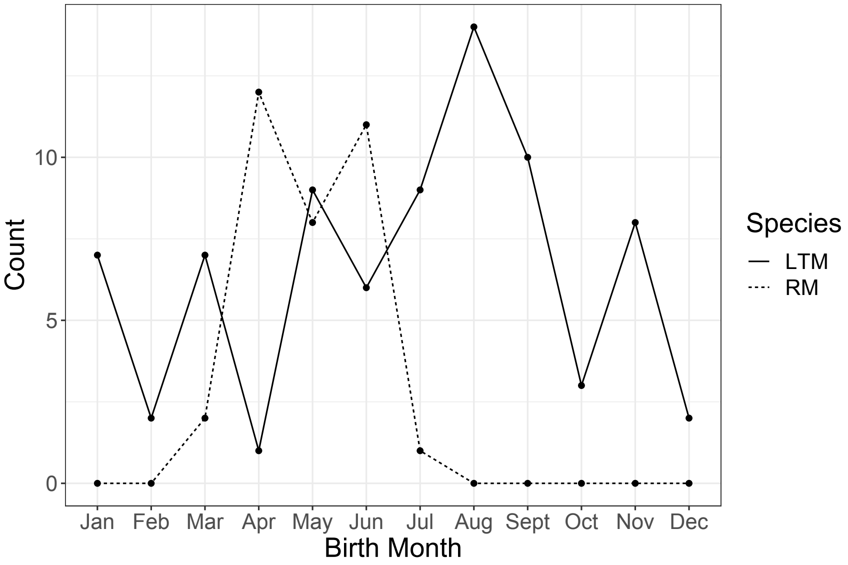


Figure 3. Birthing data for both species included in this study, rhesus and long-tailed macaques, and their distribution across months in a year. The y-axis represents the number of infants born per month of the year on the x-axis.

Female Selection Criteria

Females eligible to be included in this study were adults who had sired an infant during the study period. Females who did not sire an infant during the study period were excluded from the analysis because they may not have sired an infant due to multiple reasons that are difficult to disentangle without supplementary hormonal data. For example, some females may not have been mature enough yet to bear an infant (ex. subadult females) or it was unclear if there were additional confounding reasons the female was not reproductively active (ex. due to older age or potentially invisible abnormal cycling events). Due to this, our ability to conduct a between-subjects design was severely limited. Instead, we adopted a within-subjects design and calculated PRE and POST periods as a type of "control" for our reproductive phases of interest.

If a female in our sample gave birth to an infant during the study period, then the reproductive phases were calculated and assessed for inclusion eligibility. A female's reproductive phase was eligible for inclusion if (a) it included at least 10 focal samples and (b) it did not coincide with a visible abnormal cycling event (ex. bleeding, stillborn, young infant death). The choice of a minimum of 10 focal samples per phase was determined based on a reasonable break in the observation time per phase per individual, which showed that most individuals meeting other eligibility criteria would be included (For Females: 230 out of 311, or 74% of phases included with a minimum threshold of 10 focals, compared to 69% and 62% when removing phases with 11 and 10 focals respectively, S3).

Due to the long observation period (20 continuous months), there were some instances where a single female was observed to have given birth to more than one infant during the study period (N=20). For these females, an inter-birth interval was calculated and the expected overlap between reproductive phases was assessed (S4). In our population we observed on average a 16.3 month inter-birth interval for long-tailed macaques (N=18), whereas rhesus macaques showed on average a 12.3 month inter-birth interval (N=2). In some cases, females who had shorter inter-birth intervals resulted in more overlap in the calculated phases. Since our calculated phases on either side of the birth lasted nine months (3 months for each phase), if a female gave birth to a second infant in less than 18 months since the inception of the first infant, this would result in a significant overlap of phases. Females who had known overlapping phases were excluded from the analysis due to their ability to introduce ambiguity associated with overlapping phases (N=13).

Male Selection Criteria

To assess whether reproductive phase is measuring behavioral changes specific to females (and not some other variable experienced by both males and females at the same site, such as seasonality), we chose males in corresponding groups and rank classes (low, medium, high) to serve as matched controls. Male matched control assignments to females were performed randomly within each rank category, and then manually adjusted to maximize the amount of overlapping observation time between males and females (N=43, S3). Reproductive phase labels were assigned to males based on the overlapping period of observation with the assigned female. A male's "reproductive" phase was eligible for inclusion if it included at least 10 focal samples and it corresponded with a female phase included in the analysis.

Statistical Analyses

We fitted generalized linear mixed models (GLMMs) to test our predictions with several outcome variables including interactions with humans and human objects, interactions with conspecifics and activity budgets. For these outcome variables we treated the total number of interactions with humans, the total number of interactions with conspecifics, and the activity budget category of feeding as count data and included the total observation time of each individual as an offset variable in the corresponding models. We also treated interactions with human objects, such as feeding on human food or being on a human surface, as count data and included the total time feeding or being on a human surface as the respective offset variables. These offset variables were included in the model to account for differences in observation time across individuals in the sample. All models used a negative binomial variance structure due to overdispersion in the variance of each outcome variable tested. Data were analyzed separately for males and females to define the influence of predictor variables by sex.

For each outcome variable we ran seven GLMMs (S5 for females; S6 for males). In each model we included 'Focal ID' nested within 'Location' as random intercepts to account for within-focal as well as within-site differences in exposure to human activity. For each model, we included either observation time or total time feeding or being on a human surface as an offset variable. All test models were compared to a null model, which only included the random factors and offset variables as the first model. In the second, third and fourth models we tested each of our predictor variables separately (phase, season, rank). Due to this collinearity, we did not include phase and season in any models together. To investigate potential interactions between these variables and an individual's rank order, we ran four additional models containing additive and interactive effects between rank and phase or season respectively.

Within each model set (and as a criterion for testing additional model sets), we used AICc scores to choose the 'best-fit' model (Burnham & Anderson, 2002; Burnham, Anderson & Huyvaert, 2011). Specifically, we compared univariate models to the corresponding 'null' model. For multivariate models, we compared them to their univariate correspondents since multi-variate models are more complex and less parsimonious than univariate models (Richards, 2005). In the results we report the 'best-fit' model from each set that had the lowest AICc score. A model was considered better fit than the null when its AICc score was lowered by at least two AICc points compared to the null. If two competing models were within two AICc points, then the simpler model was deemed the best fit. All significance levels were set to two-tailed p-values < 0.05. We analyzed the data in R using the 'lme4' (Bates et al., 2015) and 'glmmTMB' packages (Brooks et al., 2017).

Ethics and Approval Declaration

The protocols used in this study were approved by the Institutional Animal Care and Use Committee (IACUC) of the University of California, Davis (protocol # 20593). The research was performed strictly in accordance with the guidelines drafted in the protocol, which complied with the legal requirements of India and Malaysia. These protocol guidelines and regulations were designed in consultation with the Himachal Pradesh Forest Department and the Indian Institute of Science Education and Research Thiruvananthapuram in India, as well as the Universiti Putra Malaysia and Universiti Sains Malaysia in Malaysia.

Results

For all outcome variables we identified a single best fit model within the model set. This was either the model with just a univariate predictor which was significantly better fit than the corresponding 'null' model, or a multivariate model that was significantly better fit than the univariate model (S5 for females; S6 for males). For the female dataset, we analyzed 63 unique individuals, with a total of 221 phases across those individuals. For the male dataset, we analyzed 43 unique individuals, with a total of 131 phases across those individuals. We summarize the main findings from these best fit models for females and males by each outcome variable in Table 3.

Outcome	**Females** (N_{unique} = 63, N_{obs} = 221)	**Males** (N_{unique} = 43, N_{obs} = 131)
Human Interactions	Phase	Season
Conspecific Interactions	Phase * Rank	Season + Rank
Activity Budget: Resting	Phase + Rank	Season
Activity Budget: Locomote	Phase	Season
Activity Budget: Feeding	Phase	Season
Feeding on Human Food	Null	Season + Rank
Time spent on Human Surface	Phase	Null

Table 3. Comparisons of best fit models for interactions with humans and conspecifics as well as activity budgets and rates of feeding on human food or being on human surfaces for males and females.

Influence of Urban Environmental Factors on Reproductive Behaviors

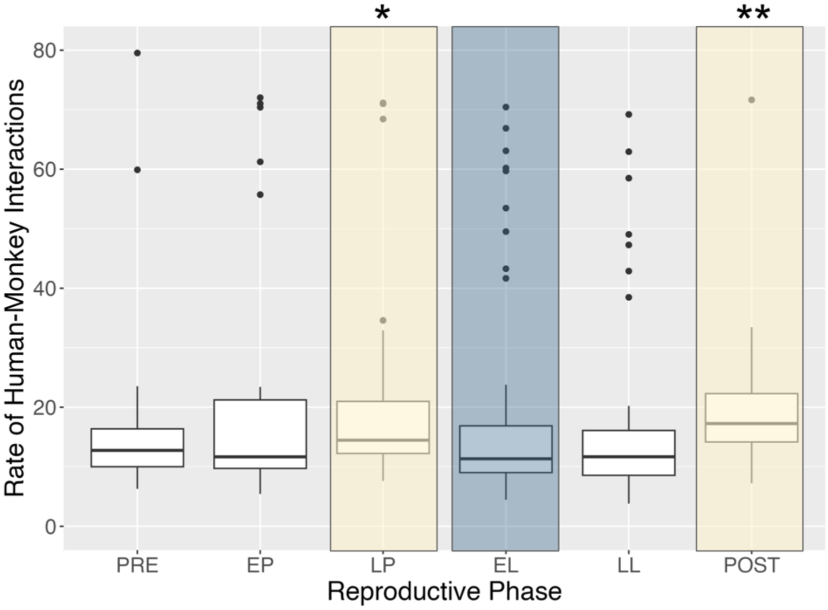


Figure 4. Rate of human-monkey interactions across female reproductive phases. The blue area is the referent category (EL = early lactation), while the yellow areas are those that were significantly different from the referent (LP = late pregnancy; POST= post-lactation cycling phase). A single asterisk above represents significance at an alpha level of 0.05, while a double asterisk is an alpha level of 0.01.

The best fit model for human interactions with females included a single predictor of phase (Table 3). Female macaques interacted with humans significantly more during pregnancy (EP & LP) and control phases (POST) compared to lactation phases (EL & LL) (EP β = 0.29, p = 0.052; LP β = 0.36, p = 0.015; POST β = 0.49, p = 0.006; S5; Figure 4). The best fit model for males included a single predictor of season (Table 3). Instead, male macaques interacted with humans significantly more during the winter season compared to monsoon season (winter β = 0.62, p = 0.015; S6). There was a similar trend for summer season, but it was not statistically significant (summer β = 0.29, p = 0.07; S6).

For females feeding on human food there were no predictors in our model set that produced a better fit model than the null. For males, the best fit model included both season and rank (Table 3; S6). Males fed significantly more on human food during the winter season compared to monsoon season (β = 0.51, p = 0.0006; S6). Males of higher rank were also significantly more likely to feed on human food than males with lower rank (β = 0.42, p = 0.008; S6).

For time spent on human surfaces, the best fit model for females included a single predictor of phase (Table 3). Specifically, females spent significantly more time on human surfaces during pregnancy (EP & LP) and control phases (PRE & POST) compared to early lactation (EL) (EP $\beta = 0.2$, $p = 0.001$; LP $\beta = 0.1$, $p = 0.04$; S5; Figure 5). Late lactation showed a similar, nonsignificant trend (LL $\beta = 0.1$, $p = 0.06$; S5). For males, there were no predictors in our model set that produced a better fit model than the null (S6).

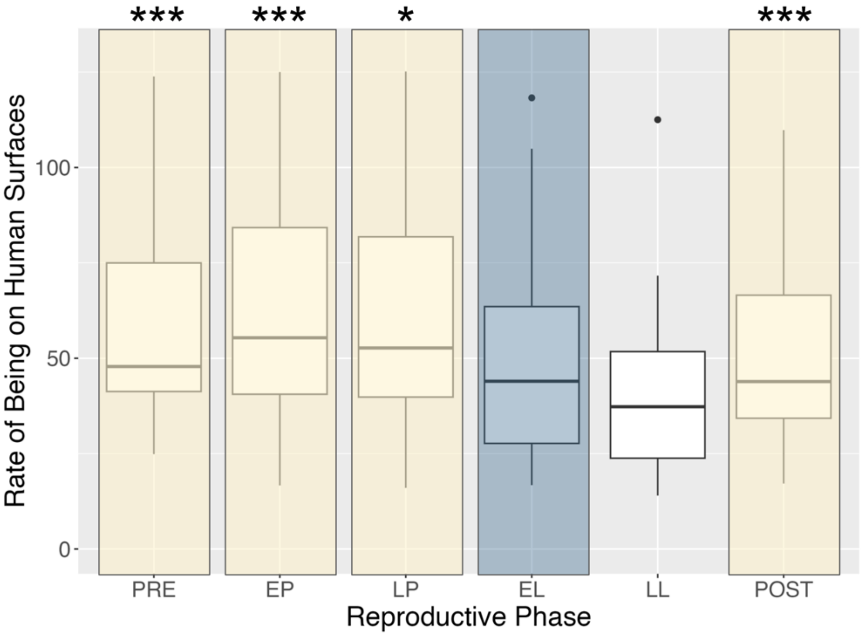


Figure 5. Rate of being on human surfaces across female reproductive phases. The blue area is the referent category (EL = early lactation), while the yellow areas are those that were significantly different from the referent (PRE = pre-pregnancy cycling, EP = early pregnancy, LP = late pregnancy; POST= post-lactation cycling phase). A single asterisk above represents significance at an alpha level of 0.05, while a double asterisk is an alpha level of 0.01, and a triple asterisk is an alpha level of 0.001.

Frequency of Conspecific Interactions

The best fit model for females included an interaction between phase and rank (Table 3, Figure 6; S5). That is, the frequency with which females interacted with conspecifics was modulated by their rank depending on the female's reproductive phase. We found a significant interaction effect between phase and rank where the influence of rank on phase was significantly lower for late pregnancy (LP) and control phases (PRE and POST) compared to early lactation (EL) (LP β = -0.6, p = 0.007; PRE β = -0.83, p = 0.0002; POST β = -0.74, p = 0.002; S5). There was a similar trend for early pregnancy (EP), but it was not statistically significant (EP β = -0.42, p = 0.068; S5).

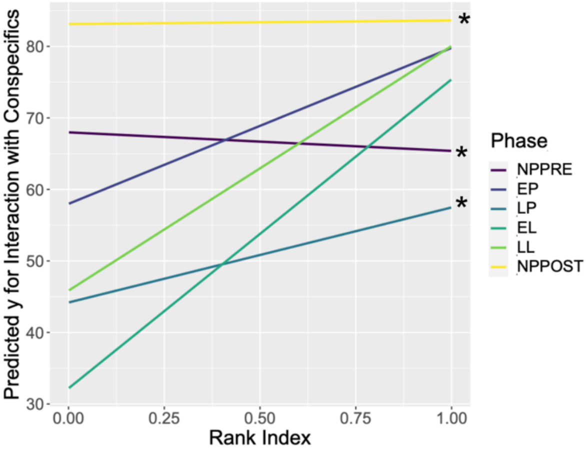


Figure 6. Interaction effect between reproductive phase, conspecific interactions, and rank index. A single asterisk above represents significance at an alpha level of 0.05.

The best fit model for males included both season and rank (Table 3; S6). Males interacted significantly more with conspecifics during the winter season compared to monsoon season (β = 0.45, p < 0.001; S6). Like females, males of higher rank were significantly more likely to interact with their conspecifics than males with lower rank (β = 0.32, p = 0.03; S6).

Activity Budgets

For all the behaviors in the female activity budget (feed, locomote, rest), the best fit model included a single predictor of phase (Table 3). Females spent significantly more time resting and less time locomoting or feeding (Figure 7) during early lactation (EL) compared to any other phase (EP, LP, LL, PRE & POST; S5).

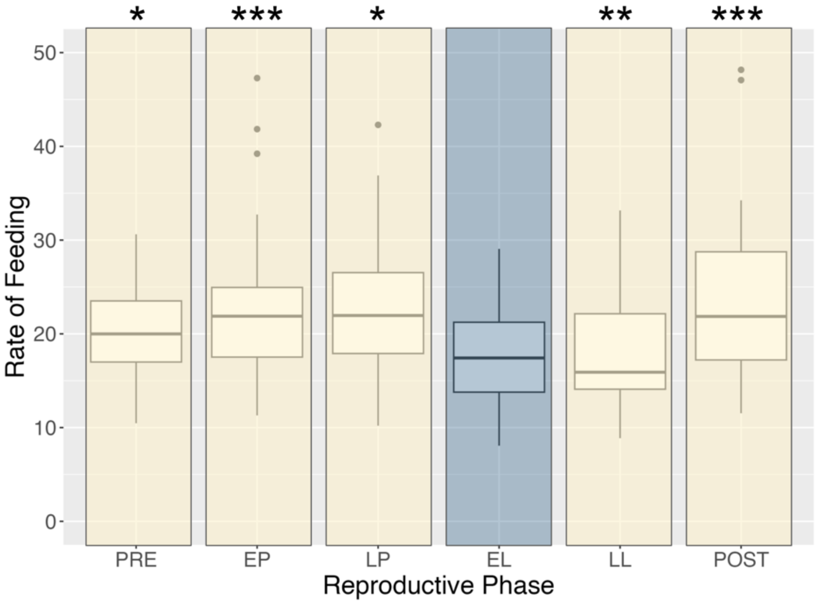


Figure 7. Rate of feeding across female reproductive phases. The blue area is the referent category (EL = early lactation), while the yellow areas are those that were significantly different from the referent (PRE = pre-pregnancy cycling, EP = early pregnancy, LP = late pregnancy; LL= late lactation; POST= post-lactation cycling phase). A single asterisk above represents significance at an alpha level of 0.05, while a double asterisk is an alpha level of 0.01, and a triple asterisk is an alpha level of 0.001.

For all the behaviors in the male activity budget (feed, locomote, rest), the best fit model included a single predictor of season (Table 3). Males spent significantly more time resting during monsoon season compared to winter or post-monsoon season (post-monsoon $\beta = -0.12$, $p = 0.002$; winter $\beta = -0.27$, $p < 0.001$; S6). Similarly, males spent significantly more time locomoting during monsoon season when compared with the summer season ($\beta = -0.26$, $p = 0.007$; S6). There was an opposite trend for post-monsoon season, but it was not significant ($\beta = 0.16$, $p = 0.075$; S6). Males were also observed feeding significantly more during the winter and summer seasons compared to the monsoon season (summer $\beta = 0.23$, $p = 0.013$; winter $\beta = 0.37$, $p < 0.001$; S6).

Discussion

Comparing Female and Male Behavior Across Reproductive Phases

Sex-dependent behaviors can reflect different strategies or priorities driven by differences in physiology or fitness. Females may be driven by offspring care schedules due to high reproductive investment, whereas males may be driven by access to mating opportunities due to female choice dynamics. In this study, we found that for nearly all behaviors explored, males were driven more by seasonality whereas females were driven more by reproductive phase. For females, this supports the idea that their behavior is dictated by either physiological needs associated with their reproductive cycle, the risks and benefits associated with offspring care schedules, or some combination of both. In the following sections we discuss the utility of exploring different behaviors (such as activity budgets and levels of interacting with the urban environment) to explore these effects and direct future research on the risks and benefits of female foraging in an urban environment. However, to truly assess the influence of energetics on these behaviors, future studies should combine observations of females across reproductive phases with physiological measurements of energetic load and expenditure, such as biological sample collection of C-peptide and/or cortisol.

The driver of seasonality for male behavior may be explained, at least in part, by the seasonal breeding nature of one of our study species, rhesus macaques. For males, many of the seasonal effects showed changes in behavior from the winter season compared to other phases such as monsoon or summer seasons. For rhesus macaques, the mating season spans across both the post-monsoon season and the winter season, with winter including the last two months of mating season (Table 2). When species show strict seasonal breeding, their behavior can shift to prioritize mating activities over other behaviors. For example, we found that males interact more with humans and conspecifics during the winter season compared to the monsoon season. This could in part be driven by an increased level of activity during the winter season, where males were found to rest more during monsoon season compared to post-monsoon and winter (which correspond with the breeding season). Additionally, males were found to feed more during the summer and winter seasons compared to monsoon season, which could either reflect increased energetic needs during the winter breeding season (perhaps due to an increase in activity) as well as increased food availability after the rainy season or an influx of tourists during the summer. Similarly, males were found to interact both with humans and conspecifics more during the winter seasons compared to monsoon seasons, potentially reflecting an overall increase in activity or engagement during the latter half of the breeding season. Like our results on females, there was a significant effect of rank on interactions with conspecifics, where high ranked males were found to interact more with conspecifics than low ranked males.

Female Behavior Across Reproductive Phases

There is ample evidence that females can adjust their behavior across their reproductive cycle, from their activity budgets to social interactions and interactions with the environment. Overall, females show reduced activity during times of high physiological or energetic requirements such as pregnancy and lactation periods when compared to cycling. This can result in females increasing their activity in preparation for these highly energetic times, when they are required to direct their energy either to the production of an offspring during pregnancy, or the care of that offspring through lactation and nursing. Our study corroborates these previous findings in that female macaques were found to be less active during the lactation periods compared to pregnancy or cycling periods. Additionally, females were also found to feed less during the lactation periods, particularly the early lactation period, compared to pregnancy or cycling periods. This suggests that females may “pack on calories” early during the pregnancy period to “ride out” the highly energetically costly period of lactation where they are constrained by carrying, feeding, and protecting their young and vulnerable infants.

Changes in female behavior across reproductive phases can also manifest socially in the frequency of interactions with other group members. For females we could expect one of two patterns to emerge. One is that females may withdraw from conspecific interactions during late pregnancy and early lactation by reducing their activity levels due to high energetic need and focusing their energy on maintaining and protecting their young infant. Another option is that females may experience a flurry of increased interactions with the birth of their newborn due to interest from other group members. In our study, we found that our best fit model for the rate of conspecific interactions included an interaction between phase and rank. This corroborates the literature suggesting that interactions with conspecifics vary across reproductive phases, where females interacted significantly more with conspecifics during pregnancy and control phases compared to lactation phases. This supports the social isolation hypothesis that females may be withdrawing from social interactions when they are focused on attending to their young and vulnerable infants. However, the effect of phase on rates of conspecific interactions was modulated by rank. That is, females with higher rank engaged with more conspecific interactions during lactation phases compared to females with lower rank. The effect of rank on phase became less influential for pregnancy phases and became negligible in control phases (Figure 3). This implies that not only does the reproductive status of females influence their interactions with conspecifics, but that the social status of the individual also plays an important role. One potential explanation for this is that occasionally low ranked females can be targeted for negative infant interest such as infant stealing and/or aggression. This may lead to low ranked females isolating more than high ranked females when they have young and vulnerable infants.

Influence of the Urban Environment on Female Reproductive Behavior

In urban areas natural food can be supplemented with human food sources and cause subsequent shifts in behavior. Sex and rank can influence an individual's access to human foods, with males and high ranking individuals gaining higher benefits (Marty et al., 2019). Additionally, sex can also influence how individuals interact with humans, with males interacting with humans more than females in a variety of ways, including a higher overall frequency of interactions, higher diversity or complexity of interactions, as well as higher likelihood of initiating interactions or exhibiting aggression towards humans (Balasubramaniam et al., 2020). However, rank can also play a role, where high ranked individuals are more likely to initiate interactions than low ranked individuals (Balasubramaniam et al., 2020).

Very little has been published on the effects of the urban environment on the behaviors of females across their reproductive phase and as a result leaves many elements to be explored. Our study provides novel information on female reproductive behavior for two highly successful urban adapters. From previous studies with other primate species, we know that provisioning from humans can increase the C-peptide levels of females compared to those who were not provisioned, thus providing an energetic incentive for females to come into proximity with humans to receive food handouts (Fürtbauer, 2020). Research on urban primate populations have shown that groups who experience high provisioning rates from humans can maintain activity and feeding rates similar to groups living in more natural areas that are not subjected to provisioning (white-faced capuchins: McKinney 2011). In fact, these patterns can persist even for individuals who may experience significant fluctuations in energetic need, such as lactating females (vervet monkeys: Saj et al., 1999). However, other investigations of activity budgets in urban compared to groups living in natural areas have shown differences in activity patterns, such as increased rates of grooming and play or object manipulation in urban groups (Jaman & Huffman, 2012). Despite the frequently observed provisioning at our field sites studied here we found that lactating females reduced their overall activity and feeding patterns compared to other reproductive phases. This suggests that the frequency, distribution, or overall rate of provisioning may modulate changes to female activity budgets. For example, provisioning can occur in urban spaces in a variety of ways, such as large dumps of food, or individual targeted handouts from humans. Furthermore, the frequency or consistency of these provisioning events may also influence shifts in subsequent urban animal behavior. We might expect that highly consistent, large provisioning events in urban spaces may lead to more homogenized activity budgets for females regardless of their reproductive phase, whereas provisioning that is more concentrated, opportunistic, or unpredictable such as direct food handouts from humans may not affect activity budgets as globally, and thus may maintain heterogeneous shifts in behavior across reproductive cycles. Further detailed research on the nature of provisioning and quantity of food being provisioned may better help tease apart the effects of provisioning on primate behavior in urban spaces.

Despite gross shifts in activity budgets, feeding behavior specifically has also shown to adjust depending on a female's reproductive phase. These adjustments include feeding on different food types across the reproductive cycle, such as feeding more on fruits or protein-rich foods during lactation and switching to a more fiber-rich diet during pregnancy or cycling (Ruvio, Stone & Fienup, 2017; Rangel Negrin et al., 2021; Serio-Silva, Hernández-Salazar & Rico-Gray, 1999; Touitou et al., 2021). One such shift in feeding behavior in the urban environment could include switching from natural food sources to more human ones. We might expect that if human foods help females more efficiently meet their energetic needs, due to a higher abundance of sugars or fats compared to natural foods (Moubarac et al., 2013), that females might preferentially choose those foods during times of higher energetic load, such as lactation, than during other phases of their reproductive cycle. However, the consistency and availability of human foods across the reproductive cycle would likely influence whether a shift from natural to human food is warranted. In our study, we found that the amount of human food females consumed did not change across phases in their reproductive cycle. This implies that females are not adjusting their dietary choices (at least based on whether it is natural or human sourced) across their reproductive cycle. Since females can access human foods both from direct human provisioning handouts as well as freely from refuse containers, this lack of adjustment across the reproductive cycle implies that human foods provide a consistent food source for females and may not necessarily represent variation in risks incurred by foraging in urban spaces.

Many studies on urban primates focus on food procurement and distribution since provisioning is considered a driving factor for attracting wild primates to urban areas. Aside from feeding on human foods, a first step in colonizing an urban area, or occupying an urban space is to be present adjacent to or directly on human surfaces. Most studies do not measure this separately from foraging efforts because being present on a human surface (such as lawns or trails maintained by humans, or man-made areas such as paved parking lots or structures) is often a requirement for feeding on human foods. However, teasing apart these variables may provide us with more information on how urban primates make decisions to occupy human-dominated areas in their pursuit of human foods. In our study, we found that lactating females spent significantly less time on human surfaces compared to pregnancy or cycling periods. This is fascinating because it elucidates a different pattern than what we found for feeding on human foods, which did not show changes across phases. This implies that willingness to spend time on human surfaces may put females at higher risks for direct interactions with people compared to simply feeding on human food, which once procured from a freely available refuse bin could be carried to a location further from risks associated with proximity to humans.

Conclusions & Future Directions

In conclusion, the reproductive status of females could be a key driver for human-wildlife interactions and result in alterations to their behavior. These behavioral adjustments could lead to a reduced fear of humans and increase the likelihood that dependent offspring are exposed to human-related risk factors, which could pose threats to their survival or fitness. For example, in dolphins it was found that females who were pregnant or lactating visited a human provisioning area more frequently than cycling females (Senigaglia & Bejder, 2020). The authors argue that these females may be exposing their dependent calves to human interactions at a critical age when they are most susceptible to behavioral conditioning. As a result, calves that have lots of experience with provisioning may show a diminished fear response of humans that could promote maladaptive behaviors such as begging that put them at increased risk of injury due to fishing line entanglements and boat strikes. Additionally, differential learning techniques for human food procurement could be driven by sex and reproductive phases in urban animals. For example, a study on free-ranging dogs in India found that both males and pregnant or lactating females consistently used a more sophisticated technique for opening a packet of food, as well as improved their food procurement performance over time, compared to cycling females (Mangalam & Singh, 2013). These results support the idea that higher energetic needs (such as those experienced in pregnancy and lactation) may facilitate a female's response to overcome risks associated with the urban environment to meet those energetic needs. Experimental studies on risk aversion in females across the reproductive cycle could provide us with crucial insights as to how females interact with novel elements of the urban environment.

For example, a captive study on vervet monkeys showed that females with young infants (> 6mo) took longer to approach a novel food container compared to females who had older infants (< 6mo) (Fairbanks & McGuire, 1993). All females with young infants showed caution, but those with older infants approached the novel food container in accordance with their dominance rank, with higher ranked individuals approaching sooner than low ranked ones. This elegant experimental study corroborates our results on macaques, showing that females adjust their interactions with novel (and potentially risky) stimuli based on the age, and vulnerability of their infants.

This study provided valuable information on how females adjust their behaviors across their reproductive phase in an urban setting. By comparing male and female behaviors, we were able to show that while male behaviors are mainly driven by seasons, female behaviors are mainly driven by their reproductive phases. Additionally, female macaques seem to show similar trends to other primates in that they reduce their time spent active and feeding during times of high energetic needs, such as early in the lactation period. Interestingly, females also showed changes in their interactions with both humans and conspecifics across phases. However, interactions with conspecifics, unlike interactions with humans, were also mediated by the females rank position. Finally, females were not shown to adjust the amount of time they spend feeding on human foods, but they did adjust how much time they spent on human surfaces by avoiding them early on in their lactation phase. Combined, these results imply that female behaviors are constrained by their energetic requirements, but they can also be adjusted based on human risks and benefits present in an urban area. Further studies would greatly benefit from a combination of behavioral and biological samples to tease apart the role of either energetics or behavioral flexibility on female behavior across the reproductive cycle.

V. Chapter 2: Problem-Solving and Innovation

Introduction

Innovation is an animal's ability to create new solutions or re-apply current solutions to a novel problem. Innovative behavior in animals has been historically restricted to anecdotal reports of individual idiosyncrasies that researchers found odd or interesting, which have frequently been related to foraging behaviors (potato washing in Japanese macaques: Kawai, 1965; coconut opening in rhesus macaques: Comins et al., 2011; milk top opening in great tits: Hawkins, 1950). Although this behavior is rare to observe in the wild (Reader & Laland, 2003), scientists have begun to study its mechanisms by inducing innovation (Reader, 2007), which requires presenting organisms with baited foraging puzzles and quantifying how they interact with and solve it. A new area of this kind of cognitive research assesses individuals in the wild using field experiments. There is evidence that innovation rates measured in captivity correlate with problem-solving ability in the wild, at least for some species (Webster and Lefebvre, 2001), making these experiments useful and relevant tests. In both birds and primates, innovation seems to correlate with relative brain size, providing evidence for this to be an indicator of cognitive abilities (Lefebvre, 2011). Thus, problem-solving has been adopted as a practice for measuring cognitive abilities and innovation success in wild animals across several taxa (birds: Griffin & Guez 2014; Sol, Griffin & Bartomeus 2012; mammals: Benson-Amram & Holekamp, 2012; Thornton &

Samson, 2012; Huebner & Fitchel, 2015). Innovation rates can also be assessed at the individual level, to reflect inter-individual differences in cognitive ability (Cauchard, 2013).

Reader and Laland (2003) predicted that several processes are important for innovation to occur: reduced responses to novelty (or risk perception), increased exploration, and behavioral flexibility. Individual risk sensitivities can be measured by neophobia – or the propensity of an individual to avoid a novel object. Individuals that are more risk-prone, and are more apt to approach a novel object, are considered more likely to innovate when encountering novel problems (Griffin & Guez, 2014). Similarly, individuals who are less neophobic, are more exploratory with novel tasks, which allows for more flexible behavior to incorporate new solutions. When individuals are exploring new problems, motor or exploratory diversity provides more variation for behavioral phenotypes. The more behaviors individuals can work with, the more likely they are able to come up with new innovative solutions. Thus, motor or exploratory diversity may represent one aspect of behavioral flexibility, since it allows individuals more behavioral options for exploring current and novel problems (Griffin & Guez, 2014). Several studies on innovation in animals have shown that increased exploratory behavior (as a measure of motor and behavioral flexibility) increased the likelihood of solving a novel task (spotted hyenas: Benson-Amram & Holekamp, 2012; racoons: Daniels et al., 2019). Further, it has been argued that measures of neophobia and neophilia (propensity to explore novel objects) are not inverses of each other, but instead may act as two separate traits that vary across individuals, lending support to measure both during individual responses to novel objects (Mettke-Hofmann, Winkler & Leisler, 2002).

Innovative behavior is thought to be adaptive when environmental conditions are highly variable, unpredictable or harsh (Sol et al., 2005a, 2005b; Mettke-Hofmann, 2014). An individual's propensity to innovate may predict its ability to survive once introduced into a novel environment (Sol et al., 2005). For example, foraging innovations may provide benefits such as accessing novel food resources. However, feeding on novel foods or taking time to solve novel problems can also incur costs such as increased predation risks (fish: Brown & Braithwaite, 2005) or poisoning (Sapolsky & Else, 1987), causing organisms to balance these tradeoffs in risky or unpredictable environments (Nowak et al., 2019). Since innovation is thought to be advantageous in unpredictable or variable environments, these traits have been proposed to be selected for in altered environments such as urban ecosystems.

Like many other cognitive abilities, attributes of individuals' may influence their ability to express behaviors such as innovation. For example, individuals without priority of access to preferred resources are those who might need to innovate the most. In primates, this is often low ranked or juvenile individuals (Laland and Reader 1999a, 1999b; Kummer and Goodall, 1985). Indeed, one study found that peripheral low ranked female hamadryas baboons were more successful with novel problems than central high ranked females (Sigg, 1980). In contrast, a meta-analysis on innovation in primates found that males and high ranked individuals have a higher incidence of innovation (Reader & Laland, 2001). This evidence suggests that rank may influence an individual's likelihood to innovate, although the relationship between the two remains unclear. For example, despite that rank determines an individual's access to preferred resources (Cole and Quinn, 2012), it does not necessarily lead to enhanced problem-solving abilities (Sigg, 1980). It is also entirely possible that individuals who are highly innovative may rise in social status to hold higher ranks, potentially as a result of reflecting a higher fitness potential through an ability to access limiting or challenging food resources. Ample plausible alternatives makes the mechanistic underpinnings of rank and innovation difficult to ascertain. Interestingly, it has been found that in birds, individuals who solve problems in captivity are less likely to engage in competitive interactions in the wild than those who do not problem-solve (Cole and Quinn, 2012). This implies that individuals with higher rank have little necessity for problem-solving, while lower ranked individuals benefit more from this ability to minimize competition with conspecifics (Aplin et al., 2013b; Thornton and Samson, 2012). Thus, despite species or population-specific responses, there may be individual differences in the drivers for cognitive abilities within groups.

A major component that cognitive studies must account for is the motivational state of the organism being tested. An individual's propensity to engage in a novel problem or foraging task is largely determined by their motivation. Persistence, or the amount of time an individual is actively engaged with a cognitive task, is one way of assessing specific task-directed motivation, which may reflect food related motivation or species specific ecologically relevant tasks (Day et al., 2003). Studies focusing on inter-individual differences have shown that persistence contributes to individual success in solving novel problems (Benson-Amram and Holekamp, 2012; Thornton and Samson, 2012). Aside from task directed motivation, there has been little evidence for a relationship between problem-solving and other measures of motivation, such as body condition or other independent behavioral measures (Cauchard et al., 2013; Bokony et al., 2013). Regardless, motivation is crucial to consider and test for, if possible, to account for individual differences and their potential contribution to problem-solving ability.

The majority of what we know about animal cognition comes from captive studies. Captivity provides a high level of control necessary for experiments requiring complex protocols, providing logistical advantages. However, it has been argued that many captive studies are too restricted and would benefit from the incorporation of natural complexity, such as the addition of competitors (Hare, 2001). A recent review emphasizes how testing individuals in social settings may be more ecologically relevant and even improve captive welfare for subjects (Cronin et al., 2017). A recent radiation of new techniques has focused on how to test cognitive abilities of free-ranging individuals in the wild (Benson-Amram & Holekamp, 2012; van de Waal et al., 2010). Although these experimental protocols can be logistically more challenging than captive ones, they provide several advantages for studying the evolution of cognitive traits. First, wild testing is more ecologically relevant than captive testing as individuals may need to balance cognitive performance with other challenges such as social interactions or predation pressure (Hare, 2001). Second, wild testing is voluntary for the subject, compared to in captivity where subjects are often involuntarily brought to an unfamiliar testing area. However, even when using wild experimental protocols, testing should be informed by a behavioral systems approach- where cognitive processes are viewed from the organism's perspective (Domjan, 2005), and problems are designed to be ecologically relevant for the study species (Healy, 2012).

Most studies on wild innovative behaviors have been conducted on birds or primates, however recently this has expanded to testing other mammal species (Lefebvre, 2011). While several studies on birds have formally investigated how habitat disturbances (such as urbanization) influence an animal's ability to innovate (great blue tits: Preiszner et al., 2017; Tebbich & Teschke, 2014) in primates there has only been a few studies (bonnet macaques: Mangalam & Singh, 2013; Pal et al., 2022; Samango monkeys: Le Roux, Mathibane & Nowak, 2019). In recent years, assessments of cognitive abilities of urban compared to rural populations of wildlife have been very useful to test questions at the intersection of cognitive and urban ecology. For instance, cognitive processes and/or behavioral changes may facilitate the invasion, spread and or success of species or individuals in highly heterogenous and dynamic environments (Logan et al., 2023). In fact, some have even asserted that complex cognitive abilities of certain animals may facilitate their success in urban habitats, leading them to be considered 'nuisance' species (Barrett, Stanton & Benson-Amram, 2019). However, very few of these studies have been conducted at the individual level and remain coarse-grained in their ability to identify individual cognitive or behavioral strategies rather than group or population level patterns. Our study fills in some of these conceptual gaps by testing the effect of individual traits and urbanization on problem-solving and innovation performance in long-tailed macaques.

Objective:

In this chapter, I investigate how urban long-tailed macaques solve problems that are either familiar or novel to them. Individuals who are familiar with a problem should have learned which behaviors acquire the correct result and subsequently canalized their behaviors to make those learned associations more efficient. However, individuals who are presented with a novel problem will face different challenges, which may require flexible and alternative behaviors. I test these ideas using two field experiments on free ranging long-tailed macaques in an urban tourist park.

To test the ability to solve a problem that is familiar, we provided individual macaques with water bottles filled with a juice reward. To test the ability to solve a problem that is completely novel, we provided individuals with a puzzle box filled with peanuts as a reward. If individuals are familiar with the bottle task, then we would expect to see evidence of proficient solving behaviors (fewer errors, shorter solve times). Similarly, we could expect that individuals may be consistent in their solving behavior due to their prior experience with these objects. However, for novel problems we may expect the opposite, where at first individuals show evidence of naïve solving behaviors (many errors, longer solve times or work times). However, over the course of several trials, individuals may show evidence of learning where errors begin to reduce and solving becomes more efficient and/or consistent.

Despite their differences in novelty, we expect that both experiments will be influenced by individual level traits such as sex, rank, or interactions with the urban environment. Long-tailed macaques are a matriarchal species that live in large social groups with despotic social hierarchies. Males slightly outweigh and outrank female counterparts, resulting in males being able to monopolize foraging resources if provided the opportunity. We expect that males or high ranked individuals may be better at innovating due to their priority of access to preferred objects and resources in the environment. However, another explanation may be that females or low ranked individuals show better performance due to higher necessity and a lack of priority of access to resources. Overall, measures of interacting with the urban environment (such as human interactions, rates of feeding on human food, and spending time on human surfaces) are thought to have a positive relationship with innovation performance since those more integrated into the urban space are thought to encounter higher rates of novel objects (Lowry, Lill & Wong, 2013).

Methods

Study Site and Subjects

Behavioral data were collected on a total of two groups of long tailed macaques (*Macaca fascicularis*) from July 2016 to February of 2018 as a part of a long-term study on human-macaque interactions (Kaburu et al., 2019; Marty et al., 2019; Balasubramaniam et al., 2020). Observations for long-tailed macaque groups were conducted just outside the city of Kuala Lumpur in Malaysia in Templar Park (3°17′58″N, 101°37′08″E). Templar Park is a recreational park in the rainforest north of Kuala Lumpur where humans come to enjoy the area for hiking, picnicking, or swimming near a series of waterfalls. These macaques feed both on natural foods and human foods either through provisioning or refuse raiding (Marty et al., 2019). The availability of preferred natural fruits is thought to follow similar patterns of nearby sites of wild long-tailed macaques (Indonesia: van Schaik & Noordwijk, 1985). Some individuals even approach and steal from humans at this location, showing high levels of planning or coordination. Work from our research group has found that groups in these urban areas experience time constraints in their natural behavior, indicating trade-offs to monitoring or interacting directly with humans (Kaburu et al., 2019; Marty et al., 2019; Balasubramaniam et al., 2020).

During behavioral data collection, both interactions between macaques and humans as well as macaque conspecifics were recorded continuously using 10-minute focal follows of all adults. The frequency of feeding on human food was collected during focal scan samples every 2 minutes along with whether the focal was observed on human or natural surfaces. The frequency of human interactions, feeding on human food, and being present on human surfaces were converted into a rate by dividing by minutes of observation time to account for differences in visibility across individuals. Rank was calculated using the Perc package in R, which is a network-based method that considers both direct and indirect dominance pathways (Fujii et al., 2020). Individual rank order was then scaled by group to account for differences in group sizes and ranged between 0 and 1, with 1 being the highest ranked individual.

Experimental Protocol

Individuals from the two observed social groups were targeted for cognitive testing to assess their problem-solving abilities. This included two tests: one where we assessed how they opened familiar water bottles and another where we tested their ability to open a completely novel puzzle box. We chose the water bottle as a familiar object because during our long-term observations of urban macaques we observed that individuals often acquire these objects from humans and that there seemed to be variation in how successful individuals were at opening them. It has also been used by other research groups to measure differences in problem-solving abilities among urban and rural groups of macaques (Mangalam et al., 2013, Pal et al., 2022). For the puzzle box, we designed it with opaque materials so individuals would be sufficiently motivated to work on the problem. Peanuts were chosen as a preferred reward since macaques seemed to favor them as they would steal them from the nearby shops. We also often observed tourists handing the peanuts out as treats to the macaques, despite feeding bans in the park.

Experimental trials were conducted between July 2018 to September 2018. The adult group composition of the two study groups is listed in Table 4. We tested individuals opportunistically once they met all beginning trial criteria. For a focal to be eligible and chosen for an experimental trial, they could not have been observed feeding in large provisioning events within 15 minutes before the trial started. This was monitored to ensure that the motivation levels of individuals to engage with our cognitive task were not affected by large recent feeding events. Additionally, for a focal to be eligible for testing it was required to be alone, as defined by no conspecifics within 3 meters. This was implemented to minimize any social interference that may affect an individual's likelihood of engaging with the task.

If both experimental criteria were met, then the experimenter would begin the trial by dropping the testing apparatus (either a bottle or a box) within a 3-meter radius of the focal individual. All trials were video recorded. At the beginning of each video, standard trial information was stated such as the date, time, session number, and focal individual. Information about the focal animal, and other individuals within close visual contact (3m) were recorded at 1-minute intervals throughout the trial. A trial would be terminated either once the problem was solved (the apparatus had been opened) or it had been abandoned for a duration of at least 5 minutes. All videos were coded using the Behavioral Observation Research Interactive Software (BORIS V.8.20.4; Friard & Gamba, 2016).

Group	Adult Males	Transient Males	Adult Females	Total
Entrance	3	1	19	22-23
Hulk	4	2	13	17-19

Table 4. Group size and composition of long tailed macaques in Templar Park (August 2018).

Water Bottle Task

Each water bottle (Ice Mountain Brand, 500mL bottles) was filled with 140mL of black currant juice as a motivational reward (Figure 8). We used this juice due to its natural coloration which may reflect its high sugar content when presented in a transparent bottle, resulting in a more effective motivator than water alone. We know from research on rhesus macaques that individuals are more motivated by sugary substances than substances that lack sugar (Johnson, 2007). After filling the bottle with the appropriate amount of juice, we would close it snugly with the original cap, so all bottles were equally difficult to open.

Figure 8. Bottles were prepared for the experiment by filling them with 140ml of black currant juice.

Puzzle Box Task

A puzzle box with a single solution was used to test individual macaques' abilities to innovate. The puzzle box is made from polycarbonate (a more durable form of plexi-glass) and steel (Figure 9). The box is designed so that it can be opened from the top, through two swinging doors that meet in the middle and are secured with a steel locking mechanism. Seven different locking mechanisms were originally tested during a pilot phase (May 2018) to identify the ability of individuals to physically solve those options in the testing environment. Two options were identified as highly feasible candidates (box top 1 & 2) due to observed variation in success levels with a non-test group of macaques living in the same area. Box top 1 had a mechanism that required the subject to pull a steel lever vertically and subsequently unhook the latch to open the doors on top (Figure 10). Box top 2 was a different type of latch that required the subject to twist a handle 90° from its original position, in either direction to unlock the box (Figure 10). The latch then needed to be lifted vertically to open the doors. The box was pre-baited before trials with six unshelled peanuts, to provide motivation for the individual to engage with the puzzle-box and work for the reward. This box required tethering to ensure the apparatus couldn't be moved significantly by a subject (< 3m). Thus, since the apparatus was immovable from the general testing area, social interference and rank effects were tested to determine their influence on the performance of individuals or their access to the testing apparatus.

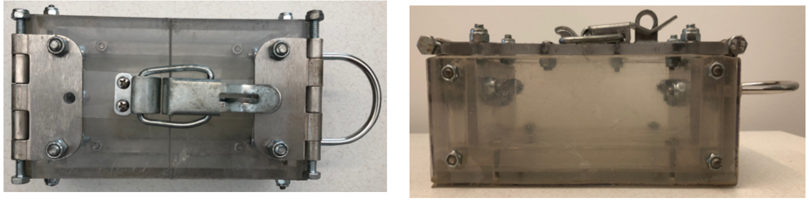


Figure 9. Top (left) and side views (right) of the single-solution puzzle box. Since the hinges have a removable pin, the doors can be changed to test different mechanisms. The steel handle on the right side of the box was used for tethering.

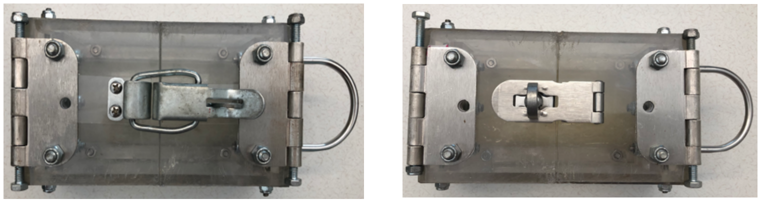


Figure 10. Box top 1 (left) is the lift latch and Box top 2 (right) is the twist latch.

Video Coding & Data Analysis

Videos of bottle & puzzle box solving behavior were analyzed in BORIS (V.8.20.4; Friard & Gamba, 2016). The trial begin time was recorded as well as once the focal first touches the object (bottle or box). When the focal solves the object, we also recorded when they first get access to the food reward (juice or peanuts). The latency to solve the object was calculated as the number of seconds elapsed from the time when the individual first contacts the object to when they get access to the food reward. We extracted all object-directed behaviors and scored them as state behaviors with unique motor patterns. Each unique object-directed behavior was summed together to calculate an exploratory diversity per individual per trial. The bottle-directed behaviors included in our ethogram are listed in Table 5. In addition to bottle-directed behaviors, we also recorded other behaviors such as the length of time in seconds the individual carried the bottle to a secondary location before working or whether they carried the bottle up into a tree during the trial.

Behavior	Definition
Sniff	Focal brings their face/nose close to the bottle but does not open their mouth or extend their tongue to contact the bottle.
Roll	Focal rotates the bottle at least 90 degrees. This could include rotating the bottle while its horizontal on the ground or tipping it over from a vertical to a horizontal position.
Touch Cap	Focal contacts the bottle by touching the cap of the bottle with their hands or feet and is attending to the cap specifically.
Touch Body	Focal contacts the bottle by touching the body of the bottle with their hands or feet. This could include simply holding the bottle in the absence of other behaviors.
Bite Cap	Focal contacts the bottle with their open mouth on the cap of the bottle specifically.
Bite Body	Focal contacts the bottle with their open mouth on the body of the bottle specifically. This includes any part of the bottle that is not the white cap or the bottom of the bottle that is not accessible when standing upright.
Bite Bottom	Focal contacts the bottle with their open mouth on the bottom of the bottle specifically. This includes only the bottom of the bottle that is not accessible when standing upright.

Table 5. Ethogram for bottle-directed behaviors in the water bottle study.

The box-directed behaviors included in our ethogram are listed in Table 6. All box trials were categorized based on whether the box was solved or not. In addition to box-directed behaviors, we also recorded other types of behaviors such as aggressive or dominance interactions among individuals in group trials, including displacements at the box. Aggressive interactions often involved open mouth threats, stiff posture and/or chasing. Displacements were defined as when an individual approached another individual and took their physical position. Displacements could be accompanied with additional social behaviors such as silent-bared teeth signals, which are often an indication of submission in macaques.

Behavior	Definition
Circle	Focal approaches the box within arms-length and walks around the perimeter of the box while attending to it.
Peer	Focal leans down to look through the sides of the box.
Sniff	Focal brings their face/nose close to the box but does not open their mouth or extend their tongue to contact the box.
Roll	Focal rotates the box at least 45 degrees, either horizontally or vertically.
Touch Top	Focal contacts the box by touching the top panel of the box with their hands or feet. This includes the latching mechanism, hinges, and corners that are adjacent to the top panel.
Touch Sides	Focal contacts the box by touching any of the four side panels of the box with their hands or feet. This includes all corner edges of the box that are perpendicular to the top and bottom panels of the box.
Touch Bottom	Focal contacts the box by touching the bottom panel of the box with their hands or feet. This includes the corners that are adjacent to the bottom panel.
Bite Top	Focal contacts the box with their open mouth on the top panel of the box. This includes the latching mechanism, hinges, and corners that are adjacent to the top panel.
Bite Sides	Focal contacts the box with their open mouth on any of the four side panels of the box. This includes all corner edges of the box that are perpendicular to the top and bottom panels of the box.
Bite Bottom	Focal contacts the box with their open mouth on the bottom panel of the box. This includes the corners that are adjacent to the bottom panel.
Pull/push	Focal uses their arms to pull or push the box to cause it to rock or experience displacement on the ground.
Carry	Lift the box off the ground and displace it some distance.
Climb	Focal lifts their body vertically on top of the box with at least 3 limbs in contact.
Lift Latch	Lift the latch vertically to unlock and unhook metal ring to open.
Twist Latch	Rotate the latch 90 degrees to unlock and lift the metal clasp to open.
Pull Knob	Pull the doors upwards to open and access inside the box.

Table 6. Ethogram for box-directed behaviors in the puzzle box study.

Statistical Methods

All statistical assessments were conducted in the statistical program R (R Core Team, 2022, V4.3.0). Nearly all tests for bottles and boxes were done using generalized linear mixed models (GLMMs) using the ‘lme4’ and ‘glmmTMB’ packages. However, for the selection of specific solving techniques in bottles we instead used a multinomial model using the ‘nnet’ package since the outcome variable was categorical rather than continuous. Due to the high monopolizable potential of the water bottles, this dataset includes predominantly individual trials, where only one individual was in contact and solved. On the other hand, puzzle boxes were fixed in space and created a scenario where individuals could be interrupted during testing. Thus, the dataset for puzzle boxes includes both individual and group trials, where group trials include multiple individuals interacting with the puzzle box. Thus, each row in the dataset corresponds to an individual adult's "participation" in the puzzle box experiments and is annotated whether it is classified as an "individual" or "group" trial.

For water bottles, we explored three aspects of solving behavior as outcome variables including the latency to solve (seconds), solving strategy chosen, and exploratory diversity score (N=42, Table 7 below). For puzzle boxes, we explored three aspects of solving behavior as outcome variables including a binary likelihood to solve, latency to solve (seconds), and exploratory diversity score (N=40, Table 7 below). For models testing predictors for the likelihood to solve the puzzle box, we used a binomial distribution. All GLMMs with binary solving behavior and exploratory diversity as outcome variables for puzzle boxes included a fixed effect of whether it was a part of a group trial or an individual trial in addition to the random effect of subject. For models testing predictors for the latency to solve either a water bottle or puzzle box, they were first tested with a Poisson distribution due to the nature of the continuous variables being a count or "count-like". These Poisson models were found to be over dispersed, so the model was shifted to a negative binomial distribution. For models testing predictors for exploratory diversity, we used a Poisson model due to no evidence of overdispersion and the count-like fashion of the diversity index. For bottles all GLMMs with latency to solve as outcome variables included solve technique as a fixed effect in addition to the random effect of subject to account for repeated trials as well as the strong influence of solve technique on solve time. However, the GLMMs exploring latency to solve for puzzle boxes only included the subject ID random effect due to power restrictions and smaller sample sizes (N=20). Additionally, the GLMMs predicting exploratory diversity for water bottles did not include the subject ID random effect due to low variation explained within individuals. Due to high consistency in solve technique within individuals across multiple presentations, all multinomial models were analyzed using only each individual's first trial presentation with the bottle object. Thus, multinomial models did not include a random effect of subject ID due to a lack of replicates in the analysis.

Outcome	**Definition**	**Water Bottles**	**Puzzle Boxes**
Solve (Y/N)	Binary outcome of solving, yes or no.	-	✓
Latency to solve (seconds)	Seconds elapsed from first touch of the object to getting access to food reward.	✓	✓
Solving Strategy	Choice of simultaneously available solving strategies (bite cap, puncture, create opening).	✓	-
Exploratory Diversity	Sum of unique motor behaviors used towards the object.	✓	✓

Table 7. Definitions for outcome variables tested in bottle and puzzle box experiments. Check marks in the two right-most columns indicate outcomes that were tested per object.

All GLMMs with more than one predictor were tested for collinearity, and variables found to be colinear were not included in the same model together but instead were tested separately. For bottles, sex was found to be correlated with technique chosen, number of trials per individual and whether they seek refuge in trees. Sex was correlated with technique chosen where females were more associated with create opening and puncture than bite cap (Figure 11; $\chi^2 = 5.81$, $p = 0.05$; Cramer's V = 0.25). Sex was also correlated with the number of trials conducted per individual, where males were associated with more repeated trials than females (Figure 13, Pearson's $r(38) = 0.28$, $p = 0.008$). Seeking refuge in trees was also found to be correlated with sex, with females entering trees with bottles more often than males (Figure 12, $\chi^2 = 5.3$, $p = 0.03$). Exploratory diversity was also found to be correlated with work time (Figure 14, Pearson's $r(38) = 0.5$, $p = 7.65 \times 10^{-3}$).

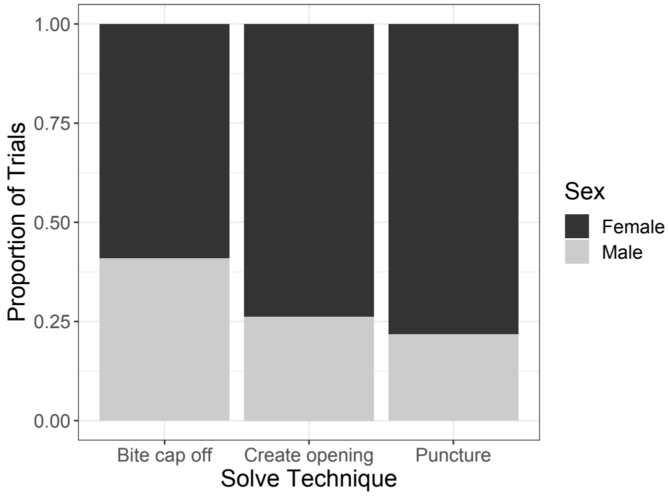


Figure 11. Solve technique plotted against the proportion of trials that were either female or male.

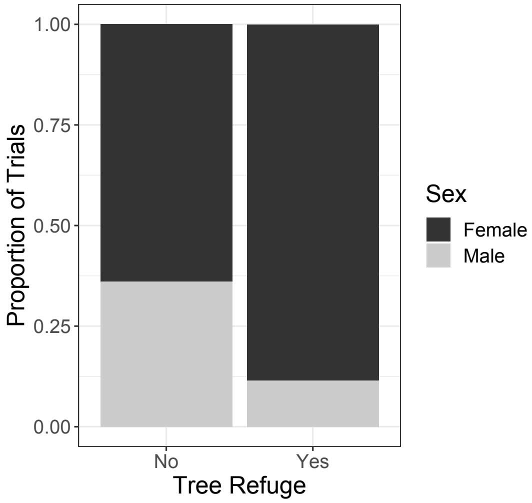


Figure 12. Bar plots of the proportion of females and males who sought tree refuge.

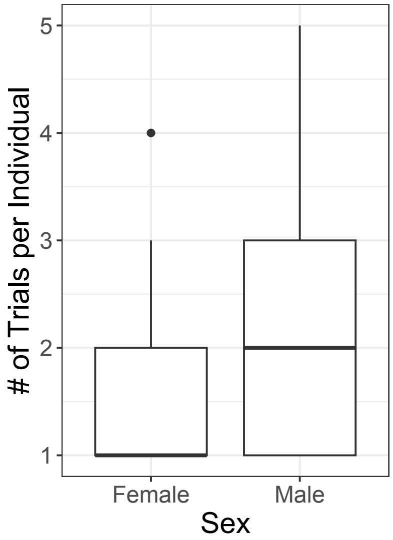


Figure 13. Boxplots of females and males and the number of trials conducted per individual.

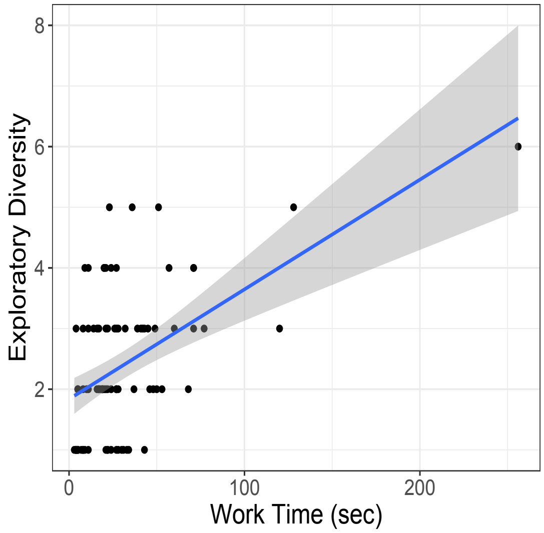


Figure 14. Positive correlation between exploratory diversity and work time (seconds) in bottle experiments.

For puzzle boxes, box top type (i.e., 1 vs. 2) was found to be moderately correlated with trial type (i.e., individual vs. group) (Figure 16; $\chi^2 = 16.68$, p = 0.0004; Cramer's V = 0.36). Box top type was also found to be correlated with exploratory diversity (Figure 17; Pearson's $r(38) = 0.35$, p = 0.001). Exploratory diversity was also found to be moderately correlated with trial type (Figure 15; $\chi^2 = 17.54$, p = 0.0509; Cramer's V = 0.4) and highly correlated with work time (Figure 18; $\chi^2 = 1046.7$, p = 0.042; Cramer's V = 0.99).

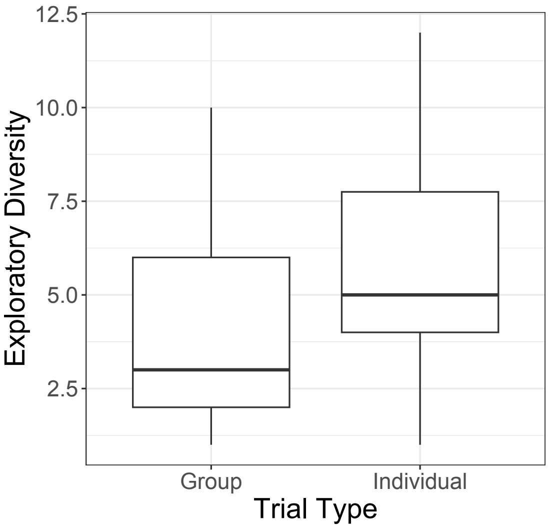


Figure 15. Boxplot of group vs. individual trials plotted against exploratory diversity scores.

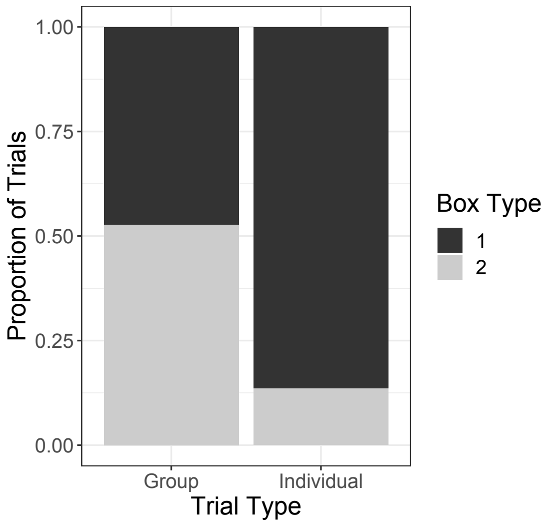


Figure 16. Trial type (group or individual) plotted against the proportion of trials that were either box top 1 (lift latch, black) or 2 (twist latch, grey).

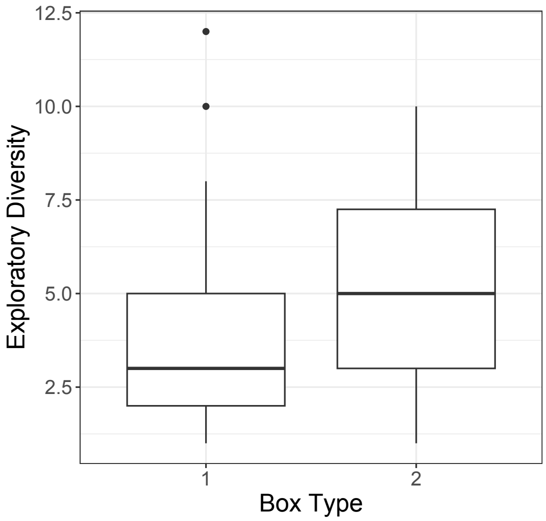


Figure 17. Boxplot of trials by box top type (top 1, lift latch, black or top 2, twist latch, grey) plotted against exploratory diversity scores.

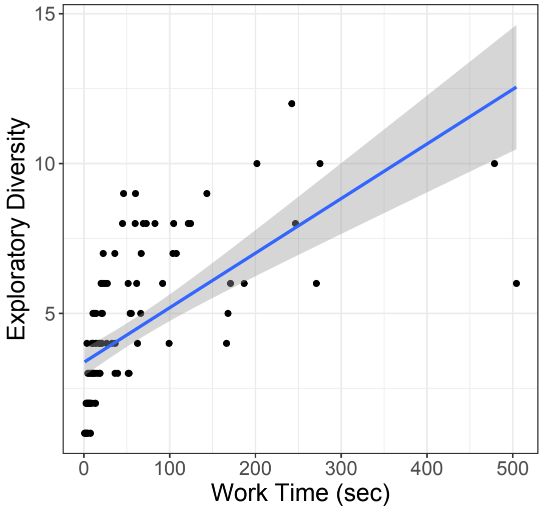


Figure 18. Work time of individuals (seconds) plotted by exploratory diversity scores for puzzle box experiments.

Ethics and Approval Declaration

The protocols used in this study were approved by the Institutional Animal Care and Use Committee (IACUC) of the University of California, Davis (protocol # 20593). The research was performed strictly in accordance with the guidelines drafted in this protocol and complied with the legal requirements of Malaysia. This protocol, along with the guidelines and regulations, was designed in consultation with the Universiti Putra Malaysia and Universiti Sains Malaysia in Malaysia.

Water Bottle Results

A total of 103 trials were conducted throughout the study period. However, a few of the files were insufficient for analysis either due to video malfunctions (4) or insufficient visibility (3) of the bottle manipulation. Additionally, one trial was completely ignored by the target subject, leaving 95 trials available for analysis from 7 unique juveniles and 42 unique adults. Due to a small sample size for juveniles, we excluded them from this analysis, resulting in 87 total adult trials included.

We were successful in testing all adult individuals at least once. To assess the consistency in solving behaviors over time we conducted repeated trials with as many individuals as possible (N=21). Overall, individuals received anywhere from 1 to 5 trials across the entire experimental period (Figure 19).

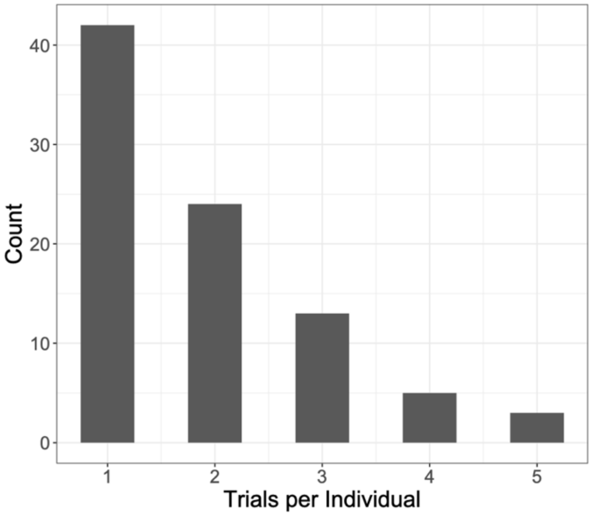


Figure 19. Histogram of number of water bottle trials per individual tested.

Overall Bottle Solving Behavior

Every adult tested was able to solve the bottle task by opening it and getting access to the juice reward inside. Overall, there were three solutions we observed. The first technique required individuals to use their mouth and/or hands to create a hole large enough to insert their hand or mouth to consume the juice (create opening). The second technique required individuals to use their mouth (usually a single canine) to create a small hole large enough for the juice to escape the bottle, from which the individuals would often drink it directly (puncture). The third and final technique required individuals to use their mouth or hands to manipulate the cap of the bottle to remove it, often resulting in individuals consuming the juice directly from the cap opening or alternatively spilling the juice onto the ground to drink it (bite cap).

We also tested the effects of group membership on bottle solving performance. However, we did not find any significant relationships between group membership and the latency to solve the bottle (S7; group Hulk $\beta = 0.01$, $p = 0.995$), solve technique (S7; bite cap & group Hulk $\beta = 1.74$, $p > 0.05$; puncture & group Entrance $\beta = 1.16$, $p > 0.05$), or exploratory diversity (S7; group Hulk $\beta = -0.02$, $p = 0.884$).

Out of these three techniques, create opening was by far the most common, followed by puncture and bite cap (Figure 20). We fitted GLMMs to test the effect of solve technique on the latency to solve the bottle. In addition to being the most common, the create opening technique took significantly longer to complete than the other two techniques (S7; create opening $\beta = 0.99$, $p = <0.001$; puncture $\beta = 0.45$, $p = 0.089$).

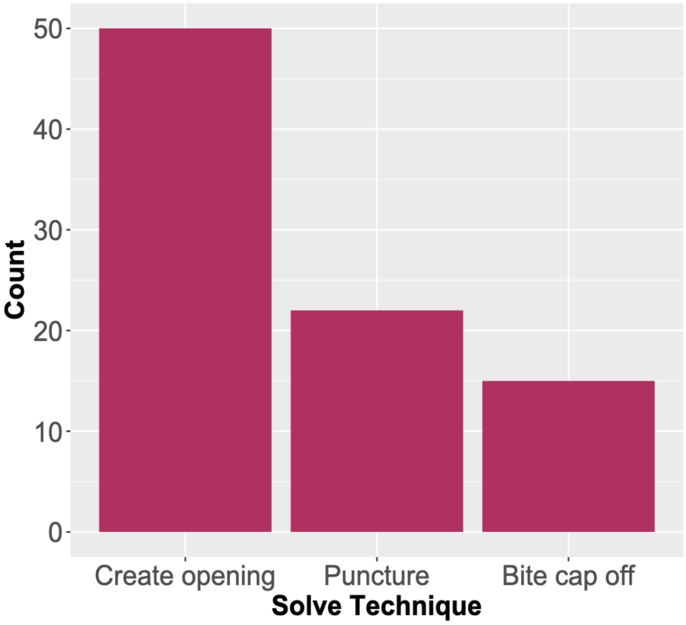


Figure 20. Bar plot of solving techniques across all bottle experiments.

Once receiving the bottle during the experiment, individuals would vary in whether they carried the bottle to a secondary location before beginning to work on opening it. Thus, we also looked at whether the amount of time it takes to carry the bottle influences how long it takes to solve the bottle to determine its importance as a control variable in our subsequent analyses on solve time. Using a GLMM we found that carry time did significantly influence solve time, with those individuals who are carrying for longer taking longer to solve the bottle problem (S7; $\beta = 0.05$, $p = <0.001$). Due to the significant influence of carry time on solve time and small effective sample sizes for testing individual predictors, we incorporated carry time into the outcome variable of latency to solve by subtracting it from the total solve time.

Individuals seemed to vary not only in whether they carried the bottle to a secondary location, but whether they took the object off the ground and into the trees to potentially seek refuge from other individuals in the group. We used GLMMs to test the influence of tree refuge on how long it takes for individuals to solve the bottle task. There was a significant effect of tree refuge where those who seek refuge in trees take significantly longer to solve the bottle than those who stay on the ground (S7; $\beta = 0.61$, $p = <0.001$).

Exploratory Diversity, Persistence and Puzzle Performance

We fitted GLMMs to test the effect of exploratory diversity on several aspects of bottle solving performance. We found that individuals with higher exploratory diversity scores took significantly longer to solve the water bottle (S7; $\beta = 0.39$, $p = <0.001$) than those who had lower exploratory diversity. However, there was no significant effect between exploratory diversity and solve technique of the bottle task (S7; bite cap & intercept $\beta = -0.29$, $p > 0.05$; puncture & intercept $\beta = -1.8$, $p > 0.1$; bite cap off & exploratory diversity $\beta = -0.4$, $p > 0.05$; puncture & exploratory diversity $\beta = 0.38$, $p > 0.05$).

Out of all the bottle-directed behaviors, we calculated which behaviors were most common in the dataset to get an idea of suites of behaviors that may be combined to solve the bottle task. Most individuals performed behaviors that were oriented towards the body region of the bottle (such as touch body, roll, or bite body). However, fewer individuals engaged in behaviors that were cap-directed or oriented towards the bottom of the bottle (such as touch/bite cap, or bite bottom; Table 8). Additionally, we calculated the intra- and inter-individual variation in exploratory diversity to get a better understanding of its potential role in bottle problem-solving behavior. There appears to be some variation in both intra- and inter-individual exploratory diversities (Figure 21), but the range is relatively low (range = 1-6). However, both forms of variation in exploratory diversity rely on the number of repeated trials conducted per individual.

Behavior	**# of Adults**	**% of Adults (out of 42 total)**
Bite Body	25	60
Roll	18	43
Touch Body	18	43
Sniff	18	43
Bite Cap	13	31
Bite Bottom	12	29
Touch Cap	5	12

Table 8. Summary of bottle-directed behaviors across adult individuals tested.

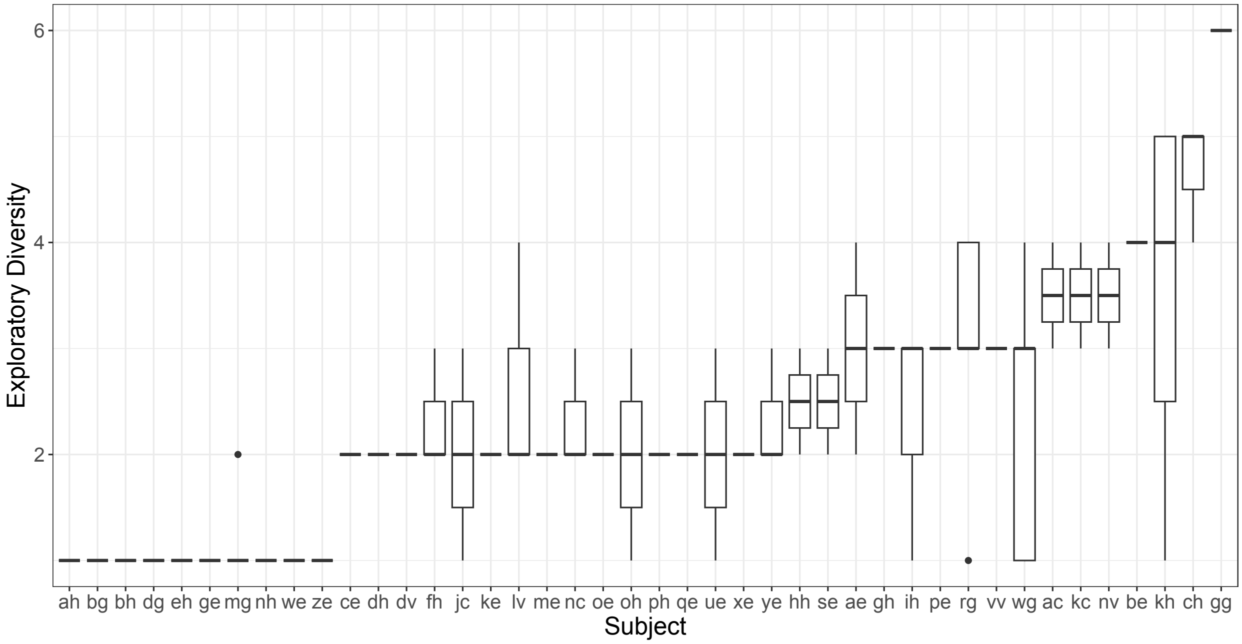


Figure 21. Variation in exploratory diversity across and within individual adults tested in the bottle task. Each boxplot represents a single individual, where individuals who only received a single trial have a single line, while individuals who received more than a single trial have a boxplot.

Individual traits & Water Bottle Performance

First, we looked at whether individual traits (such as sex or rank) as well as aspects of interacting with the urban environment (such as rate of interacting with humans, rate of feeding on human food, or rate of being present on human surfaces) influenced how long it takes for individuals to solve the bottle task using GLMMs. However, none of the predictors tested had a significant influence on the amount of time it takes to solve the bottle task (S7).

Next, we looked at whether these same individual traits influenced the likelihood to choose a particular technique when solving the bottle task. We did not find any significant effects for rank, or any aspects of interacting with the urban environment (rate of interacting with humans, rate of feeding on human food, rate of being present on human surfaces) (S7). We did find a marginally significant trend that implies that individuals who fed more on human food may be less likely to choose the bite cap technique compared to other techniques (S7; bite cap & rate of feeding human food $\beta = -17.25$, $p < 0.1$). However, we did find a significant effect for sex, whereby females were found to be significantly more likely to choose create opening than manipulating the cap (S7; bite cap & male $\beta = 2.18$, $p < 0.01$).

Finally, we used GLMMs to investigate whether individual traits (such as sex or rank) influenced within trial behaviors such as their likelihood to carry the bottle or seek refuge in trees.
For carry time and tree refuge, we did not find significant effects for rank, but we did find marginally significant trends suggesting that high ranked individuals may carry the bottle for less time than low ranked individuals (S7; $\beta = -1.26$, $p = 0.065$) and will be less likely to seek refuge in trees (S7; $\beta = -2.15$, $p = 0.078$). However, we did find a significant relationship between sex and carry time as well as tree refuge, whereby males were significantly less likely to carry the bottle to a secondary location (S7; male $\beta = -1.14$, $p = 0.007$) or seek refuge in trees (S7; male $\beta = -1.63$, $p = 0.048$) compared to females.

Water Bottle Performance over Time

Since we were able to test a subset of individuals (N=21) multiple times over the experimental period, we wanted to assess whether solving behaviors remained consistent within an individual over time. We looked at consistency in their chosen solve technique, solve time, and exploratory diversity. For solve technique, individuals were highly consistent in choosing the same technique, with over 80 percent of individuals choosing the same technique across two or more trials (17/21 individuals were consistent, Table 9; S8). Interestingly, there were six individuals who were observed to remove the cap first, but then move onto a secondary technique of create opening to gain access to the juice reward (Table 10). Using GLMMs we did not find a significant relationship between presentation order and solve time (S7; $\beta = -0.07$, $p = 0.237$) or exploratory diversity (S7; $\beta = -0.09$, $p = 0.154$), suggesting consistency within individuals for solving behaviors.

Solve Technique								
Bite Cap Off	Granny (2)	Amy (4)						
Puncture	Athena (2)	Becky (2)	Kaa (2)	Olivia (2)	Iris (3)	Katie (4)		
Create Opening	Medusa (2)	Scarlet (2)	Calypso (3)	Fleur (3)	Ursula (3)	Yedi (3)	Mario (5)	Wormtail (5)

Table 9. List of unique adult individuals who were consistent in solve technique across presentations. Values in parentheses indicate how many trials they chose a particular technique.

Combination of Techniques						
Bite Cap Off before Create Opening	Ariel (2)	Jasmine (1)	Fleur (2)	Katie (2)	Mario (1)	Trump (1)

Table 10. List of unique adult individuals who were observed to remove the cap before proceeding to solve the bottle using create opening. Values in parentheses indicate how many trials they performed this pattern of multiple sequential techniques.

Puzzle Box Results

A total of 77 puzzle box trials were conducted throughout the study period. However, a few of the files were insufficient for analysis either due to video malfunctions (4) or insufficient visibility of the box manipulation (1). Additionally, two trials were completely ignored by the target subject, leaving 70 trials available for analysis from 40 unique adults. Due to our experimental interest in the predictability of adult attributes on puzzle box performance, we only analyzed adult data despite juveniles solving the box during a portion of the experimental trials (N=21 solved box top 1; N=5 solved box top 2).

We were successful in testing nearly all adult individuals at least once aside from two shy individuals, with many adults having repeat exposures to the puzzle box. Overall, individuals received anywhere from 1 to 7 exposures to the box across the entire experimental period (Figure 22).

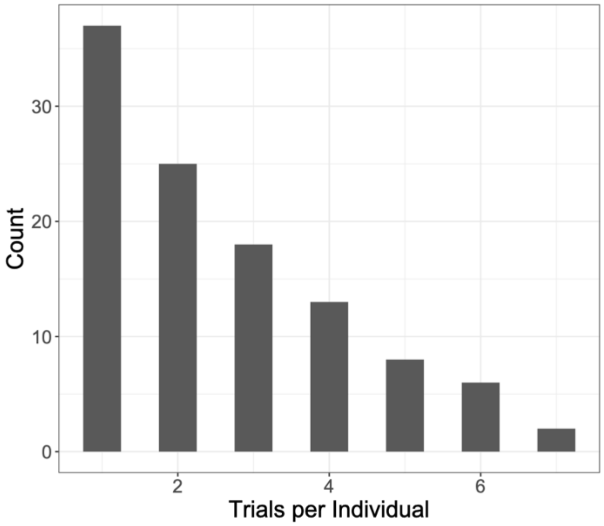


Figure 22. Histogram of the number of trials an individual interacted with the puzzle box.

Overall Puzzle Box Success

There were thirty-six trials where individuals solved the puzzle box. Solve time was calculated as the seconds elapsed between the first contact of the object and when it was solved. Work time on the other hand is the sum of seconds the individual was observed to be in contact with the object. In most cases, work time is similar to solve time when individuals are mostly in contact with the object while solving. However, solve time and work time can significantly differ when individuals have intermittent contact with the object while solving. On average, individuals solved the box in 60 seconds, and worked on the box for 55 seconds. When the box was solved, individuals had an average exploratory diversity score of 5.8 (median = 5.5, mode = 4). However, there were seventy-six instances of participation where individuals worked on the puzzle box but did not solve it. In those cases, the average amount of time individuals worked on the puzzle was 57 seconds, and their exploratory diversity averaged 3.8 (median = 3, mode = 2). Despite trial type (individual vs. group) the average solve and work times were similar, while exploratory diversity in group trials was lower (Table 11). Additionally, individuals who experienced social interactions had reduced exploratory diversity (Table 11).

	Summarizing Variable	**Mean Solve Time (sec)**	**Mean Work Time (sec)**	**Mean Exploratory Diversity (median, mode)**
Solve binary	Solve (N=36)	60	55	5.8 (5.5, 4)
	No Solve (N=76)	-	57	3.8 (3, 2)
Trial type	Individual (N=37)	60	57	6 (6, 4)
	Group (N=92)	60	59	4.1 (4. 3)

Table 11. Summary of puzzle box conditions and associated problem-solving metrics, including solve time, work time and exploratory diversity score.

We fitted GLMMs to test the effect of group membership on solving performance. We found no relationship between group membership and the likelihood to solve the box (S9; group Hulk $\beta = 0.34$, $p = 0.564$), latency to solve the puzzle box (S9; group Hulk $\beta = 0.43$, $p = 0.399$) or exploratory diversity scores (S9; $\beta = 0.07$, $p = 0.565$).

Despite the box top being tested (type 1 vs. 2), most trials tested with either mechanism resulted in high rates of success (Table 12). However, differences did emerge in the number of solvers belonging to different age classes, with more being solved by adults overall than juveniles. While the number of solvers across age classes remained relatively similar for box top 1, box top 2 showed higher rates of solving by adults when compared to juveniles (Table 12).

	Total Trials	**Solved**	**Solved by Juveniles**	**Solved by Adults**
Box Top 1	51	47	21	26
Box Top 2	19	17	5	12

Table 12. Total trials tested and solved by different age classes across the two box top types.

We fitted GLMMs to test the effect of box top type on solving performance. There was a non-significant trend that box top 2 was less likely to be solved than box top 1 (S9; $\beta = -0.77$, $p = 0.092$). Box top 2 also took significantly longer to solve (S9; $\beta = 1.48$, $p <0.001$) and was associated with significantly higher rates of exploratory diversity compared to box top 1 (S9; $\beta = 0.3$, $p = 0.002$). Unique adult individuals who participated in trials with either box top 1 or 2 are listed in Table 13.

Box Top	Unique Adult Tested
1 – lift latch	**Amy* (2)**, **Ariel (3)**, **Dory**, Emma (3), Fleur, **Gaea**, Gandalf (2), **Granny***, Kala, **Lex**, Medusa, Nala, **Olivia, Quinn**, **Scarlet (4)**, **Ursula***, **Voldemort*, Widow* (2)**
2 – twist latch	**Amy (3)**, **Ariel (2)**, Athena* (2), Becky, Bleachface*, Calypso*, **Dory**, Dracula (2), **Gaea (2)**, **Granny**, Jasmine, Kaa, **Lex (3)**, Mario (2), New Villain, Nose, **Olivia***, Ophelia, Poison, **Quinn**, **Scarlet (2)**, Trump (2), **Ursula (3)**, **Voldemort (2)**, **Widow***, Wormtail, Xena

Table 13. Unique adults engaged on different box trial types (lift latch vs. twist latch), either individual or group. Individuals who experienced both conditions are highlighted in bold. The numbers in parentheses represents the number of times that individual was tested with that box top type. Solvers are marked with an asterisk.

Social Interference & Puzzle Performance

Trials were categorized as either "individual" or "group" depending on the number of participants within a trial. For group trials, they were further divided into "instances of participation" where multiple individuals may be scored for a single trial after contacting the box. These instances of participation often happened sequentially, and more rarely they occurred simultaneously. Based on video observations, simultaneous work times seem to be more commonly performed by juveniles and only rarely with multiple adults. Overall, across all trials (individual and group), there were 106 instances of participation (i.e. animals who worked for some amount of time on the puzzle box), which are described in Table 14. There were also several instances of participation where individuals were targeted specifically for testing but did not approach or contact the box (N=22). In these cases, it is possible that the target individual either ignored the box completely or did not contact the box due to being displaced by another individual.

Trial Type	**Total**	**#Adults Solved**	**#Juveniles Solved**	**Unsolved**
Individual	37 trials/focals (24 unique adults)	21 trials/focals	9 trials/focals	5 trials/focals
Group	35 trials, 92 focals (35 unique Adults)	15 trials/focals	18 trials/focals	33 trials/76 focals

Table 14. Puzzle box trials by trial type (individual vs. group) as well as the number of trials that were solved by age class. Focal numbers represent "instances of participation" in the puzzle box analyses for group trials where more than one individual could participate in a single trial.

For trials where individuals worked on the puzzle box without interference from other individuals (i.e., individual trials, N=37), the average amount of time to solve was 60 seconds, with an average work time of 57 seconds. For those individual trials, the average exploratory diversity score was 6 (median = 6, mode = 4). There were sixteen unique individual adults who participated in individual trials, who are listed in Table 15. For trials where multiple individuals worked on the puzzle box (i.e., group trials, N=92), the average amount of time to solve was 60 seconds, with an average work time of 59 seconds. For those group trials, the average exploratory diversity score was 4.1 (median = 4, mode = 3). There were eleven unique individual adults who participated in group trials, who are listed in Table 15. Summary statistics for average solve time, work time and exploratory diversity are provided in Table 11.

Trial Type	**Unique Adults**
Individual	Amy, **Athena,** Dracula, Emma, **Fleur, Granny,** Kaa, **Kala,** Katie, Nala, New Villain, Olivia, Pippin, Trump, **Ursula, Widow**
Group	**Athena**, Bleachface, Calypso, **Fleur**, **Granny**, Iris, **Kala**, Scarlet**, Ursula,** Voldemort, **Widow**

Table 15. Unique adults engaged in different trial types, either individual or group. Individuals who experienced both conditions are highlighted in bold.

We fitted GLMMs to test the effect of trial type (individual vs. group) on several aspects of solving performance. We found that individuals who participated in individual trials were significantly more likely to solve the puzzle box (S9; $\beta = 2.3$, $p = <0.001$) and had significantly higher exploratory diversity than those who participated in group trials (S9; $\beta = 0.33$, $p = 0.002$). Due to this strong effect of trial type, we kept this variable in the null model structure for other models predicting likelihood to solve the puzzle box as well as exploratory diversity. However, we did not find any influence of trial type on the latency to solve the puzzle box (S9; $\beta = 0.28$, $p = 0.528$).

Social Interactions Within Group Trials

Out of all group trials (N=35) there were fifteen where individuals experienced a displacement. A displacement is defined by an animal occupying a position whereby upon approach by another individual the secondary individual assumes the position of the primary individual. For those who get displaced, they had an average work time on the puzzle box of 90 seconds (Table 16). Of all the individuals who were displaced, only two of them solved (Iris & Widow who took 29 seconds and 115 seconds to solve respectively). On the other hand, there were thirteen individuals who were observed to displace other individuals. For those who performed displacements, the average work time was 50 seconds, whereby four individuals solved the puzzle resulting in an average solve time of 31 seconds (Table 16).

In addition to displacements, we also observed aggressive interactions among individuals. There were three instances where individuals gave aggression to other individuals before leaving the area of the puzzle box. In all three cases, none of these individuals solved the puzzle box, resulting in an average work time of 10 seconds (Table 16). Alternatively, there were five instances where individuals received aggression from other individuals and left the area of the puzzle box. In all five cases, none of the individuals solved, resulting in an average work time of 22 seconds (Table 16).

Most instances of participation in group trials in fact did not have any overt social interactions. In these cases, individuals engaged with the puzzle box in some way (either by approaching closely or coming into contact), but then after some time (and without any social interactions such as displacements or aggression), they decide to stop interacting with the box and were defined as “abandoned”. During group trials we observed forty-two instances of “abandoned”. However, it is worth mentioning that these experiments were conducted in a wild setting, and it is possible that these animals may have decided to go do something else or were distracted by something that was not measured directly in this study. In all forty-two cases of “abandoned”, none of the individuals solved, and the average work time was measured at 61 seconds (Table 16).

Only in one instance did we observe sexual interactions between a male and a female during an experimental trial on the puzzle box. In this case, a male (New Villain) was working on the puzzle box when an adult female (Ursula) approached him in proximity. At that time, the male left the puzzle box briefly to mate with the nearby female and returned to continue working on the puzzle box shortly after. Afterwards, the male was displaced from the box by another individual and eventually the female approached and tried to solve it but was unsuccessful. The male worked on the puzzle for 504 seconds, while the female worked for 52 seconds (Table 16).

Finally, we observed only two instances where adult individuals worked simultaneously to “mutually solve” the box. For example, in one instance one adult female (Kala) lifted the metal latch mechanism while the other adult female (Ariel) pulled the doors open to gain access to the food reward. In the second example, both adult females worked simultaneously on the box for similar amounts of time (Scarlet = 25 seconds, Calypso = 12 seconds). However, one individual contributed specific actions that seemed to drive the problem-solving behavior such as lifting the latch and rolling it to open the doors (Calypso).

	Summarizing Variable	**Mean Solve Time (sec)**	**Mean Work Time (sec)**	**Mean Exploratory Diversity (median, mode)**
Interaction	Displaced (N=5)	72	90	3.6 (3, 2)
	Displacer (N=13)	31	50	3.7 (3, 3)
	Aggression Received (N=5)	-	57	4.3 (4, 2)
	Aggression Given (N=3)	-	40	4.5 (4.5, 2)
	Sexual (N=2)	-	100	5.2 (5, NA)
	Mutual Solve (N=2)	-	15	4.5 (4.5, NA)
	Abandon (N=42)	-	61	4 (3.5, 1)

Table 16. Summary of puzzle box conditions and associated problem-solving metrics, including solve time, work time and exploratory diversity score.

Exploratory Diversity, Persistence and Puzzle Performance

We fitted GLMMs to test the effect of exploratory diversity on several aspects of solving performance. We found that individuals with higher exploratory diversity scores were significantly more likely to solve the puzzle box (S9; $\beta = 0.45$, $p = <0.001$) and took significantly longer to solve the puzzle box (S9; $\beta = 0.28$, $p = 0.528$) than those who had lower exploratory diversity. Due to collinearity with work time (a measure of persistence), we could not test exploratory diversity while controlling for work time, so we tested each variable separately. There was no significant effect between work time and the likelihood to solve the puzzle box (S9; $\beta = 4.36$, $p = 0.67$). However, those who had longer work times took significantly longer to solve the puzzle than those who had shorter work times (S9; $\beta = 0.01$, $p = <0.001$).

Out of all the box-directed behaviors, we calculated which behaviors were more common in the dataset to get an idea of suites of behaviors that may be combined to solve the puzzle. Most individuals performed behaviors that were required to solve the puzzle box (such as touch top, roll, or bite top). However, many individuals engaged in behaviors that were completely unrelated to solving (such as bite sides, or touch bottom). A summary of box-directed behaviors across all trials in the study is provided in Table 17. Additionally, we calculated the intra- and inter-individual variation in exploratory diversity to get a better understanding of its potential role in problem-solving behavior. There appears to be substantial variation in both intra- and inter-individual exploratory diversities (Figure 23). However, both forms of variation in exploratory diversity rely on the number of repeated trials conducted per individual.

Behavior	**# of trials**
Touch Top	74
Roll	73
Bite Top	44
Touch Sides	46
Pull/Push	40
Pull Knob	32
Lift Latch	28
Sniff	28
Touch Bottom	27
Bite Bottom	25
Bite Sides	16
Circle	14
Twist Latch	8
Peer	4
Carry	3
Climb	1

Table 17. Summary of box-directed behaviors across all trials.

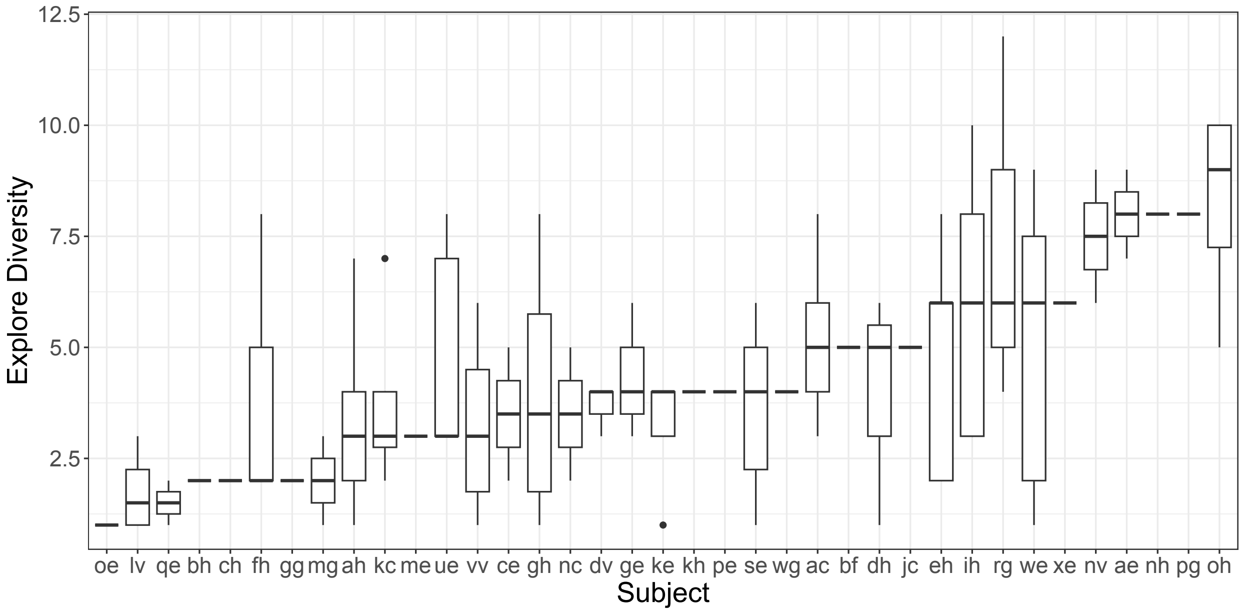


Figure 23. Variation in exploratory diversity across and within individual adults tested with the puzzle box task. Each boxplot represents a single individual, where individuals who only received a single trial have a single line, while individuals who received more than a single trial have a boxplot.

Individual Traits & Puzzle Box Performance

There were thirty-three adults who had corresponding behavioral data from the long-term dataset that we used as predictors for solving the puzzle box. We fitted GLMMs to test the effect of several individual traits on solving performance, such as the sex of the individual, their group membership, their social rank order, as well as various aspects of how they interact with the urban environment. Predictors related to the urban environment included the rate of interacting with humans, rate of feeding on human food, and rate of being present on human surfaces. However, we did not find any statistically significant effects for any of the listed predictors on the likelihood of solving the puzzle box (S9). Similarly, we did not find any significant effects for any of the same predictors on how long it takes for individuals to solve the puzzle box (S9). However, when we looked at whether any of these individual traits predicted exploratory diversity scores, we did find a significant effect for the rate of feeding on human food, where those who feed more on human food had significantly lower exploratory diversity scores than those who fed on human food less (S9; rate feeding on human food $\beta = -1.2$, $p = 0.031$).

Puzzle Box Performance over Time

We also fitted GLMMs to test the effect of presentation on aspects of puzzle box solving performance. There was a non-significant trend suggesting that individuals with higher presentations may be more likely to solve the puzzle box (S9; $\beta = 0.31$, $p = 0.09$), take less time to solve the puzzle (S9; $\beta = -0.22$, $p = 0.067$), and have lower exploratory diversity scores (S9; $\beta = -0.06$, $p = 0.061$) than those who had lower presentations.

Discussion

Overall Solving Behaviors for Water Bottles

Overall, the bottle task did not prove particularly challenging for the groups of macaques that we tested since all individuals were able to solve it and gain access to the juice reward. In previous studies on bottle solving behavior, there has been variation observed across groups that experience different environmental pressures, such as living closer to humans (Mangalam & Singh 2013; Pal et al., 2022). Differences have also been observed in the proficiency of bottle solving behaviors within groups, where some had observed lower overall rates of solving (~60%, Mangalam & Singh, 2013), while others observed much higher rates of solving (~90%, Pal et al., 2022). The lack of variation across the two groups we studied indicates that despite having distinctly separated core home ranges, both groups are likely to experience similar pressures due to equal exposure to humans and partial overlap in peripheral home ranges. However, we did observe variation in how individuals solved the task, how exploratory they were and which techniques they chose to solve. Although the three techniques varied in how long they took to solve the bottle, the absolute difference between them was not very high (ex. create opening takes on average 50s to complete, while puncture and bite cap take on average 15 to 20s to complete). This small absolute difference may provide very little (if at all) selective pressure for individuals to switch or learn techniques that are seemingly more efficient in the sense that they take a shorter amount of time to solve. Thus, it is possible that if an individual can figure out any one of these three techniques that may be sufficient for individuals to conform to that technique to get juice when they have the opportunity arise in the environment.

Although most individuals tested used a single technique to solve the bottle task, it is notable that a few individuals (N=6) were observed to remove the cap first before utilizing the final technique of create opening to get the juice reward. This is interesting because although these individuals were clearly able to remove the cap, they did not associate opening of the cap with gaining access to the juice reward since they continued to work on the problem as if they hadn't solved it yet. This contrasts to individuals who solved the bottle using the bite cap technique and immediately either consumed the juice from the cap opening or knocked the bottle over to drink the juice from the ground. One potential explanation for why individuals may have performed multiple techniques within a trial is that it might represent a fixed action pattern. That is, it is possible that removing the cap first is simply a step in a series of steps that the individual has associated with the technique of create opening as a final step. Thus, in a fixed action pattern scenario, individuals might be performing the remove cap behavior simply because it is en route to the create opening behavior. To test these ideas, future studies should conduct these experiments over a longer period to capture the process of developing or switching between bottle solving techniques.

Another potential explanation for why individuals perform multiple techniques within a trial is that they may have started to learn an association with removing the cap and solving the bottle but haven't yet made the association between bottle opening and gravitational forces (i.e., once opened, the bottle needs to be tilted to gain access to the juice from the cap). Thus, this might represent one mechanism by which animals develop different strategies, or even switch between strategies such as create opening and bite cap. This might explain why create opening is more common than bite cap since many individuals can figure out how to simply rip the bottle open with their teeth, but it takes more associative learning steps to figure out the relationship between the cap and the bottle (as a mechanism for procuring juice) as well as the relationship between bottle orientation and gravitational forces (where the orientation of the bottle determines the ability to gain access to the juice). This may be a particularly fruitful area of research in the future where we can examine the sequences of behaviors individuals are using to solve the bottle task and see if those strings remain consistent across trials. If this is the case, this might better support the idea of a fixed action pattern. However, if individuals are using the same behaviors across trials but changing the sequence of those behaviors, that may suggest that they have more flexibility in combining behaviors together to get to a desired (solved) outcome.

Role of Individual Traits for Solving Water Bottles

Next, we wanted to investigate whether individual traits influenced the solving behavior for opening water bottles. Although we predicted a direct relationship between traits (such as sex or rank) on solving performance, instead we found that these traits can sometimes have a more indirect influence on solving behavior. For example, although sex or rank were not significant in predicting latency to solve, traits like sex did indicate that females were significantly more likely to choose the create opening technique, which takes significantly longer as a technique to solve than other techniques. In previous studies on bottle manipulation in macaques, females have either been found to be more successful in opening bottles (Mangalam & Singh, 2013), or no influence of sex on success was found (Pal et al., 2022). Thus, in problem-solving studies it may be important to consider both the direct and indirect influences of traits on solving behavior, otherwise these relationships might be missed. One might wonder why female macaques may be more likely to choose the create opening technique compared to males. One potential reason for this might be due to the matriarchal structure of macaque societies, where females often possess strong bonds with other females that may facilitate a process of "conformity" to the strategies that other females are using to solve foraging problems. Males, on the other hand, are the dispersing sex and as a result may experience a wider variety of environmental variation that may lead to diverging solution types for foraging problems. For example, it is note-worthy that we observed seven males using the rarer technique of bite cap, where four of those males had recently migrated into the group. In a recent study on bottle manipulation in bonnet macaques, they mention similar anecdotes where they observed several males immigrate into their study groups that were able to successfully open water bottles, with several males using ‘sophisticated techniques’ such as manipulating the cap (Pal et al., 2022).

It is curious that all aspects of interacting with the urban environment did not prove significant in any of our analyses on bottle solving behavior. One potential reason for this might be that the behavioral predictors characterizing interactions with the urban environment were collected over a long period (2 years of data collection) which may not accurately represent the behaviors of the individuals at the time of the experimental testing. It is also possible that our sample sizes were insufficient to detect these effects if they in fact are present due to the reduced sample size of individuals who had corresponding data from the long-term study (N=33). Another suggestion might be due to the nature of how common these water bottle objects are in the urban environment. It’s possible that all individuals, regardless of the traits they possess, can interact with these objects both outside of the context of human interactions as well as feeding on human food since these objects are scattered throughout the environment as rubbish and are freely available. Thus, it might not matter how often you interact with people or feed on human food, but rather on how much exposure you get to these objects in the environment before being tested on solving performance. For example, previous studies that have quantified the amount of direct provisioning by humans found that groups with higher rates of provisioning showed higher frequencies of cap-directed bottle techniques (Pal et al., 2022). However, they did not measure this on an individual scale as we did in our study, which requires the consistent identification of unique individuals. Additionally, despite quantifying the availability of water bottles in the environment, they did not find a correlation with bottle-directed manipulative techniques across the four study groups they sampled (Pal et al., 2022). We encourage future studies to test multiple groups living at varied ecological conditions to help better tease apart the influence of individual traits with environmental influences on solving behavior.

When conducting experiments in the wild, social dynamics are important to consider because they can lead to interference in individual performance. Due to the high monopolizable potential of the bottle object, we expected that social dynamics would play a minimal role in the solving behavior of individuals. Although infrequent, we did have experimental trials where individuals experienced social interactions with others such as displacements or aggression. In only a single trial, we observed a male open a bottle and drink some juice, before mating with a nearby female, after which the female got control of the juice bottle and consumed the rest. In another trial we observed a female holding the water bottle while being sexually mounted by a male, afterwards she continued working on the bottle and eventually solved the task.

However, it was much more common for individuals to perform additional behaviors, presumably to avoid social interference with others such as carrying the bottle to a secondary location or entering trees to seek refuge from others. Our results that females were significantly more likely to carry the bottle rather than males is indicative that animals with different traits experience different social pressures that may influence aspects of problem-solving performance. Many studies on problem-solving in the wild use measurements such as how long it takes for individuals to solve as a measure of their cognitive performance (lizards: Cooper et al., 2019; lions: Borrego & Dowling, 2016; beagle dogs: Nippak & Milgram, 2005). Additionally, previous studies on Samango monkeys (Le Roux, Mathibane & Nowak, 2019) have shown that problem-solving performance is mediated by whether the testing apparatus is placed in a more sheltered forested environment compared to an open urban environment. Thus, it is important to consider both the social dynamics and level of risk in the environment as predictors of performance on wild cognitive tests to get a more accurate idea of the pressures for problem-solving under different conditions.

Consistency in Water Bottle Solving Behavior

Due to repeated sampling across individuals we tested to see if there was consistency in solving behavior over time. When testing for the effect of repeated presentations of the object on the solve technique chosen, the latency to solve and the level of exploratory diversity when solving – all results pointed towards consistency. This supports our original assumption (and observations of this behavior prior to testing) that individuals in this population are already familiar with this problem and how to solve it. Additionally, with no observable relationship between sex or rank and consistency of solving behaviors, this suggests that access to these objects is not a challenge for developing bottle solving behaviors. If this were the case, we'd expect that only those who have priority of access to these objects (males or high ranked individuals) would be consistent, while those who do not have priority of access (females and low ranked individuals) would be inconsistent.

Overall Solving Behavior for Puzzle Boxes

Regardless of whether the box was solved or not, individuals worked on the puzzle box on average for the same amount of time (~60s). Interestingly, when the box was solved, it was often solved in the same amount of time as the average work time (~60s). This might suggest that these animals have generalized experience with encountering "novel problems" in the urban environment and use a simple heuristic such as "if I haven't gotten a reward in 60s, move onto a new problem". Alternatively, it is possible that these animals have already gained experience with a similar type of object in the urban environment (such as trash cans with locked lids) and have learned that on average it takes ~60s to open these complex containers, after which the returns on that investment are no longer worth the effort. This timing pattern also seems to remain consistent even when split between individual and group trials (Table 11). Curiously, even when looking at solving behavioral patterns when individuals experience social interactions with others, the average work and solve time often vary around the 60 second mark (Table 11). Although further investigation is warranted to test the idea of a tipping point, consistent timing may be indicative of tradeoffs for individuals foraging in the urban environment according to optimal foraging theory. That is, individuals may use optimal foraging heuristics to forage efficiently depending on the costs of acquiring foods such as search or processing costs as well as the benefits acquired from specific food items such as caloric content. Shorter work times may suggest that search costs for additional calories are low, providing individuals with greater benefits to leave a difficult to procure food patch in search of additional patches. Studies seeking to test these assumptions would need to measure these costs and benefits more directly to assess their respective influences on problem-solving behavior.

When we instead look at the exploratory behavior of individuals across both solved and unsolved puzzle box trials, we find that those who do solve seem to show significantly higher exploratory diversity scores compared to those who do not solve. This means that individuals who are more exploratory towards novel objects are more likely to solve them than those who are less exploratory. Similarly, when looking at the effects of exploratory diversity on the amount of time it takes to solve, those with higher exploratory diversity scores take significantly longer to solve the puzzle. This implies that exploratory behavior may incur some ecological tradeoffs that may prove important for solving behavior. For example, higher exploratory tendencies may be beneficial for solving new or novel problems, but this may be offset by costs in time-constraints invested in expressing exploratory behaviors instead of other essential activities such as feeding and socializing. These potential time-constraint costs may inhibit the expression of exploratory behaviors in a setting where information is changing rapidly and is unlikely to be reliable over short time spans.

In our experiment we tested two different mechanisms for solving with the same puzzle box, which resulted in differences in solving behavior. When tested with box top 1 (a mechanism that requires the solver to lift a latch vertically) the puzzle box had a trend towards being more likely to be solved when compared to box top 2 (a mechanism that requires the solver to twist a latch horizontally). Additionally, individuals tested with box top 1 solved significantly faster than those tested with box top 2. Finally, individuals tested with box top 2 showed significantly higher exploratory diversity scores than those tested with box top 1. These results together indicate that the twist latch on box top 2 may have been a more difficult solution than the lift latch on box top 1. This idea is further supported by the distribution of solvers by age category. Individuals who solved box top 1 were relatively evenly distributed across the adult and juvenile categories (26 and 21 respectively), while individuals who solved box top 2 had nearly double the number of adults when compared to juveniles (12 and 5 respectively). Based on the literature, juveniles are known for being more exploratory towards novel objects, show less neophobia (mynas: Miller, Garcia-Pelegrin & Danby, 2022) and are often more likely to solve novel problems than adults (birds: Biondi, Bo & Vassallo, 2010). However, some studies have found that adults are associated with higher rates of exploration and innovation due to the need for experience or technical competency of older individuals (callitrichid monkeys: Kendal, Coe & Laland, 2005; meerkats: Thornton & Samson, 2012; spotted hyenas: Benson-Amram, Weldele & Holekamp, 2013). Thus, the influence of age on problem solving behaviors warrants further investigation. In our experiments, the reduction in solving by juveniles for box top 2 might indicate that this is a more difficult problem that requires more manual dexterity afforded by experienced adults. Overall, it is worth noting that although differences exist in the solving behaviors across box top 1 and 2, most trials that tested either condition resulted in high rates of success (92% and 89% respectively). However, there was only one savvy adult female who was observed to solve both box types across the experimental period (Widow).

Social Interactions & Puzzle Box Solving Behavior

Cognitive experiments conducted under field conditions are often subjected to social interactions or interference by other individuals. Since social interference is likely to influence solving behavior, it is important to distinguish between trials that are conducted with individuals alone without interference compared to those conducted with individuals in the presence of others that may be subject to interference. In our experiments we had nearly half the trials conducted with alone individuals (individual trials), while the other half tested individuals in the presence of others (group trials). Interestingly, regardless of whether individuals were tested individually or in groups, the amount of time individuals work on and solve these novel puzzles is similar, averaging around 60 seconds. However, those who were tested individually were significantly more likely to solve the puzzle box, as well as shown to have significantly higher exploratory diversity scores than those who were tested in group settings. It is possible that this increased likelihood of solving and exploratory behavior in individual trials is afforded by the release of social pressure present in group trials. When looking at the identity of specific individual solvers, there are a few individuals (N=6) that experienced both individual and group trial conditions. However, most individuals only experienced one type of experimental condition, individual or group (10 and 5 individuals respectively). Although we do not have the sample size to investigate whether traits of certain individuals are more likely to participate during individual versus group trials, it is worth noting that this dichotomy for solving may exist. Future studies on solving behavior in the field should consider these differences and strive for large enough sample sizes that afford experimenters to tease apart the effects of these social dynamics from the problem-solving behaviors themselves.

Experimental trials can vary wildly in the number of individuals that encountered the box ranging anywhere from 1 to 30 individuals in a single trial (Figure 24). While most trials included only a handful of individuals (>5), there were a few trials that included many individuals (<5). Thus, simply categorizing trials by whether they were conducted individually compared to in groups may not appropriately represent the nuances of social interference on problem-solving behavior. To explore the diversity of social interactions occurring during group trials we labeled individual instances of participation as whether they occurred in the presence of other well-defined social interactions among individuals, such as displacements, aggression, or sexual activity. We also had many instances of participation in group trials that did not experience any of these social interactions, so we categorized these instances as those who had "abandoned" the problem without explicit evidence of interference from others. Of these defined social interactions, the most common one observed during group trials were displacements, followed by aggressive interactions. Interestingly, in instances where individuals were observed to "abandon" without specific social interactions their average work time on the puzzle box averaged to the same amount of time observed for average solving times and work times regardless of social interference (~60 seconds). In most group trials, individuals would approach and work on the puzzle box sequentially. However, in rare situations multiple individuals would work on the puzzle simultaneously. Simultaneous working on the puzzle box by multiple individuals was more common for juvenile participants than adult individuals, which only happened rarely. Working together with another individual to solve the puzzle may be beneficial in that you might be more likely to solve it and get the food reward. However, it may also be costly in that one partner may not share the food reward, rendering the partnership particularly costly for one participant. For example, there were a handful of events where the puzzle box was solved by one individual, but other individuals nearby came and either consumed the entire reward, or a part of the reward as a scrounging event.

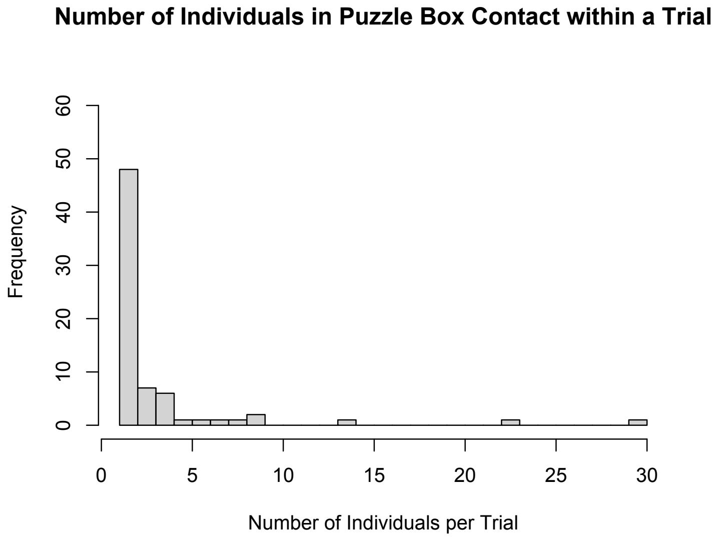


Figure 24. Histogram of the number of individuals that contacted the puzzle box within a trial.

Role of Individual Traits for Solving Puzzle Boxes

One main goal of this study was to explore the predictive power of individual traits on problem-solving behavior. We tested the effect of individual traits such as sex, rank order, as well as several aspects of how individuals interact with the urban environment. Surprisingly, none of these traits influenced the likelihood of individuals to solve the puzzle box or the amount of time it takes to solve the puzzle box. However, when investigating which individual traits influenced exploratory behavior, we found that individuals who fed more on human foods were less exploratory than those who feed less on human foods. This may be counter-intuitive since we might expect a priori that those who interact more frequently with the urban environment would be better at solving due to higher exposure to novel objects. However, upon reflection it makes sense that those who are provisioned at a higher rate would be less likely to exhibit exploratory behaviors since these individuals are afforded a release from individual performance on foraging tasks (such as solving novel food puzzles) since they are more frequently presented with a freely available high caloric food option. Thus, conditions with frequent provisioning or feeding events may favor individuals who have reduced exploratory behaviors due to the potential tradeoffs for imposing time constraints on the time budgets afforded for other behaviors. Interestingly, in a recent study on object manipulation in bonnet macaques, researchers found that provisioning rate was positively correlated with "sophisticated" bottle solving techniques (Pal et al., 2022). These results together might suggest that exploratory diversity is one mechanism through which individuals can learn solving techniques when foraging problems are novel, while environmental attributes such as handling of human objects through provisioning may cause a reduction in exploratory tendencies as solving strategies are developed and honed through behavioral canalization.

Consistency in Puzzle Box Solving Behavior

Specific individuals were targeted for cognitive testing throughout the experimental period with the aim of distributing testing equally across individuals. For individuals who experienced multiple exposures (or presentations), we tested whether they maintained consistency in their solving behaviors across presentations or whether they changed over time as a measure of gaining experience with the task. Although we did not find any significant differences, we did find some trends to suggest that later exposures to the puzzle box may result in a higher likelihood of solving. Similarly, later presentations may be more likely to have shorter solve times and lower scores of exploratory diversity. These trends suggest that individuals may be gaining experience with the task across multiple exposures and as a result are solving the box more often, solving the box quicker as well as canalizing their behaviors toward the puzzle box as a result of honing particular behaviors that are more likely to lead to solving the box.

Conclusions & Future Directions

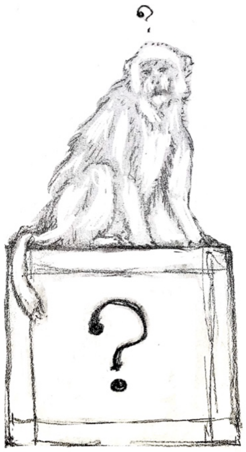
There seems to be great utility in measuring both familiar problems and novel problems with the same population. By knowing the behavioral signature of how individuals approach problems they are very familiar with, we can better interpret behaviors towards objects that are assumed to be completely novel to them. For example, in the familiar water bottle task all individuals were able to solve (N=42) and were highly consistent in their solving behaviors. On the other hand, in the puzzle box task only some individuals were able to solve the box (N=20), and individuals varied in their solving behaviors. One potential reason for this discrepancy in solving success across tasks may be due to the monopolizable potential of each object. For the puzzle box, it was tethered to a single location and was thus highly susceptible to social interference by other individuals during cognitive trials. However, water bottles could be better monopolized by the target individuals and thus were less subjected to social interference. Puzzle solvers with corresponding rank data (N=15) seemed to be evenly distributed across rank orders. Thus, it does not seem likely that access to the puzzle box is likely to influence the ability to solve it. However, even with a novel problem such as the puzzle box, there were some individuals who seemed to not engage in trial and error at all and instead solved the box nearly immediately without exploration. It is hard to say with those individuals whether they were employing insight learning (where you can solve a problem without fiddling by trial and error), or whether they had some previous experience with similar objects, thus facilitating their solving proficiency. It is also possible that these individuals may have gained experience with this task through observing other individuals interact with it. Future analyses of the puzzle box dataset will consider potential mechanisms of social learning through proximity scoring during trials across the experimental period.

Although much of the solving behaviors in the dataset were addressed in the analyses described above, there are several additional analyses that may be interesting for future studies. For example, it would be interesting to investigate the efficiency of consuming the liquid juice reward in the water bottle experiments, since individuals were observed to use different techniques with varying timing tradeoffs. For example, some individuals would remove the bottle cap and drink the juice directly from the bottle opening in a short amount of time. Alternatively, other individuals may open the bottle using the create opening technique and proceed to use their hand to soak up the juice and consume it indirectly over a longer time. These categorized drink techniques could then be paired with the bottle solve techniques to see if certain techniques are more often paired together and whether certain combinations allow for either greater consumption of the juice reward (i.e., less juice lost) or consumption of the juice in a shorter timeframe (latency to consume all juice). Similarly, another interesting analysis on both the bottle and box datasets would be to look at combinations of specific task-directed behaviors to uncover more mechanistic angles to task performance. For example, the variation in the combination or sequence of behaviors used towards objects could provide us with more information on whether individuals are approaching objects the same way every time or whether they adjust their specific behaviors over subsequent presentations. Combinations or strings of behaviors may be adjusted over time as individuals learn solutions for the tasks and further canalize those behaviors to lead to higher rates of success. Future studies on this dataset, and other studies like this, could use methods such as information theory (Reznikova, 2023; Owoeye, Musolesi & Hailes, 2018; Bergman & Beehner, 2023) to detect meaningful patterns that may exist within behavioral strings or combinations when solving foraging tasks.

Despite vast differences in solving success across the two problem solving tasks, there also seemed to be some consistent patterns in solving behaviors. For example, the amount of time it took individuals in this population to solve or work on either the water bottle task or the puzzle box was similar (~60s), regardless of whether the task was solved or not. Although there was variation in both tasks in solve and work time across individuals, the averages across tasks are starkly similar. Despite the novelty of the puzzle box, and the potential differences in difficulty across box top types, most individuals spend on average one minute working on a foraging extraction task such as opening a water bottle or puzzle box. This convergence of timing patterns across different foraging tasks may imply similar time constraints when foraging in the urban environment and provide further support for an optimal foraging heuristic. It is possible that due to the availability of alternative resources in the urban environment, individuals may have learned over time that one minute is an optimal time frame for exploring new foraging options without incurring exceeding costs of missed foraging opportunities.

Although the availability of human objects was not measured directly in this study, in hindsight we would have greatly benefited from that information. This would have provided an idea of how common these types of human induced foraging problems are to this macaque population to assess their influence through familiarity or novelty. Although researchers who have measured these variables did not find any correlations between bottle availability in the environment and solving performance for familiar problems (Pal et al., 2022), this negative result is useful for knowing whether availability is driving performance. Interestingly, in our study on bottles we found that at the individual level there was no effect of the rate of feeding on human food on bottle performance or solution technique, while others have found that the rate of direct provisioning influenced the frequency of cap-directed techniques at the group level (Pal et al., 2022). Furthermore, when we tested individual performance on puzzle boxes, we found that provisioning had a significantly negative effect on exploratory diversity. This suggests that greater experience with human foods may canalize individual behavioral diversity by only retaining behaviors that are most successful for solving. This particular result may have large implications for urban wildlife, where exploratory or complex behaviors may be lost with increased human pressures (chimpanzees: Kuhl et al., 2019). These combined results show the utility of testing both familiar and novel problems with the same population. It also illustrates the potential tradeoffs between focusing on a higher gross level of analysis (such as the group level) compared to a more fine-grained level of analysis (such as the individual level). Future studies would benefit from considering sample sizes that can accommodate both levels of analysis to tease apart individual from group level effects since clearly there are mechanisms operating at multiple levels of organization in urban spaces.

VI. Ch 3. Innovation, Flexibility, and Inhibitory Responses



Introduction

Behavioral flexibility is defined as when an animal makes an adaptive behavioral change in response to changes in their external or internal environment. Behavioral flexibility and plasticity are terms that have been used interchangeably in the literature, resulting in a wide variety of processes being described under these terms. This has made defining what one means by behavioral flexibility very important (Audet & Lefebvre, 2017). In the previous chapter, we examine behavioral flexibility as a measure of exploratory diversity, which has been shown to be instrumental for cognitive problem solving. To build upon this, in the current chapter we measure behavioral flexibility both in terms of exploratory diversity and inhibitory responses, as measured by a modified reversal learning task.

When environments are rapidly changing, behavioral flexibility can be advantageous since flexible individual responses act more quickly than multi-generational responses that have been shaped by natural selection (Price et al 2003). It is thought that behavioral flexibility can be acquired by an organism either through activational or developmental pathways (Snell-Rood, 2012). Activational flexibility assumes that individuals have a repertoire of responses innately available to them and being in a particular environmental context cues the expression of a single preferred response. This is advantageous in rapidly changing environments because it is an innate and fast-acting neural response. Developmental plasticity instead is based on more learned processes and can alter individuals' responses throughout their lifetime as they gain experience. Both processes can result in similar behavioral outcomes; however, it is useful to mention these different pathways as they may pose different advantages when the success or utility of flexible behavior depends on the quickness of the response.

Regardless of the mechanism for behavioral flexibility, its expression rests on the costs and benefits it brings to species under particular environmental conditions (Van Buskirk and Steiner, 2009). For example, developmental plasticity acquired through processes such as learning can be costly in time and brain power, which can also be energetically costly to maintain (Lefebvre & Sol, 2008; Laughlin et al., 1998). These processes take time to complete, and thus would select for organisms with slower life-history strategies (Snell-Rood, 2012). Additionally, an increase in plasticity can result in a higher diversity of motor behaviors, which requires more neural space or capacity (Catania & Kaas, 1997). Further, the costs of plasticity can vary depending on life stage. For example, with developmental plasticity, neural investment is high during early life stages when individuals are sampling a wide variety of behaviors. These behavior patterns, and their associated neurons, are pruned and consolidated over the process of learning (Huttenlocher, 1979), which is thought to considerably reduce the costs of continual adjustment.

The role of environmental predictability on behavioral plasticity has already been discussed at length in our introduction. However, it is worth mentioning here that high variation between generations should favor developmental plasticity, while high variation within generations should favor activational plasticity. This allows individuals to either adjust over their lifetime to current conditions or activate different underlying networks under different conditions, respectively. Similarly, the ability of animals to reverse plastic responses also depends on the heterogeneity of environmental variation (Snell-Rood, 2012). When plasticity is irreversible, coarse-grained variation favors plasticity since it is most likely to closely match the current environment due to few fluctuations over time. However, reversible plasticity is favored with fine-grained environmental variation due to high variability in these parameters over an individual’s lifetime.

While the topic of behavioral flexibility has been widely investigated, assessments of how these traits affect wildlife facing urbanization pressures is relatively new. Despite this, the benefits of plasticity in urban environments are widely accepted (Miranda, 2017). Elements of developmental plasticity such as learning processes have been shown to be able to quickly shift adaptive peaks to new optima (Hinton & Nolan, 1987), providing significant fitness advantages. Once flexible individuals have shifted to new adaptive peaks, the constraints of plasticity should select for refining of the selected phenotype, reducing overall plasticity. For example, wildlife living in areas with high human density have been observed to adaptively shift their activity patterns to either better avoid humans when persecution is common (wolves: Theuerkauf et al., 2003) or increase their overlap with humans when persecution is low (Sclater's monkey: Baket er al., 2014). The possession of traits such as behavioral flexibility and larger brain sizes has been emphasized as a crucial factor in the colonization and persistence of several wildlife species in cities (Sol et al., 2005, 2008). Further, larger brained organisms with more flexibility have been shown to be more successful at increasing levels of human presence in both urban and rural areas (birds: Carrete & Tella, 2011). Even animals who face persecution, such as chimpanzees injured by human snares, have shown behavioral flexibility in compensating for those injuries in complex food processing tasks (Stokes & Byrne, 2001). This shows that organisms can employ behavioral flexibility in a variety of ways to cope with the environmental changes and direct effects of human disturbance.

A classic test of behavioral flexibility is the reversal learning paradigm. In this test, individuals are trained to receive a reward that is paired with a particular cue such as color (e.g. the yellow cup gets consistently baited). Once the subject learns this rule, the experimenter reverses the contingency and measures how long it takes for the subject to inhibit the previously correct response (e.g. choose the yellow cup) and begin exploring alternative options (e.g., choose the grey cup instead). A major drawback to using this classic paradigm is that it requires training of individuals before testing their inhibitory responses. Due to this, the reversal learning paradigm has been extensively used to test the abilities of captive animals (sparrows: Aljadeff & Lotem, 2021; capuchin monkeys: Beran et al., 2017; cottontop tamarins: Gaudio & Snowdon, 2008), but there are relatively few examples of animals being tested in the wild (vervet monkeys: Kumpan, Smeltzer & Teichroeb, 2020; blue tits: Cauchoix et al., 2017) due to the lack of experimental control of subjects. Additionally, little is known about the influence of the training process itself on inhibitory control performance. Thus, a need for testing the inhibitory responses of individuals without active training is warranted for accurate experimental assessments of behavioral flexibility. One way to do this is to allow subjects to explore multi-solution objects naturally, and reverse contingencies that they learn on their own through exploration of the object. A multi-access puzzle box that has solutions that can be locked once they have been learned is one way of creating a modified reversal learning paradigm that probes natural behavioral tendencies and is feasible under field or captive conditions.

Although the multi-access box reversal learning paradigm has been used to test many captive species (reviewed in Shaw & Schmelz, 2017; spotted hyenas: Johnson-Ulrich et al., 2020, raccoons: Daniels et al., 2019; Great apes: Manrique et al., 2013), only a few studies have attempted this with wild populations (described in Auersperg et al., 2012; mouse lemurs: Henke-von der Malsburgh & Fichtel, 2018; red-fronted lemurs: Huebner & Fichtel, 2015). In these studies, inhibition of previous responses was highly predictive of individuals solving multiple solutions. However, these multi-solution puzzle box techniques have never been used to test rhesus macaques, a species often described as having high potential for behavioral flexibility. A recent study on barbary macaques investigated problemsolving abilities using a multi-step foraging problem, but instead of requiring subjects to inhibit previous responses it required them to build upon previously successful responses to maintain success in solving further iterations of the task (Amici et al., 2020). Inhibition in the barbary study was also measured simply by attempts to reach directly through the plexiglass box compared to reaching around through an open door rather than the classic reversal learning measure where individuals must inhibit previously rewarded latch responses to explore new latches with different motor actions (Amici et al., 2020). The careful choice of study species and experimental design makes our study a useful contribution to understanding how individual variation influences innovation and inhibitory responses in rhesus macaques. Testing captive macaques with a reversal learning paradigm that does not require training, will provide us with greater experimental control as well as help us more accurately measure inhibitory responses as they would be represented in the wild.

Finally, the role of neophobia in problem-solving abilities has been studied extensively across a variety of species, however, tests have shown mixed results. Some studies found that juveniles are less neophobic but not necessarily more likely to solve the problem (meerkats: Thornton and Samson, 2012; spotted hyenas: Benson-Amram and Holekamp, 2012), while others found adults to be more innovative than juveniles (Callitrichid monkeys: Kendal et al., 2005). Thus, the relationship between neophobia and innovation clearly needs further exploration, especially in species that have yet to be tested, such as the rhesus macaques.

Objective:

Here we test two major lines of research investigating: (1) the ability for female captive macaques to solve novel problems (i.e., innovation) and (2) their ability to behave flexibly in a modified reversal learning paradigm. To solve more than one novel problem in a multi-access puzzle box (i.e. open more than one door), individuals must employ behavioral flexibility (in terms of exploratory diversity and switching to new solutions) and behavioral inhibition (the suppression of a previously learned response). When individuals first approach the apparatus, it should theoretically be identified as a novel object that they have never encountered before. We expect that individuals who are initially less neophobic with these novel objects will be more likely to solve the puzzle box during testing trials.

In this study we explore whether the inhibition of previously learned responses influences a macaque’s likelihood to solve multiple solutions on a multi-access puzzle box. We also assess the influence of individual traits on innovation of single solutions as well as the likelihood to solve multiple solutions. We expect that inhibitory control enhances success with multiple solutions, where those who interact for a shorter duration of time (or lower frequency of interactions) with previously preferred solutions will be more likely to solve more than one solution of the multi-access puzzle box. Individuals who have higher exploratory diversity scores and are more persistent at working on the puzzle are also expected to be more successful at repeated innovation. However, individual traits may also influence innovation with the multi-access puzzle box. For example, if priority of access to preferred resources is a major factor that influences solving behaviors, we might expect that high ranked or older individuals will be more likely to solve at least one door solution. However, if necessity to gain access to resources instead drives solving behavior, we expect that low ranked or younger individuals will be more likely to solve at least one solution. Furthermore, subjects that possess particular types or combinations of personality traits (which may or may not correlate with rank order) may be more likely to innovate. For example, those who are bolder or are more likely to interact with novel objects may be more likely to solve the multi-access puzzle box. Additionally, individuals who are calmer or gentler may be better able to focus on the task, resulting in a higher likelihood to solving the multi-access puzzle box.

Methods

Study Site and Subjects

All data were collected at the California National Primate Research Center (CNPRC) in Davis, California. The CNPRC is a non-human primate research facility associated with the University of California, Davis. Multi-access puzzle box (MAB) experiments were conducted with fifty adult female rhesus macaques (*Macaca mulatta*). All females selected for this study had one main selection criteria that they had been raised outdoors in large social group enclosures prior to living in indoor paired housing at the time of testing. We also preferentially chose subjects who possessed behavioral predictors from other previously collected datasets, including rank data our lab collected on these individuals years ago when living in large social group enclosures, as well as the BioBehavioral Assessment (BBA) program that has been conducted at the CNPRC for over a decade (Golub et al., 2009; Gottlieb et al., 2018; Capitanio et al., 2017).

We used these rank and BBA measures as predictors for individuals being tested with the multi-access puzzle box. Additionally, subjects were split between two distinct health statuses that may be relevant for captive primates. Nearly half the subjects had been bred as a lineage to eliminate specific pathogens (SPF), whereas the other half had not been isolated for specific breeding purposes (conventional). The health status of this population has been suggested to play a role in the expression of behavioral inhibition in captive rhesus macaques (Capitanio, 2019) and was thus tested here for its significance in how individuals approach novel foraging problems. Additionally, since all subjects had been raised in the large outdoor social enclosures, individuals varied in how much time they had spent living indoors since their relocation. Thus, we calculated the number of months individuals had spent indoors prior to testing to assess whether behavioral inhibition with the MAB may be linked to the length of time since being relocated to indoor housing, which is significantly more constricted in terms of space and social partner opportunities.

Trials were conducted for two months, from March 7th to May 19th of 2022. Experimental testing was mainly conducted in the morning, from 8am to 12pm, but on a few rare occasions it extended until 2pm. Subjects were fed twice daily and provided with water ad libitum in their home cages and during the experimental trials. On the day of testing, subjects were transported from their home cages to the testing cage and given a minimum of 15 minutes to acclimate to the new space. This test enclosure is the same structure as their home cage and is comprised of two adjacent compartments separated by a small door in the center, allowing to keep test subjects separated from the experimental stimuli (MAB) before the trial began (Figure 25). All trial data were video recorded using two cameras, (a SONY Handycam and a Canon Rebel 5) to obtain both zoomed out and close-up views. Once a subject had concluded all experimental testing for the day, they would be transported back to their home cage and reunited with their conspecific social partner.

Figure 25. Photo of our testing location with two adjacent enclosures connected by a small pairing door that allows the focal individual to move between the holding enclosure (right) and the test enclosure containing the multi-access puzzle box (left).

Multi-Access Puzzle Box Task

For this experiment we built a multi-access puzzle box with three solutions, one on each adjacent side, with the last side blank and without a solution (similar design to Daniels et al., 2019). Each side has a different type of latching mechanism to open the box and receive the reward (lifting hook, horizontal slide, or twist; Figure 26). Each one of these solutions (hook, slide, twist) also required the individual to pull the door towards themselves once the latch was in the open position. Another important component of the design is that each solution can be locked during testing, rendering that solution obsolete. The side panels of the box are interchangeable within the aluminum frame, allowing for easy randomization of panel orientation across individuals while minimizing the potential effects of side bias (Guo et al., 2009). We placed a single grape inside the box as a motivating food reward, which is a common favorite treat amongst our captive rhesus macaque population.

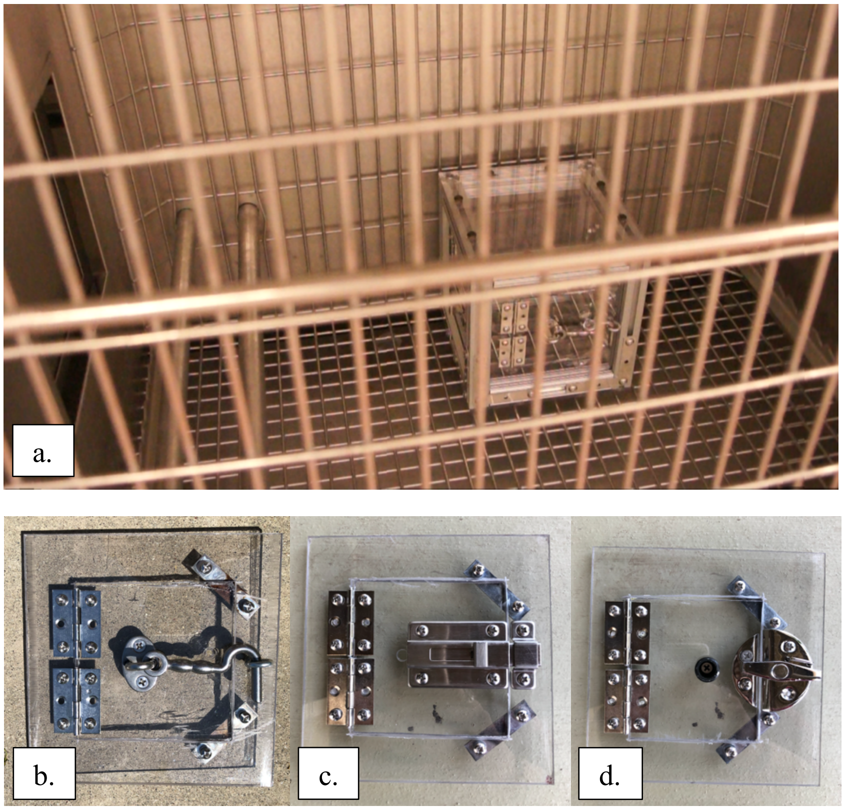


Figure 26. Multi-access puzzle box placement in the testing cage (a), as well as the three door locking mechanisms used in the experiment (b) hook (c) slide (d) twist.

Experimental Protocol

Before test trials began, we provided all subjects with a habituation trial to allow them to first acclimate to the device. During habituation trials, the subject was presented with the MAB but with all the doors unlatched and open so that the grape reward is easy to get by just reaching inside the box. All the subjects must do to pass the habituation trial is reach inside and grab the grape reward. Once subjects passed this habituation trial, they moved onto the testing trial sequence.

During test trials individuals were presented with the puzzle-box with all three solution types in the closed but unlocked position (Figure 27). Thus, individuals can choose to solve any solution type in the first set of trials. The orientation of the three doors was randomized for each individual to avoid potential side bias. We tested individuals a minimum of three times, and a maximum of six times per testing day. If an individual opened the box by solving one of the solution types, the box was rebaited in the same condition (all solutions unlocked) and re-presented to the same focal individual. Test trials ended either when the subject solved a solution, or at a maximum of 10 minutes. If the individual was in contact with the MAB at the 10-minute mark, the individual was given an additional 5 minutes to solve the puzzle. If an individual was able to open the box within the first three trials, individuals would continue to receive the box until they had solved the box three times using the same solution, or the individual failed to solve the box in three consecutive trials (Daniels et al., 2019). Successful individuals were considered those that solved the box at least three times using the same solution. Those individuals would receive the box again on a subsequent day, but with the previously preferred solution locked. Thus, individuals would need to open each solution type a minimum of three times to reach the end of all experimental trials. If individuals solved multiple solutions within a single day, then the solution used most frequently was locked in subsequent trials, while other solutions remained open.

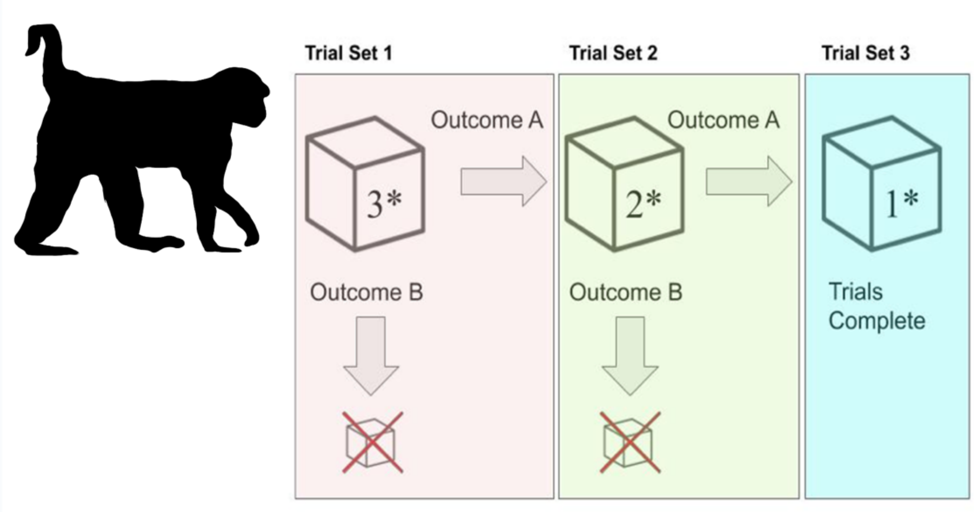


Figure 27. Experimental protocol for the multi-access puzzle box study. The asterisk represents the number of solutions available to the subject to solve. Outcome A represents when an animal solves a single solution consistently a minimum of three times and continues onto the next day of experimentation. Outcome B represents when an animal does not solve a single solution a minimum of three times and drops out of the experiment.

Video Coding & Data Analysis

Videos of MAB solving behavior were analyzed in BORIS (V. 8.20.4, Friard & Gamba, 2016). Prior to beginning each experimental trial, unique information was recorded such as the date, subject tested, as well as the experimental condition such as habituation, day 1, day 2 or day 3 testing. The trial start time was recorded as well as once the subject first touches the MAB. If the subject solved any one of the doors of the MAB, the time was recorded when the subject opens the door as well as when they take the grape reward from inside the box. The latency to solve a particular door was calculated as the number of seconds elapsed from the time when the individual first contacts the box to when they open the door and take the grape reward. All box-directed behaviors were extracted and scored as state behaviors with unique motor patterns. Each unique box-directed behavior was summed together to calculate an exploratory diversity score per individual per trial (range = 1-17). The behaviors included in our ethogram are listed in Table 18. In addition to box-directed behaviors, we also recorded other types of behaviors such as aggressive threats directed towards the human experimenter, stereotypic behaviors, and overall activity levels. For subjects who consistently solved a door on day 1 and moved onto day 2 or day 3 testing, the number of errors or duration of interacting with a previously rewarded door solution was calculated. This error rate would be expected to have a negative relationship with flexibility, where those who perform less errors are more flexible at rule switching or exploring multiple solution choices.

Behavior	**Definition**
Circle	Focal approaches within arm's length and walks around it while attending to it.
Peer	Focal approaches within arm's length and leans down to look through the sides of the box.
Sniff/Lick	Focal brings their face to the box to contact either with or without the tongue extended.
Touch Top	Focal contacts the box by touching the top panel of the box with their hands or feet, including the corners that are adjacent to the top panel.
Touch Front	Focal contacts the box by touching the front panel of the box with their hands or feet, including the latching mechanism.
Touch Left	Focal contacts the box by touching the left panel of the box with their hands or feet, including the latching mechanism.
Touch Right	Focal contacts the box by touching the right panel of the box with their hands or feet, including the latching mechanism.
Bite Top	Focal contacts the box with their open mouth on the top panel of the box, including the corners that are adjacent to the top panel.
Bite Front	Focal contacts the box with their open mouth on the front panel of the box, including the latching mechanism.
Bite Left	Focal contacts the box with their open mouth on the left panel of the box, including the latching mechanism.
Bite Right	Focal contacts the box with their open mouth on the right panel of the box, including the latching mechanism.
Climb	Focal lifts their body up perpendicular to the front of the box using their front limbs.
Stand on	Focal climbs on top of the box, including a minimum of three limbs.
Pull/Push	Focal uses their arms to pull or push the box to cause it to rock but not be displaced due to the fasteners.
Cage Shake	Focal climbs on top of the box, including a minimum of three limbs, and uses their body weight to cause the entire enclosure to shake.
Raise	Lift the latch vertically to unlock and unhook the metal hook to open.
Slide	Slide the latch horizontally to open.
Twist	Twist the latch 90 degrees clockwise to open.
Pull Knob	Pull the door towards the focal to open the door and gain access to the food reward.

Table 18. Ethogram of MAB-directed behaviors.

Behavioral Predictors & Long-term Data

A subset of subjects (N=25) had behavioral data collected by our lab when they lived in large social group enclosures several years prior to testing. These data were collected as a part of the social networks and health project (SNH) from 2013 to 2015 where adult dyadic behaviors were recorded to better understand social interactions and health outcomes in rhesus macaques (McCowan et al., 2016; Balasubramaniam et al., 2018). Dyadic dominance interactions including displacements and aggression were used to calculate ordinal ranks with a network-based calculation using the Perc package in R (Fujii et al., 2020). Ordinal ranks were then scaled to better compare scores across groups of different sizes by dividing ordinal ranks by the total group size. This resulted in a rank index that ranges from 0 to 1, where individuals with 1 represent a high rank, and zero represent a low rank.

Another subset of test subjects (N=27) had been tested on a variety of metrics through the BBA program when they were young infants. The Biobehavioral Assessment consists of separating infants from their mothers at roughly 3-4 months of age and exposing them to a battery of tests over the course of 25 hours. During BBA, infants were assessed on how well they acclimate to the testing space by measuring their activity levels and level of emotionality at the beginning of the separation and again at the end of the testing period. Infants were also scored on a likert scale from 1-7 on 16 individual personality metrics which were later used to calculate four grouping factor scores: Vigilance, Confidence, Gentleness and Nervousness (Table 19). Scale names are based on the highest, positive loading for each scale. Definitions of individual personality measures can be found in S10 while calculations for the testing cage activity and emotionality responses and temperament scales are described in Golub et al., 2009.

Temperament Metric	Definition
Vigilant	Vigilant, NOT depressed, NOT tense, NOT timid
Confident	Gentle, calm, flexible, curious
Gentle	Confident, bold, active, curious, playful
Nervous	Nervous, fearful, timid, NOT calm, NOT confident

Table 19. Definitions for factor scales for temperament in the BBA program at the CNPRC.

Statistical Analysis

We fitted generalized linear mixed models (GLMMs) to test differences in innovation and flexibility with the multi-access puzzle box. All statistical assessments were conducted in the program R using the ‘lme4’ and ‘glmmTMB’ packages (R Core Team, 2022, V4.3.0). For models testing predictors for the likelihood to solve a single door consistently on the multi-access box on day 1, day 2 and day 3 of testing, we used a binomial distribution. For models testing predictors for the latency to solve a solution on the first trial of day 1 of testing we first used a Poisson distribution due to the nature of the continuous variables being count-like (i.e. the number of seconds to solve). These Poisson models were found to be over dispersed and were then shifted to a negative binomial distribution. For models testing predictors for exploratory diversity on the first trial of day 1 of testing we used a Poisson distribution due to lack of evidence for over dispersion and the nature of exploratory diversity being count-like (range = 3-16). For models testing predictors for the number of unique doors solved on day 1 of testing we used a Poisson distribution due to the count-like fashion of number of doors solved which showed no evidence of overdispersion. Predictors related to rank were scaled between zero and one to account for variation in group sizes and its influence on ordinal rank. Predictors related to BBA were z-scored within a yearly cohort of animals tested to control for inter-annual variation.

Ethics and approval declaration

The protocols used in this study were approved by the Institutional Animal Care and Use Committee (IACUC) of the University of California, Davis (protocol # 22691). The research was performed strictly in accordance with the guidelines drafted in this protocol and complied with the legal requirements of National Primate Research Facilities and NIH regulations. This protocol, along with the guidelines and regulations, was designed in consultation with the animal care staff and behavioral management unit of the CNPRC in Davis, California, USA.

Results

Overall Multi-Access Puzzle Box Performance

Out of the fifty females tested, forty-seven of them passed habituation by taking the grape inside the box during the habituation trial (Table 20). Of those who moved onto the testing phase, twenty-one females solved at least one door. Seventeen females solved a door consistently and moved onto day 2 testing. On day 2, ten individuals solved a second door with nine of those solving a second door consistently allowing them to move onto day 3 testing. On day 3, there were seven animals that solved a third door, with six of them solving a third door consistently, completing the testing regime. Although most individuals had short time lags between testing days (2 days max), there was one female who had a longer lag in testing (longer than all other subjects, >3 days) between day 2 and day 3. Although this female solved consistently on both day 1 and day 2, they did not solve on day 3. It is hard to discern whether this lag in testing may have contributed to the lack of solving on day 3 for this individual as it is possible that they may have lost the association between door solves across the interim period between day 2 and day 3 testing sessions.

Condition	N	Solved a Door	Solved Consistently
Habituation	50	N/A	N/A
Day 1	47	21	17
Day 2	17	10	9
Day 3	9	7	6

Table 20. Testing conditions during the MAB experiment including counts of individuals tested (N), those who solved a door, and those who solved a door consistently (i.e. three times within the same session).

Individuals varied in which doors they solved on different testing days. On day 1 most individuals solved the hook door, while a few solved the slide door (Table 21). However, on day 2 when most individuals no longer have access to the hook door because it is locked, it becomes a bit more random regarding which door gets chosen between the slide and twist mechanisms. Twist was solved overall much less often (6/32 solved trials) compared to the other door mechanisms such slide (10/32) and hook (16/32).

Condition	N	Hook	Slide	Twist	(Majority) %
Day 1	50	14	3	0	(Hook) 82%
Day 2	17	1	5	3	(Slide) 55%
Day 3	9	1	2	3	(Twist) 50%

Table 21. Count of individual solvers by testing condition (day 1, day 2, or day 3) and solution type, either hook, slide or twist. The majority of solvers was then calculated for each testing condition and converted into a percentage.

Due to the differences in motor patterns used to solve each solution type, we looked at the average solve time per solution type (i.e. hook, slide or twist) to get an idea of how easy or difficult each solution might be for the subjects. Overall, we found that on day 1 of testing, subjects were on average quicker to solve the hook solution, followed by the slide and twist solutions (Table 22). However, it is notable that there was a significant amount of variation in solve time for all three solutions, which could be attributable to differences in sample size or individual variation in solving behaviors.

Solution Type	N	Mean Solve Time (sec)	SD
Hook	47	134.72	150.01
Slide	14	151.5	111.95
Twist	4	273.5	254.37

Table 22. Solved solutions on Day 1 with the number of trials (N) where that solution was solved, the average solve time in seconds, and the standard deviation of solve time (SD).

Individual Traits & MAB Performance on Day 1

We tested the influence of individual traits of females on the likelihood to solve and latency to solve a single solution consistently on the first day of testing. Some traits were calculated at the time of testing per individual, including age, health status and number of months living indoors. For age, there was a non-significant trend suggesting that younger individuals may be less likely to solve a door on day 1 (S11; $\beta = -0.14$, $p = 0.065$). Younger individuals also had significantly higher exploratory diversity scores than adults (S11; $\beta = -0.03$, $p = 0.007$) and were able to solve significantly more unique doors on day 1 (S11; $\beta = -0.1$, $p = 0.029$) than older individuals. Based on a chi-squared test for categorical data, there appeared to be no significant relationship between an individual's health status and the likelihood to solve a door on day 1 ($\chi^2 = 1.67$, $p = 0.239$). However, there appeared to be a marginally significant relationship between an individual's health status and the likelihood to solve a door on day 2 ($\chi^2 = 4.29$, $p = 0.059$). Using GLMM methods, there also did not seem to be a relationship between an individual's health status and the latency to solve a door on day 1 (S11; $\beta = -0.12$, $p = 0.735$). Finally, there was no effect of the number of months the animal had been living indoors prior to testing on the likelihood to solve (S11; $\beta = -0.001$, $p = 0.862$) or latency to solve (S11; $\beta = -0.0006$, $p = 0.929$) on day 1.

Other individual traits of interest were pulled from previously collected datasets on the same individuals, including rank information for individuals previously living in outdoor enclosures and temperament ratings and behaviors from the BBA Program at the CNPRC. For rank, we found that high ranked individuals take significantly longer to solve a door on day 1 than low ranked individuals (S11; $\beta = 3.28$, $p = 0.0004$). Additionally, high ranked individuals were found to have a nonsignificant trend that implies that high ranked individuals may have higher exploratory diversity scores than low ranked individuals (S11; β = 0.61, p = 0.078). For BBA metrics, we did not find any significant relationships between the same individual predictors, but we did find a marginally significant trend for likelihood to solve on day 1. This trend suggests that females who score high on nervous temperament ratings (S11; β = 1.15, p = 0.058) may be more likely to solve on day 1. We also found two marginally significant trends predicting the latency to solve that suggest that those who score low on gentle (S11; β = -0.53, p = 0.056) and high on nervous (S11; β = 0.52, p = 0.098) temperament ratings may solve the puzzle faster on day 1. The last BBA metric investigated was the acclimation patterns of subjects as measured by the activity and emotionality scores on both day 1 and day 2 of BBA. For activity scores we found a non-significant trend that suggests individuals who are more active on the first day of BBA may be more likely to solve more than one unique door on day 1 than those who were less active on day 1 of BBA (S11; β = 0.54, p = 0.086).

Within-Trial Behaviors and MAB Performance on Day 1

Within-trial behaviors can include behaviors performed within an experimental trial (such as threats towards the experimenter, or stereotypies) as well as puzzle box directed behaviors such as neophobia, work time and exploratory diversity. Neophobia here was simply measured as the latency for an individual to take the grape from inside the open box during the habituation trial. Individuals who took longer to reach inside and take the grape reward were considered to have greater neophobia. Those who scored higher on neophobia had a trend towards being less likely to solve a door on day 1 (S11; β = -0.007, p = 0.091) and solve fewer unique doors on day 1 (S11; β = -0.004, p = 0.061). Those with greater neophobia scores were also observed to have significantly lower exploratory diversity scores (S11; β = 0.0009, p = 0.005).

When investigating the predictive influence of exploratory diversity and work time we found some interesting results. Unsurprisingly, higher exploratory diversity scores (S11; β = 0.16, p = 0.0006) and longer work times (S11; β = 0.008, p = <0.001) were both associated with longer latencies to solve a door on day 1. However, only exploratory diversity significantly predicted likelihood to solve on day 1 (S11; $\beta = 0.31$, $p = 0.006$), whereas work time was not significant (S11; $\beta = -0.001$, $p = 0.664$). Additionally, those with higher exploratory diversity scores solved significantly more unique doors on day 1 (S11; $\beta = 0.19$, $p = 0.001$) whereas work time did not. Work time was also a significant predictor of exploratory diversity, where longer work times had higher exploratory diversity scores (S11; $\beta = 0.002$, $p < 0.001$). In terms of individual traits predicting exploratory diversity, younger individuals had significantly higher scores than older individuals (S11; $\beta = -0.03$, $p = 0.007$). For rank there was a non-significant trend indicating higher ranked individuals may have higher exploratory diversity scores than lower ranked individuals (S11; $\beta = 0.61$, $p = 0.078$). We did not find any significant relationships between within trial behaviors such as stereotypies or threats towards the experimenter and either the likelihood to solve (S11; $\beta = 0.007$, $p = 0.338$) or latency to solve on day 1 (S11; $\beta = 0.11$, $p = 0.355$).

Out of all the MAB-directed behaviors, we calculated which behaviors were more common in the dataset to get an idea of suites of behaviors that may be combined to solve the MAB task. The majority of individuals (Table 21, grey shading) performed behaviors that were related to touching the box, circling, or sniffing the box, climbing or standing on it as well as biting the top. However, fewer individuals performed other MAB-directed behaviors such as biting the right, front or left sides, peering through the side of the box, pulling or pushing the box, performing a cage shake while in contact with the box, as well as solving behaviors (i.e., Raise, Slide, Twist, Pull knob). A summary of MAB-directed behaviors across individuals in the study is provided in Table 21. Additionally, we calculated the intra- and inter-individual variation in exploratory diversity to get a better understanding of its potential role in MAB solving behavior. There appears to be a lot of variation across individual exploratory diversities on the first trial of day 1 (Figure 19; range = 3-16).

Behavior	**# of individuals**	**% of individuals (out of 50 total)**
Touch Top	50	100
Climb	39	78
Sniff/Lick	38	76
Touch Front	34	68
Circle	32	64
Stand on	31	62
Bite Top	28	56
Touch Left	25	50
Peer	23	46
Touch Right	21	42
Bite Front	21	42
Pull/Push	21	42
Pull Knob	19	38
Bite Right	13	26
Raise	13	26
Bite Left	12	24
Cage Shake	5	10
Slide	4	8
Twist	2	4

Table 23. Frequency of MAB-directed behaviors observed across subjects on day 1 trial 1. Grey shading represents the majority of individuals (50% and above), while no shading represents the minority of individuals (49% and below).

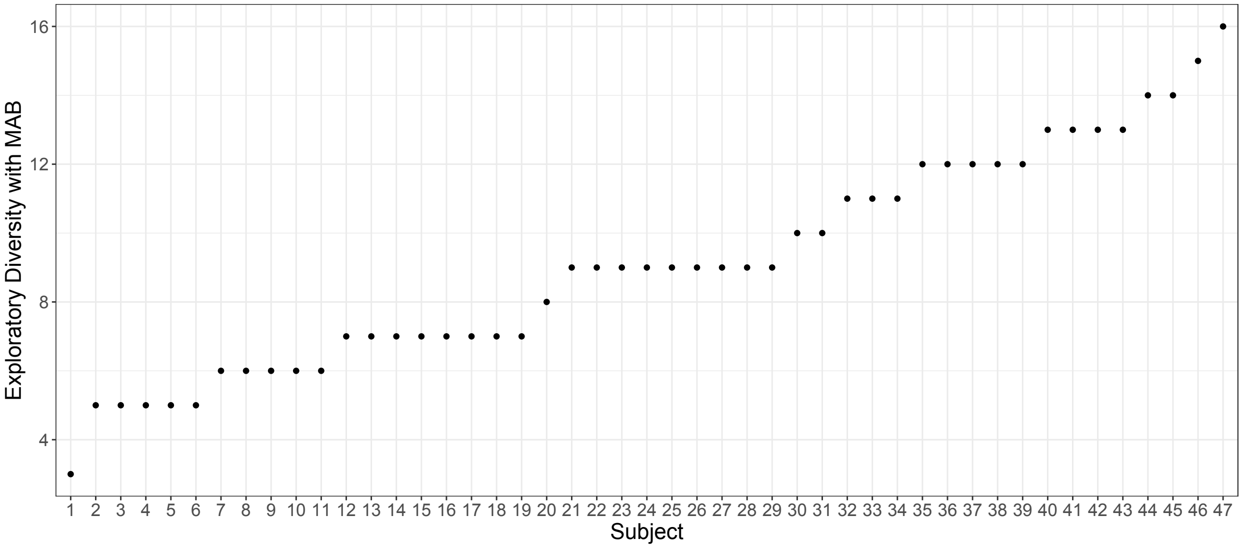


Figure 28. Variation in exploratory diversity across individual adult females tested on Trial 1 of Day 1 of testing with the MAB. Subject names are dummy coded with numbers from 1-47.

Individual Traits & Within-Trial Behaviors on Day 2

Once individuals showed their competency of solving a single door consistently on day 1, they would move to day 2 testing (N=17). To test what makes individuals more likely to innovate across multiple days, and inhibit previously learned responses, we used GLMMs to predict likelihood to solve on day 2. We found that individuals who solved more unique doors on day 1 (S11; $\beta = 0.19$, $p = 0.001$) and had higher exploratory diversity scores (S11; $\beta = 0.32$, $p = 0.017$) were significantly more likely to solve on day 2. From BBA specific predictors, we had two non-significant trends that suggest that those who score high on nervous temperament ratings (S11; $\beta = 1.16$, $p = 0.078$) as well as those who are more active on day 1 of BBA testing (S11; $\beta = 1.1$, $p = 0.081$) may be more likely to solve on day 2. Due to more restricted sample sizes, we did not test the influence of individual traits on the likelihood to solve on day 3.

Reversal Learning & Flexibility in MAB Performance

For individuals who solved on day 1, they moved onto day 2 for additional testing (N=17). To test behavioral flexibility more directly, we calculated the number of errors the individuals made, which was defined as the frequency or duration of behaviors directed towards the previously learned and rewarded side. However, we did not find any significant relationships between either the frequency or duration of errors and the likelihood to solve on either day 2 (S11; frequency $\beta = -0.02$, $p = 0.401$; duration $\beta = 0.005$, $p = 0.314$) or day 3 (S11; frequency $\beta = -0.01$, $p = 0.877$; duration $\beta = 0.001$, $p = 0.939$). Interestingly, the more unique doors an individual solved on day 1 the more likely they were to solve a second door on day 2 (S11; $\beta = 3.16$, $p = 0.002$) but not day 3 (S11; $\beta = 0.11$, $p = 0.691$).

Discussion

Overall MAB Performance

Out of all individuals tested, less than half were able to solve a single door consistently on day 1. The hook solution seemed to be the favored solution on day 1, perhaps due to it being easier than the other two latch mechanisms (Table 22). It is not terribly surprising that neophobia was negatively associated with most solving behaviors with the MAB. Animals who were originally more neophobic towards the box showed lower exploratory diversity scores and had trends to be less likely to solve as well as solve fewer unique doors on day 1. This supports the idea that individuals who are more cautious around novel objects than others will be less successful in extracting food from them, which may reflect a general variation among individuals in risk aversion and successful foraging strategies with novel food objects.

We also found that individuals who differed in health status showed differences in MAB performance. Although there was no detectable relationship between health status and the likelihood to solve a door on day 1, there was a nearly significant relationship with day 2. Females who had been bred without pathogens (i.e. SPF) tended to be less likely to solve a door on day 2. This is counter-intuitive given that previous research has shown that SPF animals have been shown to be more likely to exhibit behavioral inhibition, as defined by withdrawing from novel situations. I hesitate to interpret this finding too much as I suspect it may be a spurious result due to it being a trend and not reaching statistical significance.

Individual Traits & MAB Performance

Regarding the predictability of individual traits on MAB performance, age was a strong predictor of solving on day 1. Younger individuals had higher exploratory diversity scores and solved more unique doors on day 1 as well as trended towards being more likely to solve any door on day 1. This corroborates previous literature that often asserts that juveniles are more commonly described as innovators for new problems and are generally found to be more exploratory than adults. However, age no longer predicted the likelihood to solve a door on day 2, indicating that age may be a more important factor for initial innovation abilities rather than flexibility involved in switching between solving strategies.

Like age effects, there were some significant influences of rank on individual MAB performance on day 1. High ranked individuals were observed to take longer to solve a door on day 1 as well as trended towards greater exploratory diversity scores. Under normal social conditions for macaques, high ranked individuals may not experience strong pressures to work on foraging problems due to priority of access to preferred resources and social dynamics to oversee and maintain. For example, high ranked individuals might spend a considerable amount of time keeping track of the social interactions of others, either to police aggressive interactions among group members or monitor sexual relations among conspecifics, instead of spending time innovating on foraging problems. Animals living under captive conditions with small group sizes or pair-housing such as the subjects in this study may allow for females to express their natural exploratory tendencies upon release from time constraints, foraging costs, and social pressures in the wild. Despite the significant amount of time between when the rank data were collected and when individuals were tested with the MAB, there was still an effect of rank on solving performance. Rank orders in primates have been shown to be relatively stable across years (Shively & Kaplan, 1991; Mori, Watanabe & Yamaguchi, 1989). Due to this, rank effects may be difficult to disentangle with individual temperament as measured by an open field test or observer ratings, which are also considered to be consistent over time and across contexts (Capitanio, 1999). The parallel study of rank effects and temperament ratings may provide useful insights into predictive individual differences in problem solving behavior in the wild. For example, high ranked individuals may be more likely to possess personality traits such as high nervousness and low gentleness, which may contribute to their exploratory tendencies as mechanisms for improved problem-solving abilities. In addition to the BBA temperament scores, there were some nonsignificant trends from the activity scores from day 1. We found that individuals with higher activity scores on the first day of BBA may be more likely to solve on day 2 as well as solve more unique doors on day 1. This result is surprising because, anecdotally, overall activity levels seemed to vary significantly among subjects and those who were more active seemed to be more successful with the

MAB. This might suggest that animals who are overall more reactive to a novel testing environment (as measured in activity levels on day 1 of BBA) may exhibit more exploratory behaviors, overall activity levels and success in solving when tested with a novel foraging puzzle years later.

Within-Trial Behaviors & MAB Performance

Interestingly, exploratory diversity seemed to be more predictive of likelihood to solve on day 1 and day 2 rather than day 3. This may be explained by the fact that individuals with higher exploratory diversity scores solved significantly more unique doors on day 1 than those with lower exploratory diversity. This greater diversity of solving techniques learned on day 1 of testing could provide subjects with alternative options for solving when presented with a locked solution on day 2. However, the influence of exploratory diversity was no longer significant when tested against the likelihood to solve on day 3. This might be explained by the fact that for individuals who had solved on days 1 and 2, the last remaining door was the twist mechanism, which may have been a more difficult latch when compared to the hook and slide mechanism (Table 22). Despite exploratory diversity scores on day 3, individuals may not have solved the door due to the greater level of movement in the latch mechanism itself, requiring the latch to be in a particular singular position before proceeding with the opening of the doors. These overall patterns suggest that exploratory diversity is particularly important when individuals are confronting novel problems. It is hard to say with certainty whether the lack of influence of exploratory diversity of solving on day 3 is due to reduced sample sizes, memory between testing days, or overall difficulty of the third latching mechanism.

Conclusions & Future Directions

Overall, it has become clear that despite living in captive conditions, animals are not inherently more motivated to work for a food reward. Under captive living conditions, rhesus macaques have been observed to work voluntarily for regularly provided foods such as monkey chow (Reinhardt, 1994). Thus, we expected that captive rhesus macaques would be highly motivated to interact with the MAB in our study when the food reward provided was a highly preferred treat that the monkeys only receive during training sessions or on special occasions. However, this did not seem to be the case since most animals tested did not interact with the MAB enough to solve it and get the grape food reward. In fact, some individuals were simply content with not interacting with the puzzle box very much despite having taken the grape in the open habituation treatment. Future studies on MAB performance may consider testing subjects who are more often foraging in a complex environment or need to make more frequent foraging decisions. It is possible that the low rate of solving in our sample was due to the indoor pair-housing conditions of the animals, which is relatively barren or simple compared to a wild environment. For example, indoor pair-housed animals are rationed twice daily and have minimal competitive influences due to being housed with only one other animal, and thus may not be motivated to work on a foraging puzzle. This suggestion that indoor pair-housing influences motivation for interacting with foraging puzzles is further supported by the fact that a different study at the CNPRC with rhesus macaques housed in small outdoor social groups showed high rates of interaction and solving success for a single-solution puzzle box despite having the same single grape food reward (Mayazumder et al., in progress). This implies that the single grape food reward is motivating enough for most animals housed under highly social conditions to work on the puzzle box. Future studies may also benefit greatly from manipulating foraging complexity of test subjects before MAB testing to better understand the relationship between environmental complexity and motivation to work on novel foraging puzzles or overall exploratory tendencies. For example, studies who have provided environmental enrichment to rhesus macaques in small social groups have found it to increase overall exploratory behaviors (Byrne & Suomi, 1991). In combination with other knowledge on rhesus behavior towards novel food puzzles under different housing and social conditions, our current study provides some suggestions that despite a relatively low complexity home environment, there is still natural variation in individual motivations to explore a novel food puzzle.

There were several individual traits that were predictive of solving success with the MAB. Overall, individuals who were less neophobic and younger were more likely to show higher exploratory diversity scores, which is the main factor likely to influence their innovation success on days 1 and 2. Additionally, associated behavioral traits such as rank order or personality traits seem to facilitate exploration and success in solving novel foraging problems. However, replicating these studies with a larger sample size of subjects would allow us to test whether these personality traits are indeed statistically significant, rather than a non-significant trend. Behavioral and urban ecology theories posit that different environmental pressures may select for the expression of different combinations of behaviors or personality traits. Thus, replicating these studies with behavioral rank data that is collected closer to the time of experimental testing as well as more directly comparable between captive and wild conditions would be an interesting addition. Further investigations into this dataset might include looking at combinations of behaviors directed towards the MAB to better understand sequences in the development of solving strategies or approaches to novel foraging tasks. By measuring the frequency and sequence of different combinations of behaviors we may be better able to understand the role of flexibility in problem-solving strategies. Additionally, studies with more time or funding may also benefit from a conducting a set of food preferences before beginning with the puzzle box testing. Our study works under the assumption that grapes are a widely accepted and loved treat for macaques since they are often only used for special circumstances. However, we do know that individuals can hold unique food preferences (Martin et al., 2018), so controlling for this potential condition would help to confirm the motivational state of the subject at the time of testing.

Finally, it is curious that our measures of flexibility (such as the frequency or duration of errors on locked doors) did not have any predictive power for solving on day 2 or day 3. It is hard to discern whether these patterns are because flexibility truly does not have implications for innovating repeatedly or whether there are other ways that we could have measured flexibility that may better represent these processes. Some studies on innovation and flexibility have looked at the intersection between neophobia, problem-solving ability, and flexibility using separate unique tests (Logan et al., 2022; Logan et al., 2023) and while some have found relationships between these independent assays, others have found mixed results. For example, aside from the reversal learning paradigm another classic test of flexibility is the detour task, where subjects must inhibit their immediate impulse to grab food directly out of a clear tube, and instead reach around to the side of the clear tube to grab the food reward (Amici, Aureli & Call, 2008). Adding additional flexibility measures such as the detour task may better help us discern the validity of independent flexibility assessments as well as whether there is consistency in performance across tasks aimed at measuring flexibility. Furthermore, additional assessments that may not measure flexibility directly but may contribute to the expression of flexibility may also prove useful in understanding the role of flexibility in solving novel foraging problems. For example, independent novel object testing both with and without food rewards would be a worthy contribution aimed at teasing apart general exploratory tendencies with novel objects rather than exploratory tendencies with novel food objects, and the role of these traits with behavioral flexibility expression.

VII. Discussion

This thesis provides a comprehensive overview of methods that could be used to investigate the role of behavioral flexibility in animals. Behavioral flexibility can be measured simply as the adjustment or change of behaviors to match current environmental conditions. Flexibility is also often touted as a beneficial trait for solving novel foraging puzzles and innovating in rapidly changing environments. Throughout the three chapters presented here, we use both approaches to measure different types of individual and within trial traits to get a more holistic understanding of the mechanistic underpinnings of behavioral flexibility as well as their natural manifestations in wild behavioral repertoires.

In chapter 1 we found that adult female macaques can employ behavioral flexibility in the urban environment and adjust their behaviors based upon their reproductive phases. To perform optimal flexible behavior individuals must presumably balance the costs and benefits of shifting behaviors based on changing environmental conditions. For example, based on our results adult female macaques were observed to reduce their frequency of interactions with humans when their infants were young and vulnerable. Alternatively, females increased interactions with humans during late pregnancy when energetic needs are expected to be higher than cycling periods, but without the risk of exposing young and vulnerable infants to human interactions that could result in injury or death. Finally, by comparing males and females we show that different sexes can flexibly adjust their behaviors based upon different underlying variables, where females are mainly driven by reproductive phase while males are more driven by seasonality. This study provides supporting evidence that even using purely observational techniques can help to discern patterns of behavior that may be more labile or flexible in response to novel or dynamic changes in the environment. Arguably, these types of observational studies are particularly relevant for assessing behavioral shifts in the urban environment due to the assumed higher level of heterogeneity and unpredictability in environmental variables under these conditions. Observational studies such as these may provide anecdotal evidence of object manipulation and problem-solving in urban spaces. For example, many instances of object manipulation (such as bottle and human food containers) were observed frequently during the long-term study on urban macaque behavior. These observations then fueled the inspiration to conduct cognitive trials on this population to measure flexibility and novel foraging abilities with both wild and captive macaques.

In chapter 2, we used experimental tasks to better understand how individuals solve different types of foraging problems in the urban space. Overall, what we learned from these two sets of experiments is that individual traits can play a significant role in problem-solving behavior, and the role of these individual traits depends upon the familiarity of the task and the monopolizable potential of the testing apparatus. In the familiar water bottle task, there were very few individual traits that predicted performance since all individuals were able to solve it relatively quickly. However, in the novel puzzle box task, there was more variation in ability for individuals to solve the task. Additionally, traits such as feeding more often on human food seemed to reduce exploratory diversity in these individuals which can indirectly affect solving performance. Furthermore, only the novel puzzle box task had an effect of presentation per individual on solving performance, where individuals who were tested repeatedly were more likely to solve, trended towards solving the puzzle quicker, and had lower exploratory diversity scores. The contrasting results from the bottle and box experiments conducted in the same population illustrate the importance of measuring (or verifying) the novelty of a particular stimulus before formal testing to better help with the interpretation of findings during the analysis stage. Furthermore, testing different devices that are presumed to be at different stages of learning or difficulty for the population are helpful to include in the experimental design to facilitate discerning between innate problem-solving abilities and learning processes through experience with objects and solving. For example, the differences in solving behaviors between box top 1 and box top 2 show that even with the same task, individuals can adjust their solving behaviors to match the difficulty of the problem to ensure solving success. Despite the differences between the bottle and box testing paradigms and despite seemingly few potential solutions to the problem, individuals can find unique and new ways to solve the problem that lie outside of the procedures to which most of the population conforms. For example, in the bottle task a few individuals were able to figure out a seemingly rarer technique of removing the bottle cap to consume the juice. On the other hand, for the box task a few individuals were able to solve the box simply by unhooking the latch and rolling the box, so the doors opened on their own without intentional pulling. In one unique case, a female was able to solve the puzzle box by sheer force where upon extreme tension from her canines, she was able to pop open the twist mechanism without deliberate latch manipulation. There were similar anecdotes in chapter 3 with the multi-access puzzle box, where individuals were able to shake the entire cage (i.e. cage shake) to dislodge the hook latch, and subsequently was able to open the doors without explicit latch manipulation. Essentially, even when you think you know what the monkeys will do, they always seem to find a way to surprise experimenters in their level of innovation.

It is particularly interesting to compare the problem-solving and innovation performance across chapters 2 and 3, due to the ability to investigate different types of predictors requiring different types of data collection or datasets. For example, the puzzle boxes in the wild measured interactions with the urban environment as well as group social dynamics as behavioral predictors of solving performance. However, the captive multi-access puzzle box measured personality assessments as a part of the BioBehavioral Assessment at infancy. The personality assessments at infancy would not have been feasible for wild populations due to our data collection period only lasting a few years (per funding allowances), whereas captive facilities have been conducting long term data associated with these assessments regularly on infants as a part of larger base grant initiatives (Biobehavioral characterization of infant rhesus monkeys, Grant No: P51OD011107). The only trait that is shared across wild and captive puzzle box projects is the social rank index variable. Comparing the influence of rank across the two projects is interesting because rank was not a significant predictor in wild groups but was a significant predictor in captive individuals. Most studies investigating the role of social rank on problem-solving performance in wild animals have shown no relationship, which corroborates our wild findings with long-tailed macaques (Amici et al., 2020; Mangalam & Singh, 2013). However, in captivity we found that high ranked individuals had longer latencies to solve on day 1 and lower exploratory diversity. It is interesting in and of itself that these rank effects have persisted despite the behavioral data having been collected years prior to experimental testing. One possible explanation for these results is that when individuals are living in larger social groups, high rankers may have multiple goals vying for their attention, time and energy, such as socializing with others and taking advantage of foraging opportunities. However, when animals are relocated (and tested) in indoor asocial conditions, they may experience less competition for socializing with conspecifics or foraging opportunities, allowing them to express innate exploratory behaviors due to a release of time constraints. It is also possible that high ranked individuals may possess certain personality traits such as being more nervous and less gentle which may lead to higher success and faster solving as supported by our results in chapter 3. Despite both species being categorized in the same social style category, it is also possible that rank effects may be more salient in rhesus macaques compared to long-tailed macaques due to their more highly despotic societies with strict dominance hierarchies. Species differences such as these may explain why we see observed rank effects for captive rhesus macaques but not for wild long-tailed macaques.

Finally, when further comparing experimental assessments of innovation and flexibility between chapters 2 and 3, it seems that despite a release from competitive pressures captive rhesus macaques interact with and solve the testing apparatus at comparable levels to wild long-tailed counterparts (captive rhesus macaques: 17/50 tested & solved; wild long-tailed macaques: 20/42 tested & solved). A priori one may expect that captive individuals might be more motivated or able to solve these types of novel foraging problems due to a lack of complex environmental enrichment and social interference. However, it is also possible that an opposite behavioral pattern may result from a lack of environmental enrichment, where individuals instead become more behaviorally inhibited overall due to a lack of stimulation. Behavioral inhibition has been proposed as an important model for understanding the natural development of behavioral tendencies in primates and humans (Chun & Capitanio, 2015) and is characterized by a propensity to withdraw from novel situations or social interactions. Behavioral inhibition and has also been shown to be predicted by certain individual traits such as captive health status (Capitanio, Sommet & Del Rosso, 2022) and genetic traits (Rogers et al., 2008). The influence of health status on MAB performance showed that females who were bred without pathogens (i.e. SPF) may be less likely to solve a door on day 2, indicating that isolated breeding regimens may influence natural behavioral tendencies and lead to behavioral inhibition. Investigations into whether behavioral inhibition is a significant impediment to the expression of behavioral flexibility is a topic warranted for investigation in future studies to tease apart innate behavioral versus learned environmental influences on the expression of flexibility both in wild and captive populations.

Despite differences in experimental results between chapter 2 and 3, there are some traits such as within trial behaviors which can effectively be compared across studies. Exploratory diversity and work time (i.e. persistence on a problem) are two measures that are often involved in innovation and problem-solving processes. Overall, it seems that despite the type of novel puzzle box (single solution or multi-solution) higher exploratory diversity scores are predictive of a subject's ability to innovate on a novel foraging problem. Similarly, work time is often correlated with exploratory diversity such that those who are more persistent on a problem (i.e. have higher work times) are more likely to have higher exploratory diversity scores. However, these patterns only emerge for novel problems, and are not present when testing problems that have already been learned or are familiar to the population being tested.

Another variable that could potentially have been compared across chapters is neophobia, which is measured as the latency to approach and interact with novel objects. However, due to the unique conditions of testing long-tailed macaques in the wild, it was difficult to standardize the beginning of each trial per individual to test neophobia. For example, often we would attempt to target specific individuals for novel puzzle box testing, and in doing so would wait for those individuals to be alone before deploying the apparatus. However, individuals would often see the apparatus as it was being set up and tethered, during which they could have approached in close distance before the trial even began. Thus, measuring neophobia as the latency to first touch the novel puzzle box was difficult to standardize across individuals in the field. However, in the captive study on rhesus macaques experimenters had significantly greater control over the beginning of trials such that presentation of the puzzle box to subjects was far more standardized across individuals, allowing for a clean standardized measurement for neophobia. In future studies on innovation in wild populations, protocols could be adjusted such that experiments are set up in areas where animals could naturally approach and discover the puzzle box (without being associated with a human experimenter) and those approach behaviors could be recorded from a distance to get a measurement of neophobia in the wild. However, researchers interested in implementing this type of protocol should be warned that conducting enough trials to get a worthy enough sample size to test the effects of individual traits may take significantly longer using this strategy than the targeted subject's strategy.

The three projects outlined in this thesis look at both direct mechanisms of behavioral flexibility, as well as how organisms may employ flexibility in foraging decisions. Overall, these projects contribute to our understanding of how individuals vary in behavioral flexibility, how flexibility is employed to solve problems within their environment, and how macaques can use flexibility to cope with and thrive in urban environments that are highly dynamic. These projects have broad implications for the conservation or coexistence of species alongside humans, by considering their cognitive abilities to employ effective management strategies and avoid a "cognition-arms race" for nuisance species (Barrett, Stanton & Benson-Amram, 2018). While many studies in comparative cognition have taken a top-down approach (de Waal & Ferrari, 2010), we employ both a top-down observational approach to measure natural variation in behavioral flexibility as well as a bottom-up approach to investigate potential mechanisms of behavioral flexibility in macaques. This combination of approaches is particularly useful because a better understanding of mechanisms for behavioral flexibility may allow for more effective comparison across species. We combine these technical assessments with more holistic examinations of behavioral flexibility in individual behavior to better understand how organisms may employ flexibility in everyday foraging problems. These theoretical approaches provide a framework to explore how mechanisms of flexibility are employed by wildlife in other systems, particularly under differing levels of predictability. These methods may prove effective in forming predictions for how organisms may cope with rapidly changing environments, especially human-induced rapid environmental change.

In closing, it is incredibly valuable to take a multi-faceted approach to studying a topic like behavioral flexibility because it allows you to test different types of predictor variables to get a deeper or more unified understanding of the subject in question. For example, in chapter 1 we measured how naturally occurring behaviors can be flexible for macaques over time and contexts. In the subsequent chapters we dive into experimental techniques where we tested both wild conditions (chapter 2) and captive (chapter 3) conditions, allowing us different affordances or previously collected datasets to use as predictors. Captive animals have lifelong documented histories, that are rich with systematic personality assessments requiring high levels of experimental control. Wild animals on the other hand have more limited background behavioral data. Captive conditions also provide ample experimental control over how the research is conducted, while in the wild there are no limits to the interruptions or number of variables at play during experimental tests. For example, I had plenty of humans walk through or near the puzzle box during experimental trials which could have affected the subject's solving behaviors. There was also ample social interference or observing by conspecifics during the puzzle box trials, whereas in captive groups individuals were purposefully isolated before testing. All in all, this thesis has leveraged the power of observational and experimental approaches to studying behavioral flexibility mechanisms such as problem-solving as well as manifestations at both the individual and population level.

VIII. References

Abegg, C. (2002). Macaque evolution and dispersal in insular south-east Asia. *Biological Journal of the Linnean Society*, *75*(4), 555-576.

Aljadeff, N., & Lotem, A. (2021). Task-dependent reversal learning dynamics challenge the reversal paradigm of measuring cognitive flexibility. *Animal Behaviour*, *179*, 183-197.

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, *49*(3-4), 227-266.

Altmann, J., & Samuels, A. (1992). Costs of maternal care: infant-carrying in baboons. *Behavioral ecology and sociobiology*, *29*(6), 391-398.

Amici, F., Aureli, F., & Call, J. (2008). Fission-fusion dynamics, behavioral flexibility, and inhibitory control in primates. *Current Biology*, *18*(18), 1415-1419.

Amici, F., Caicoya, A. L., Majolo, B., & Widdig, A. (2020). Innovation in wild Barbary macaques (Macaca sylvanus). *Scientific Reports*, *10*(1), 4597.

Aplin, L. M., Sheldon, B. C., & Morand-Ferron, J. (2013a). Milk bottles revisited: social learning and individual variation in the blue tit, Cyanistes caeruleus. *Animal Behaviour*, *85*(6), 1225-1232.

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cole, E. F., Cockburn, A., & Sheldon, B. C. (2013b). Individual personalities predict social behaviour in wild networks of great tits (Parus major). *Ecology letters*, *16*(11), 1365-1372.

Archie, E. A., Altmann, J., & Alberts, S. C. (2014). Costs of reproduction in a long-lived female primate: injury risk and wound healing. *Behavioral ecology and sociobiology*, *68*(7), 1183-1193.

Ardito, G. (1976). Check-list of the data on the gestation length of primates. *Journal of human evolution*, *5*(2), 213-222.

Audet, J. N., & Lefebvre, L. (2017). What's flexible in behavioral flexibility?. *Behavioral Ecology*, *28*(4), 943-947.

Auersperg, A. M., Gajdon, G. K., & von Bayern, A. M. (2012). A new approach to comparing problem solving, flexibility and innovation. *Communicative & integrative biology*, *5*(2), 140-145.

Balasubramaniam, K., Beisner, B., Guan, J., Vandeleest, J., Fushing, H., Atwill, E., & McCowan, B. (2018). Social network community structure and the contact-mediated sharing of commensal E. coli among captive rhesus macaques (Macaca mulatta). *PeerJ*, *6*, e4271.

Balasubramaniam, K. N., Marty, P. R., Samartino, S., Sobrino, A., Gill, T., Ismail, M., Saha, R., Beisner, B., Kaburu, S., Bliss-Moreau, E., Arlet, M., Ruppert, N., Ismail, A., Sah, S. A. M., Mohan, L., Rattan, S., Kodandaramaiah, U., & McCowan, B. (2020). Impact of individual demographic and social factors on human–wildlife interactions: a comparative study of three macaque species. *Scientific Reports*, *10*(1), 21991.

Bardi, M., Shimizu, K., Fujita, S., Borgognini-Tarli, S., & Huffman, M. A. (2001). Social behavior and hormonal correlates during the perinatal period in Japanese macaques. *Hormones and Behavior*, *39*(3), 239-246.

Baker, L. R., Olubode, O. S., Tanimola, A. A., & Garshelis, D. L. (2014). Role of local culture, religion, and human attitudes in the conservation of sacred populations of a threatened 'pest' species. *Biodiversity and conservation*, *23*(8), 1895-1909.

Barrett, L. P., Stanton, L. A., & Benson-Amram, S. (2019). The cognition of 'nuisance' species. *Animal behaviour*, *147*, 167-177.

Bates, D., Mächler, M., Bolker, B. M. & Walker, S. C. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*. 67, 20 (2015).

Battles, A. C., & Kolbe, J. J. (2019). Miami heat: Urban heat islands influence the thermal suitability of habitats for ectotherms. *Global change biology*, *25*(2), 562-576.

Benson-Amram, S., & Holekamp, K. E. (2012). Innovative problem solving by wild spotted hyenas. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1744), 4087-4095.

Beran, M. J., Klein, E. D., Evans, T. A., Chan, B., Flemming, T. M., Harris, E. H., Washburn, D. A. & Rumbaugh, D. M. (2008). Discrimination reversal learning in capuchin monkeys (Cebus apella). *The Psychological Record*, *58*, 3-14.

Bergman, T. J., & Beehner, J. C. (2023). Information Ecology: an integrative framework for studying animal behavior. *Trends in Ecology & Evolution*.

Berman, C. M., Li, J., Ogawa, H., Ionica, C., & Yin, H. (2007). Primate tourism, range restriction, and infant risk among Macaca thibetana at Mt. Huangshan, China. *International Journal of Primatology*, *28*(5), 1123-1141.

Bernstein, I. S., Weed, J. L., Judge, P. G., & Ruehlmann, T. E. (1989). Seasonal weight changes in male rhesus monkeys (Macaca mulatta). *American Journal of Primatology*, *18*(3), 251-257.

Biondi, L. M., Bó, M. S., & Vassallo, A. I. (2010). Inter-individual and age differences in exploration, neophobia and problem-solving ability in a Neotropical raptor (Milvago chimango). *Animal cognition*, *13*, 701-710.

Bókony, V., Lendvai, Á. Z., Vágási, C. I., Pătraş, L., Pap, P. L., Németh, J., Vincze, E., Papp, S., Preiszner, B., Seress, G. & Liker, A. (2014). Necessity or capacity? Physiological state predicts problem-solving performance in house sparrows. *Behavioral Ecology*, *25*(1), 124-135.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist*, *161*(1), 1-28.

Borrego, N., & Dowling, B. (2016). Lions (Panthera leo) solve, learn, and remember a novel resource acquisition problem. *Animal cognition*, *19*, 1019-1025.

Brooks M. E., Kristensen K., van Benthem K. J., Magnusson A., Berg C. W., Nielsen A., Skaug H. J., Maechler M., Bolker B. M. (2017). "glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling." *The R Journal*, *9*(2), 378–400.

Brotcorne, F., Giraud, G., Gunst, N., Fuentes, A., Wandia, I. N., Beudels-Jamar, R. C., Poncin, P., Huynen, M. C., & Leca, J. B. (2017). Intergroup variation in robbing and bartering by long-tailed macaques at Uluwatu Temple (Bali, Indonesia). *Primates*, *58*, 505-516.

Brown, C., & Braithwaite, V. A. (2005). Effects of predation pressure on the cognitive ability of the poeciliid Brachyraphis episcopi. *Behavioral Ecology*, *16*(2), 482-487.

Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral ecology and sociobiology*, *65*, 23-35.

Burnham, K. P., & Anderson, D. R. (2002). Model selection and multimodel inference: a practical-theoretical approach. *Journal of Wildife Management.*

Buyantuyev, A., & Wu, J. (2009). Urbanization alters spatiotemporal patterns of ecosystem primary production: A case study of the Phoenix metropolitan region, USA. *Journal of Arid Environments*, *73*(4-5), 512-520.

Byrne, G. D., & Suomi, S. J. (1991). Effects of woodchips and buried food on behavior patterns and psychological well-being of captive rhesus monkeys. *American Journal of Primatology*, *23*(3), 141-151.

Cano-Huertes, B., Rangel-Negrín, A., Coyohua-Fuentes, A., Chavira-Ramírez, D. R., Canales-Espinosa, D., & Dias, P. A. D. (2017). Reproductive energetics of female mantled howlers (Alouatta palliata). *International Journal of Primatology*, *38*, 942-961.

Capitanio, J.P., Blozis, S.A., Snarr, J., Steward, A., McCowan, B.J. Do "birds of a feather flock together" or do "opposites attract"? Behavioral responses and temperament predict success in pairings of rhesus monkeys in a laboratory setting. American Journal of Primatology, 2017, 79:1-11. PMC5344041.

Capitanio, J. P., & Mason, W. A. (2019). Personality as adaptation: Perspectives from nonhuman primates.

Capitanio, J. P. Behavioral inhibition in nonhuman primates: The elephant in the room. Pp. 17-33 in K. Pérez-Edgar, N. A. Fox, Behavioral Inhibition, 2019. Springer.

Capitanio, J. P. (1999). Personality dimensions in adult male rhesus macaques: Prediction of behaviors across time and situation. *American Journal of Primatology: Official Journal of the American Society of Primatologists*, *47*(4), 299-320.

Capitanio, J. P., Sommet, N., & Del Rosso, L. (2022). The relationship of maternal rank, 5-HTTLPR genotype, and MAOA-LPR genotype to temperament in infant rhesus monkeys (Macaca mulatta). *American Journal of Primatology*, *84*(6), e23374.

Carrete, M., & Tella, J. L. (2011). Inter-individual variability in fear of humans and relative brain size of the species are related to contemporary urban invasion in birds. *PloS one*, *6*(4).

Catania, K. C., & Kaas, J. H. (1997). Somatosensory fovea in the star-nosed mole: behavioral use of the star in relation to innervation patterns and cortical representation. *Journal of Comparative Neurology*, *387*(2), 215-233.

Cauchard, L., Boogert, N. J., Lefebvre, L., Dubois, F., & Doligez, B. (2013). Problem-solving performance is correlated with reproductive success in a wild bird population. *Animal Behaviour*, *85*(1), 19-26.

Cauchoix, M., Hermer, E., Chaine, A. S., & Morand-Ferron, J. (2017). Cognition in the field: comparison of reversal learning performance in captive and wild passerines. *Scientific reports*, *7*(1), 12945.

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem.

Chun, K., & Capitanio, J. P. (2016). Developmental consequences of behavioral inhibition: A model in rhesus monkeys (Macaca mulatta). *Developmental science*, *19*(6), 1035-1048.

Cole, E. F., & Quinn, J. L. (2012). Personality and problem-solving performance explain competitive ability in the wild. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1731), 1168-1175.

Cole, E. F., Morand-Ferron, J., Hinks, A. E., & Quinn, J. L. (2012). Cognitive ability influences reproductive life history variation in the wild. *Current Biology*, *22*(19), 1808-1812.

Comins, J. A., Russ, B. E., Humbert, K. A., & Hauser, M. D. (2011). Innovative coconut-opening in a semi free-ranging rhesus monkey (Macaca mulatta): a case report on behavioral propensities. *Journal of ethology*, *29*(1), 187-189.

Cooper, T., Liew, A., Andrle, G., Cafritz, E., Dallas, H., Niesen, T., Slater, E., Stockert, J., Vold, T., Young, M., & III, J. M. (2019). Latency in problem solving as evidence for learning in varanid and helodermatid lizards, with comments on foraging techniques. *Copeia*, *107*(1), 78-84.

Cunningham, E., & Janson, C. (2007). A socioecological perspective on primate cognition, past and present. *Animal Cognition*, *10*(3), 273-281.

Dall, S. R., Giraldeau, L. A., Olsson, O., McNamara, J. M., & Stephens, D. W. (2005). Information and its use by animals in evolutionary ecology. *Trends in ecology & evolution*, *20*(4), 187-193.

Dang, D. C., Chaouat, G., Delmas, A., Hureau, J., Hidden, G., & Lassau, J. P. (1992). Assessment of factors responsible for variability of birth weight in the long-tailed macaque (Macaca fascicularis). *Folia Primatologica*, *59*(3), 149-156.

Daniels, S. E., Fanelli, R. E., Gilbert, A., & Benson-Amram, S. (2019). Behavioral flexibility of a generalist carnivore. *Animal cognition*, *22*(3), 387-396.

Devictor, V., Julliard, R., & Jiguet, F. (2008). Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos*, *117*(4), 507-514.

De Waal, F. B., & Davis, J. M. (2003). Capuchin cognitive ecology: cooperation based on projected returns. *Neuropsychologia*, *41*(2), 221-228.

De Waal, F. B., & Ferrari, P. F. (2010). Towards a bottom-up perspective on animal and human cognition. *Trends in cognitive sciences*, *14*(5), 201-207.

Dias, P. A. D., Rangel-Negrín, A., & Canales-Espinosa, D. (2011). Effects of lactation on the time-budgets and foraging patterns of female black howlers (Alouatta pigra). *American Journal of Physical Anthropology*, *145*(1), 137-146.

Dickman, A. J. (2012). From cheetahs to chimpanzees: a comparative review of the drivers of human-carnivore conflict and human-primate conflict. *Folia Primatologica*, *83*(3-6), 377-387.

Dingemanse, N. J., Kazem, A. J., Réale, D., & Wright, J. (2010). Behavioural reaction norms: animal personality meets individual plasticity. *Trends in ecology & evolution*, *25*(2), 81-89.

Donihue, C. M., & Lambert, M. R. (2015). Adaptive evolution in urban ecosystems. *Ambio*, *44*(3), 194-203.

Domjan, M. (2005). Pavlovian conditioning: A functional perspective. *Annu. Rev. Psychol.*, *56*, 179-206.

Dufour, D. L., & Sauther, M. L. (2002). Comparative and evolutionary dimensions of the energetics of human pregnancy and lactation. *American Journal of Human Biology*, *14*(5), 584-602.

Dukas, R. (2004). Causes and consequences of limited attention. *Brain, Behavior and Evolution*, *63*(4), 197-210.

Dunham, A. E., Erhart, E. M., & Wright, P. C. (2011). Global climate cycles and cyclones: consequences for rainfall patterns and lemur reproduction in southeastern Madagascar. *Global Change Biology*, *17*(1), 219-227.

Dunham, N. T., & Rodriguez-Saona, L. E. (2018). Nutrient intake and balancing among female Colobus angolensis palliatus inhabiting structurally distinct forest areas: Effects of group, season, and reproductive state. *American Journal of Primatology*, *80*(7), e22878.

Dunlap, A. S., & Stephens, D. W. (2009). Components of change in the evolution of learning and unlearned preference. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1670), 3201-3208.

Eccard, J. A., & Liesenjohann, T. (2014). The importance of predation risk and missed opportunity costs for context-dependent foraging patterns. *PloS one*, *9*(5).

Fa, J. E., & Lindburg, D. G. (Eds.). (1996). *Evolution and ecology of macaque societies*. Cambridge University Press.

Fairbanks, L. A., & McGuire, M. T. (1993). Maternal protectiveness and response to the unfamiliar in vervet monkeys. *American Journal of Primatology*, *30*(2), 119-129.

Feeney, M. C., Roberts, W. A., & Sherry, D. F. (2011). Mechanisms of what-where-when memory in black-capped chickadees (Poecile atricapillus): Do chickadees remember "when"?. *Journal of comparative psychology*, *125*(3), 308.

Fooden, J. (1982). Ecogeographic segregation of macaque species. *Primates*, *23*(4), 574-579.

Foster, R. J., Harmsen, B. J., & Doncaster, C. P. (2010). Habitat use by sympatric jaguars and pumas across a gradient of human disturbance in Belize. *Biotropica*, *42*(6), 724-731.

Friard, O., & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in ecology and evolution*, *7*(11), 1325-1330.

Fuentes, A., & Gamerl, S. (2005). Disproportionate participation by age/sex classes in aggressive interactions between long-tailed macaques (Macaca fascicularis) and human tourists at Padangtegal monkey forest, Bali, Indonesia. *American Journal of Primatology*, *66*(2), 197-204.

Fujii, K., Jin, J., Vandeleest, J., Shev, A., Beisner, B., McCowan, B., Fushing, H. (2020). Perc: Using Percolation and Conductance to Find Information Flow Certainty in a Directed Network. R package version 0.1.5. https://CRAN.R-project.org/package=Perc

Fürtbauer, I., Christensen, C., Bracken, A., O'Riain, M. J., Heistermann, M., & King, A. J. (2020). Energetics at the urban edge: Environmental and individual predictors of urinary C-peptide levels in wild chacma baboons (Papio ursinus). *Hormones and Behavior*, *126*, 104846.

Gaudio, J. L., & Snowdon, C. T. (2008). Spatial cues more salient than color cues in cotton-top tamarins (Saguinus oedipus) reversal learning. *Journal of Comparative Psychology*, *122*(4), 441.

Gehrt, S. D., Brown, J. L., & Anchor, C. (2011). Is the urban coyote a misanthropic synanthrope? The case from Chicago. *Cities and the Environment (CATE)*, *4*(1), 3.

Ginsburg, S., & Jablonka, E. (2010). The evolution of associative learning: A factor in the Cambrian explosion. *Journal of theoretical biology*, *266*(1), 11-20.

Girard-Buttoz, C., Heistermann, M., Rahmi, E., Marzec, A., Agil, M., Fauzan, P. A., & Engelhardt, A. (2014). Mate-guarding constrains feeding activity but not energetic status of wild male long-tailed macaques (Macaca fascicularis). *Behavioral ecology and sociobiology*, *68*(4), 583-595.

Golub, M.S., Hogrefe, C.E., Widaman, K.F., Capitanio, J.P. Iron deficiency anemia and affective response in rhesus monkey infants. Developmental Psychobiology, 2009, 51, 47-59. PMC3443197

Gottlieb, D. H., Del Rosso, L., Sheikhi, F., Gottlieb, A., McCowan, B., & Capitanio, J. P. (2018). Personality, environmental stressors, and diarrhea in Rhesus macaques: an interactionist perspective. *American journal of primatology*, *80*(12), e22908.

Gould, L., Power, M. L., Ellwanger, N., & Rambeloarivony, H. (2011). Feeding behavior and nutrient intake in spiny forest-dwelling ring-tailed lemurs (Lemur catta) during early gestation and early to mid-lactation periods: Compensating in a harsh environment. *American Journal of Physical Anthropology*, *145*(3), 469-479.

Griffin, A. S., & Guez, D. (2014). Innovation and problem solving: a review of common mechanisms. *Behavioural Processes*, *109*, 121-134.

Grove, M. (2012). Space, time, and group size: a model of constraints on primate social foraging. *Animal Behaviour*, *83*(2), 411-419.

Gumert, M. D., Hamada, Y., & Malaivijitnond, S. (2013). Human activity negatively affects stone tool-using Burmese long-tailed macaques Macaca fascicularis aurea in Laem Son National Park, Thailand. *Oryx*, *47*(4), 535-543.

Gumert, M. D., & Malaivijitnond, S. (2012). Marine prey processed with stone tools by burmese long-tailed macaques (Macaca fascicularis aurea) in intertidal habitats. *American Journal of Physical Anthropology*, *149*(3), 447-457.

Guo, K., Meints, K., Hall, C., Hall, S., & Mills, D. (2009). Left gaze bias in humans, rhesus monkeys and domestic dogs. *Animal cognition*, *12*(3), 409-418.

Han, J. Y., Baik, J. J., & Lee, H. (2014). Urban impacts on precipitation. *Asia-Pacific Journal of Atmospheric Sciences*, *50*(1), 17-30.

Hare, B. (2001). Can competitive paradigms increase the validity of experiments on primate social cognition?. *Animal Cognition*, *4*(3-4), 269-280.

Harrison, M. J. (1983). Age and sex differences in the diet and feeding strategies of the green monkey, Cercopithecus sabaeus. *Animal Behaviour*, *31*(4), 969-977.

Harrison, X. A., Donaldson, L., Correa-Cano, M. E., Evans, J., Fisher, D. N., Goodwin, C. E., & Inger, R. (2018). A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ*, *6*, e4794.

Haus, T., Ferguson, B., Rogers, J., Doxiadis, G., Certa, U., Rose, N. J., Teepe, R., Weinbauer, G. F., & Roos, C. (2014). Genome typing of nonhuman primate models: implications for biomedical research. *Trends in Genetics*, *30*(11), 482-487.

Hawkins, T. H. (1950). Opening of milk bottles by birds. *Nature*, *165*(4194), 435-436.

Healy, S. D. (2012). Animal cognition: the trade-off to being smart. *Current Biology*, *22*(19), R840-R841.

Henke-von der Malsburg, J., & Fichtel, C. (2018). Are generalists more innovative than specialists? A comparison of innovative abilities in two wild sympatric mouse lemur species. *Royal Society open science*, *5*(8), 180480.

Horrocks, J. A., & Baulu, J. (1988). Effects of trapping on the vervet (Cercopithecus aethiops sabaeus) population in Barbados. *American Journal of Primatology*, *15*(3), 223-233.

Huebner, F., & Fichtel, C. (2015). Innovation and behavioral flexibility in wild redfronted lemurs (Eulemur rufifrons). *Animal cognition*, *18*(3), 777-787.

Hinton, G. E., & Nowlan, S. J. (1987). How learning can guide evolution. *Complex systems*, *1*(3), 495-502.

Hoelzer, G. A. (1996). Evolutionary relationships of the macaques. *Evolution and ecology of macaque societies*, 3-19.

Hsu, M. J., Kao, C. C., & Agoramoorthy, G. (2009). Interactions between visitors and Formosan macaques (Macaca cyclopis) at Shou-Shan Nature Park, Taiwan. *American Journal of Primatology*, *71*(3), 214-222.

Huebner, F., Fichtel, C., & Kappeler, P. M. (2018). Linking cognition with fitness in a wild primate: fitness correlates of problem-solving performance and spatial learning ability. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1756), 20170295.

Huttenlocher, P. R. (1979). Synaptic density in human frontal cortex-developmental changes and effects of aging. *Brain Res*, *163*(2), 195-205.

Isden, J., Panayi, C., Dingle, C., & Madden, J. (2013). Performance in cognitive and problem-solving tasks in male spotted bowerbirds does not correlate with mating success. *Animal Behaviour*, *86*(4), 829-838.

Jacobson, S. L., Puitiza, A., Snyder, R. J., Sheppard, A., & Plotnik, J. M. (2021). Persistence is key: investigating innovative problem solving by Asian elephants using a novel multi-access box. *Animal Cognition*, (25), 657-669.

Jaman, M. F., & Huffman, M. A. (2013). The effect of urban and rural habitats and resource type on activity budgets of commensal rhesus macaques (Macaca mulatta) in Bangladesh. *Primates*, *54*(1), 49-59.

Johnson, E. C. (2007). Rhesus macaques (Macaca mulatta) are not neophobic toward novel food with a high sugar content. *American Journal of Primatology: Official Journal of the American Society of Primatologists*, *69*(5), 591-596.

Kaburu, S. S., Beisner, B., Balasubramaniam, K. N., Marty, P. R., Bliss-Moreau, E., Mohan, L., & McCowan, B. (2019). Interactions with humans impose time constraints on urban-dwelling rhesus macaques (Macaca mulatta). *Behaviour*, *1*(aop), 1-28.

Kawai, M. (1965). Newly-acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima Islet. *Primates*, *6*(1), 1-30.

Keagy, J., Savard, J. F., & Borgia, G. (2009). Male satin bowerbird problem-solving ability predicts mating success. *Animal Behaviour*, *78*(4), 809-817.

Keagy, J., Savard, J. F., & Borgia, G. (2011). Complex relationship between multiple measures of cognitive ability and male mating success in satin bowerbirds, Ptilonorhynchus violaceus. *Animal Behaviour*, *81*(5), 1063-1070.

Kendal, R. L., Coe, R. L., & Laland, K. N. (2005). Age differences in neophilia, exploration, and innovation in family groups of callitrichid monkeys. *American Journal of Primatology*, *66*(2), 167-188.

Key, C., & Ross, C. (1999). Sex differences in energy expenditure in non–human primates. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *266*(1437), 2479-2485.

Koganezawa, M., & Imaki, H. (1999). The effects of food sources on Japanese monkey home range size and location, and population dynamics. *Primates*, *40*(1), 177-185.

Kühl, H. S., Boesch, C., Kulik, L., Haas, F., Arandjelovic, M., Dieguez, P., & Ayimisin, E. A. (2019). Human impact erodes chimpanzee behavioral diversity. *Science*, *363*(6434), 1453-1455.

Kumpan, L. T., Smeltzer, E. A., & Teichroeb, J. A. (2020). Animal cognition in the field: performance of wild vervet monkeys (Chlorocebus pygerythrus) on a reversal learning task. *Animal Cognition*, *23*, 523-534.

Kylafis, G., & Loreau, M. (2008). Ecological and evolutionary consequences of niche construction for its agent. *Ecology letters*, *11*(10), 1072-1081.

Laland, K. N., & Reader, S. M. (1999). Foraging innovation in the guppy. *Animal Behaviour*, *57*(2), 331-340.

Laland, K. N., & Reader, S. M. (1999). Foraging innovation is inversely related to competitive ability in male but not in female guppies. *Behavioral Ecology*, *10*(3), 270-274.

Lappan, S. (2009). The effects of lactation and infant care on adult energy budgets in wild siamangs (Symphalangus syndactylus). *American Journal of Physical Anthropology*, *140*(2), 290-301.

Laughlin, S. B., van Steveninck, R. R. D. R., & Anderson, J. C. (1998). The metabolic cost of neural information. *Nature neuroscience*, *1*(1), 36-41.

Lefebvre, L., & Sol, D. (2008). Brains, lifestyles and cognition: are there general trends?. *Brain, behavior and evolution*, *72*(2), 135-144.

Lefebvre, L. (2011). Taxonomic counts of cognition in the wild. *Biology letters*, *7*(4), 631-633.

Le Roux, A., Mathibane, N., & Nowak, K. (2019). Wild Samango Monkeys, Cercopithecus mitis, Balance Risk and Opportunity to Interact with Novel Objects in Village Gardens. *International Journal of Primatology*, 1-10.

Logan, C., McCune, K., LeGrande-Rolls, C., Marfori, Z., Hubbard, J., & Lukas, D. (2023). Implementing a rapid geographic range expansion-the role of behavior changes. *Peer Community Journal*, *3*.

Logan, C., Lukas, D., Blaisdell, A., Johnson-Ulrich, Z., MacPherson, M., Seitz, B., Sevichik, A. & McCune, K. (2023). Behavioral flexibility is manipulable and it improves flexibility and innovativeness in a new context. *Peer Community Journal*, *3*.

Logan, C. J., McCune, K. B., MacPherson, M., Johnson-Ulrich, Z., Rowney, C., Seitz, B., Blaisdell, A., Deffner, D., & Wascher, C. A. (2022). Are the more flexible individuals also better at inhibition. *Anim Behav Cogn*, *9*, 14-36.

Lowry, Hélène, Alan Lill, and Bob BM Wong. "Behavioural responses of wildlife to urban environments." *Biological reviews* 88.3 (2013): 537-549.
Maestripieri, D. (1999). Changes in social behavior and their hormonal correlates during pregnancy in pig-tailed macaques. *International Journal of Primatology*, *20*(5), 707-718.

Luncz, L. V., Svensson, M. S., Haslam, M., Malaivijitnond, S., Proffitt, T., & Gumert, M. (2017). Technological response of wild macaques (Macaca fascicularis) to anthropogenic change. *International Journal of Primatology*, *38*, 872-880.

Maestripieri, D., & Wallen, K. (1995). Interest in infants varies with reproductive condition in group-living female pigtail macaques (Macaca nemestrina). *Physiology & Behavior*, *57*(2), 353-358.

Maestripieri, D. (1999). Changes in social behavior and their hormonal correlates during pregnancy in pig-tailed macaques. *International Journal of Primatology*, *20*(5), 707-718.

Malaivijitnond, S., Lekprayoon, C., Tandavanittj, N., Panha, S., Cheewatham, C., & Hamada, Y. (2007). Stone-tool usage by Thai long-tailed macaques (Macaca fascicularis). *American Journal of Primatology*, *69*(2), 227-233.

Mandalaywala, T. M., Higham, J. P., Heistermann, M., Parker, K. J., & Maestripieri, D. (2014). Physiological and behavioural responses to weaning conflict in free-ranging primate infants. *Animal behaviour*, *97*, 241-247.

Mangalam, M., & Singh, M. (2013). Flexibility in food extraction techniques in urban free-ranging bonnet macaques, Macaca radiata. *Plos One*, *8*(12).

Manrique, H. M., Völter, C. J., & Call, J. (2013). Repeated innovation in great apes. *Animal Behaviour*, *85*(1), 195-202.

Marshall, H. H., Carter, A. J., Coulson, T., Rowcliffe, J. M., & Cowlishaw, G. (2012). Exploring foraging decisions in a social primate using discrete-choice models. *The American Naturalist*, *180*(4), 481-495.

Martin, P., & Bateson, P. (1993). Measuring Behaviour. Cambridge University Press.

Martin, A. L., Franklin, A. N., Perlman, J. E., & Bloomsmith, M. A. (2018). Systematic assessment of food item preference and reinforcer effectiveness: Enhancements in training laboratory-housed rhesus macaques. *Behavioural processes*, *157*, 445-452.

Marty, P. R., Beisner, B., Kaburu, S. S., Balasubramaniam, K., Bliss-Moreau, E., Ruppert, N., & McCowan, B. (2019a). Time constraints imposed by anthropogenic environments alter social behaviour in longtailed macaques. *Animal behaviour*, *150*, 157-165.

Marty, P. R., Balasubramaniam, K. N., Kaburu, S. S., Hubbard, J., Beisner, B., Bliss-Moreau, E., & Mohan, L. (2019b). Individuals in urban dwelling primate species face unequal benefits associated with living in an anthropogenic environment. *Primates*, 1-7.

Matsumura, S. (1999). The evolution of "egalitarian" and "despotic" social systems among macaques. *Primates*, *40*(1), 23-31.

McCabe, G. M., & Fedigan, L. M. (2007). Effects of reproductive status on energy intake, ingestion rates, and dietary composition of female Cebus capucinus at Santa Rosa, Costa Rica. *International Journal of Primatology*, *28*, 837-851.

McCowan, B., Beisner, B., Bliss-Moreau, E., Vandeleest, J., Jin, J., Hannibal, D., & Hsieh, F. (2016). Connections matter: social networks and lifespan health in primate translational models. *Frontiers in Psychology*, *7*, 433.

McLinn, C. M., & Stephens, D. W. (2006). What makes information valuable: signal reliability and environmental uncertainty. *Animal Behaviour*, *71*(5), 1119-1129.

McKinney, T. (2015). A classification system for describing anthropogenic influence on nonhuman primate populations. *American Journal of Primatology*, *77*(7), 715-726.

McKinney, T. (2011). The effects of provisioning and crop-raiding on the diet and foraging activities of human-commensal white-faced capuchins (Cebus capucinus). *American Journal of Primatology*, *73*(5), 439-448.

Melin, A. D., Young, H. C., Mosdossy, K. N., & Fedigan, L. M. (2014). Seasonality, extractive foraging and the evolution of primate sensorimotor intelligence. *Journal of Human Evolution*, *71*, 77-86.

Mettke-Hofmann, C., Winkler, H., & Leisler, B. (2002). The significance of ecological factors for exploration and neophobia in parrots. *Ethology*, *108*(3), 249-272.

Mettke-Hofmann, C (2014). Cognitive ecology: ecological factors, life-styles, and cognition. *Wiley Interdisciplinary Reviews: Cognitive Science, 5*(3), 345-360.

Meulman, E. J., Sanz, C. M., Visalberghi, E., & van Schaik, C. P. (2012). The role of terrestriality in promoting primate technology. *Evolutionary Anthropology: Issues, News, and Reviews*, *21*(2), 58-68.

Mikula, P., Šaffa, G., Nelson, E., & Tryjanowski, P. (2018). Risk perception of vervet monkeys Chlorocebus pygerythrus to humans in urban and rural environments. *Behavioural processes*, *147*, 21-27.

Miller, R., Garcia-Pelegrin, E., & Danby, E. (2022). Neophobia and innovation in Critically Endangered Bali myna, Leucopsar rothschildi. *Royal Society Open Science*, *9*(7), 211781.

Miranda, A. C. (2017). Mechanisms of behavioural change in urban animals: the role of microevolution and phenotypic plasticity. In *Ecology and conservation of birds in urban environments* (pp. 113-132). Springer, Cham.

Mitani, J. C., Gros-Louis, J., & Richards, A. F. (1996). Sexual dimorphism, the operational sex ratio, and the intensity of male competition in polygynous primates. *The American Naturalist*, *147*(6), 966-980.

Moll, R. J., Cepek, J. D., Lorch, P. D., Dennis, P. M., Robison, T., Millspaugh, J. J., & Montgomery, R. A. (2018). Humans and urban development mediate the sympatry of competing carnivores. *Urban Ecosystems*, *21*(4), 765-778.

Morand-Ferron, J., & Quinn, J. L. (2015). The evolution of cognition in natural populations. *Trends in cognitive sciences*, *19*(5), 235-237.

Mori, A., Watanabe, K., & Yamaguchi, N. (1989). Longitudinal changes of dominance rank among the females of the Koshima group of Japanese monkeys. *Primates*, *30*, 147-173.

Morzillo, A. T., de Beurs, K. M., & Martin-Mikle, C. J. (2014). A conceptual framework to evaluate human-wildlife interactions within coupled human and natural systems. *Ecology and Society*, *19*(3).

Moubarac, J. C., Martins, A. P. B., Claro, R. M., Levy, R. B., Cannon, G., & Monteiro, C. A. (2013). Consumption of ultra-processed foods and likely impact on human health. Evidence from Canada. *Public health nutrition*, *16*(12), 2240-2248.

Murray, C. M., Lonsdorf, E. V., Eberly, L. E., & Pusey, A. E. (2009). Reproductive energetics in free-living female chimpanzees (Pan troglodytes schweinfurthii). *Behavioral Ecology*, *20*(6), 1211-1216.

Negrín, A. R., Fuentes, A. C., de la Torre Herrera, A., Huertes, B. C., Cruz, E. R., Ceccarelli, E., Espinosa, E. G., Ramirez, D. C., Espinoza, D. M., Canales-Espinosa, D., Lastra, N. M., Miros, P. C., Santiago, S. C., Garau, S., & Dias, P. A. (2021). Female reproductive energetics in mantled howler monkeys (Alouatta palliata): A follow-up study. *American Journal of Physical Anthropology, 174* (3), 396-406.

Nippak, P. M., & Milgram, N. W. (2005). An investigation of the relationship between response latency across several cognitive tasks in the beagle dog. *Progress in Neuro-Psychopharmacology and Biological Psychiatry*, *29*(3), 371-377.

Nowak, K., Wimberger, K., Richards, S. A., Hill, R. A., & Le Roux, A. (2017). Samango monkeys (Cercopithecus albogularis labiatus) manage risk in a highly seasonal, human-modified landscape in Amathole Mountains, South Africa. *International journal of primatology*, *38*(2), 194-206.

Nunn, C. L. (1999). The number of males in primate social groups: a comparative test of the socioecological model. *Behavioral Ecology and Sociobiology*, *46*(1), 1-13.

O'Connor, V. L., Thomas, P., Chodorow, M., & Borrego, N. (2022). Exploring innovative problem-solving in African lions (Panthera leo) and snow leopards (Panthera uncia). *Behavioural Processes*, *199*, 104648.

Odling-Smee, L. C., Boughman, J. W., & Braithwaite, V. A. (2008). Sympatric species of threespine stickleback differ in their performance in a spatial learning task. *Behavioral ecology and sociobiology*, *62*(12), 1935-1945.

Oro, D., M. Genovart, G. Tavecchia, M. S. Fowler, and A. Martínez-Abraín. 2013. Ecological and evolutionary implications of food subsidies from humans. Ecology Letters 16:1501-1514.

Owoeye, K., Musolesi, M., & Hailes, S. (2018). Characterizing animal movement patterns across different scales and habitats using information theory. *bioRxiv*, 311241.

Pal, A., Mahato, S., Leca, J. B., & Sinha, A. (2022). Blowing the lid off! Bottle-directed, extractive foraging strategies in synurbic bonnet macaques Macaca radiata in southern India. *Frontiers in Psychology*, *13*, 973566.

Petit, O., Abegg, C., & Thierry, B. (1997). A comparative study of aggression and conciliation in three cercopithecine monkeys (Macaca fuscata, Macaca nigra, Papio papio). *Behaviour*, *134*(5-6), 415-432.

Plavcan, J. M. (2001). Sexual dimorphism in primate evolution. *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists*, *116*(S33), 25-53.

Pravosudov, V. V., & Roth II, T. C. (2013). Cognitive ecology of food hoarding: the evolution of spatial memory and the hippocampus. *Annual Review of Ecology, Evolution, and Systematics*, *44*, 173-193.

Preiszner, B., Papp, S., Pipoly, I., Seress, G., Vincze, E., Liker, A., & Bókony, V. (2017). Problem-solving performance and reproductive success of great tits in urban and forest habitats. *Animal cognition*, *20*(1), 53-63.

Proops, L., Grounds, K., Smith, A. V., & McComb, K. (2018). Animals remember previous facial expressions that specific humans have exhibited. *Current Biology*, *28*(9), 1428-1432.

Queller, D. C. (1997). Why do females care more than males?. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *264*(1388), 1555-1557.

Quinn, G. P., & Keough, M. J. (2002). *Experimental design and data analysis for biologists*. Cambridge university press.

R Core Team. (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2012.

Reader, S. M., & Laland, K. N. (2001). Primate innovation: sex, age and social rank differences. *International Journal of Primatology*, *22*(5), 787-805.

Reader, S. M., & Laland, K. N. (Eds.). (2003). *Animal innovation* (Vol. 10). Oxford: Oxford University Press.

Reader, S. M. (2007). Environmentally invoked innovation and cognition. *Behavioral and Brain Sciences*, *30*(4), 420-421.

Rehage, J. S., & Sih, A. (2004). Dispersal behavior, boldness, and the link to invasiveness: a comparison of four Gambusia species. *Biological Invasions*, *6*(3), 379-391.

Reinhardt, V. (1994). Caged rhesus macaques voluntarily work for ordinary food. *Primates*, *35*, 95-98.

Reitsema, L. J., Partrick, K. A., & Muir, A. B. (2016). Inter-individual variation in weaning among rhesus macaques (Macaca mulatta): Serum stable isotope indicators of suckling duration and lactation. *American Journal of Primatology*, *78*(10), 1113-1134.

Reznikova, Z. (2023). Information Theory Opens New Dimensions in Experimental Studies of Animal Behaviour and Communication. *Animals*, *13*(7), 1174.

Richard, A. F., Goldstein, S. J., & Dewar, R. E. (1989). Weed macaques: the evolutionary implications of macaque feeding ecology. *International Journal of Primatology*, *10*(6), 569.

Richards, S. A. (2005). Testing ecological theory using the information-theoretic approach: examples and cautionary results. *Ecology*, *86*(10), 2805-2814.

Rogers, J., Shelton, S. E., Shelledy, W., Garcia, R., & Kalin, N. H. (2008). Genetic influences on behavioral inhibition and anxiety in juvenile rhesus macaques. *Genes, Brain and Behavior*, *7*(4), 463-469.

Rosati, A. G. (2017). Foraging cognition: reviving the ecological intelligence hypothesis. *Trends in cognitive sciences*, *21*(9), 691-702.

Rose, L. M. (1994). Sex differences in diet and foraging behavior in white-faced capuchins (Cebus capucinus). *International Journal of Primatology*, *15*(1), 95-114.

Ruvio, L. V., Stone, A. I., & Fienup, M. (2017). Reproductive status affects the feeding ecology and social association patterns of female squirrel monkeys (Saimiri collinsi) in an Amazonian rainforest. *American Journal of Primatology*, *79*(6), e22657.

Saj, T., Sicotte, P., & Paterson, J. D. (1999). Influence of human food consumption on the time budget of vervets. *International Journal of Primatology*, *20*, 977-994.

Schülke, O., Heistermann, M., & Ostner, J. (2014). Lack of evidence for energetic costs of mate-guarding in wild male Aaaamese macaques (Macaca assamesis). *International Journal of Primatology*, *35*(3-4), 677-700.

Senigaglia, V., & Bejder, L. (2020). Pregnancy cravings: visitation at a food-provisioning site is driven by the reproductive status of bottlenose dolphins. *Tourism in Marine Environments*, *15*(3-4), 237-248.

Serio-Silva, J. C., Hernández-Salazar, L. T., & Rico-Gray, V. (1999). Nutritional composition of the diet of Alouatta palliata mexicana females in different reproductive states. *Zoo Biology*, *18*(6), 507-513.

Seyfarth, R. M., & Cheney, D. L. (2015). Social cognition. *Animal Behaviour*, *103*, 191-202.

Shaw, R. C., & Schmelz, M. (2017). Cognitive test batteries in animal cognition research: evaluating the past, present and future of comparative psychometrics. *Animal cognition*, *20*(6), 1003-1018.

Shively, C. A., & Kaplan, J. R. (1991). Stability of social status rankings of female cynomolgus monkeys, of varying reproductive condition, in different social groups. *American Journal of Primatology*, *23*(4), 239-245.

Short, K. H., & Petren, K. (2008). Boldness underlies foraging success of invasive Lepidodactylus lugubris geckos in the human landscape. *Animal Behaviour*, *76*(2), 429-437.

Sih, A., & Bell, A. M. (2008). Insights for behavioral ecology from behavioral syndromes. *Advances in the Study of Behavior*, *38*, 227-281.

Silk, Joan, et al. "Gestation length in rhesus macaques (Macaca mulatta)." *International Journal of Primatology* 14.1 (1993): 95-104.

Snell-Rood, E. C. (2013). An overview of the evolutionary causes and consequences of behavioural plasticity. *Animal Behaviour*, *85*(5), 1004-1011.

Sol, D. (2009). The cognitive-buffer hypothesis for the evolution of large brains'. *Cognitive ecology II*, 111-136.

Sol, D., Duncan, R. P., Blackburn, T. M., Cassey, P., & Lefebvre, L. (2005a). Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences*, *102*(15), 5460-5465.

Sol, D., Lefebvre, L., & Rodríguez-Teijeiro, J. D. (2005b). Brain size, innovative propensity and migratory behaviour in temperate Palaearctic birds. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1571), 1433-1441.

Sol, D., Griffin, A. S., Bartomeus, I., & Boyce, H. (2011). Exploring or avoiding novel food resources? The novelty conflict in an invasive bird. *PLoS One*, *6*(5).

Sol, D., Griffin, A. S., & Bartomeus, I. (2012). Consumer and motor innovation in the common myna: the role of motivation and emotional responses. *Animal Behaviour*, *83*(1), 179-188.

Spelt, A., Soutar, O., Williamson, C., Memmott, J., Shamoun-Baranes, J., Rock, P., & Windsor, S. (2021). Urban gulls adapt foraging schedule to human-activity patterns. *Ibis*, *163*(1), 274-282.

Stephens, D. W. (1981). The logic of risk-sensitive foraging preferences. *Animal Behaviour*, 29(2), 628-629.

Stephens, D. W. (2008). Decision ecology: foraging and the ecology of animal decision making. *Cognitive, Affective, & Behavioral Neuroscience*, *8*(4), 475-484.

Stokes, E. J., & Byrne, R. W. (2001). Cognitive capacities for behavioural flexibility in wild chimpanzees (Pan troglodytes): the effect of snare injury on complex manual food processing. *Animal Cognition*, *4*(1), 11-28.

Szabo, B., Damas-Moreira, I., & Whiting, M. J. (2020). Can cognitive ability give invasive species the means to succeed? A review of the evidence. *Frontiers in Ecology and Evolution*, *8*, 187.

Tarlow, E. M., & Blumstein, D. T. (2007). Evaluating methods to quantify anthropogenic stressors on wild animals. *Applied Animal Behaviour Science*, *102*(3-4), 429-451.

Tebbich, S., & Teschke, I. (2014). Coping with uncertainty: woodpecker finches (Cactospiza pallida) from an unpredictable habitat are more flexible than birds from a stable habitat. *PLoS One*, *9*(3).

Teichroeb, J. A., & Chapman, C. A. (2014). Sensory information and associative cues used in food detection by wild vervet monkeys. *Animal cognition*, *17*(3), 517-528.

Thatcher, H. R., Downs, C. T., & Koyama, N. F. (2019). Positive and negative interactions with humans concurrently affect vervet monkey (Chlorocebus pygerythrus) ranging behavior. *International Journal of Primatology*, *40*, 496-510.

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

Thierry, B., Singh, M., & Kaumanns, W. (Eds.). (2004). *Macaque societies: a model for the study of social organization* (Vol. 41). Cambridge University Press.

Thompson, M. (2013). Comparative reproductive energetics of human and nonhuman primates. *Annual Review of Anthropology*, *42*, 287-304.

Thornton, A., & Samson, J. (2012). Innovative problem solving in wild meerkats. *Animal Behaviour*, *83*(6), 1459-1468.

Touitou, S., Heistermann, M., Schülke, O., & Ostner, J. (2021). The effect of reproductive state on activity budget, feeding behavior, and urinary C-peptide levels in wild female Assamese. *Behavioral Ecology and Sociobiology*, *75*(9), 1-22.

Van Buskirk, J., & Steiner, U. K. (2009). The fitness costs of developmental canalization and plasticity. *Journal of evolutionary biology*, *22*(4), 852-860.

van Schaik, C. P. V., & Noordwijk, M. A. V. (1985). Interannual variability in fruit abundance and the reproductive seasonality in Sumatran long-tailed macaques (Macaca fascicularis). *Journal of Zoology*, *206*(4), 533-549.

van Schaik, C. P., & Deaner, R. O. (2003). Life history and cognitive evolution in primates. *Animal social complexity*.

van De Waal, E., & Bshary, R. (2010). Contact with human facilities appears to enhance technical skills in wild vervet monkeys (Chlorocebus aethiops). *Folia Primatologica*, *81*(5), 282-291.

van de Waal, E., Renevey, N., Favre, C. M., & Bshary, R. (2010). Selective attention to philopatric models causes directed social learning in wild vervet monkeys. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1691), 2105-2111.

Webster, S. J., & Lefebvre, L. (2001). Problem solving and neophobia in a columbiform–passeriform assemblage in Barbados. *Animal Behaviour*, *62*(1), 23-32.

Werner, R. M., Montrey, R. D., Roberts, C. R., Tsoy, A. C. T., & Huxsoll, D. L. (1980). *Establishment of a cynomolgus monkey (Macaca fascicularis) breeding colony in Malaysia: a feasibility study*. Institute for Medical Research Kuala Lumpur (Malaysia).

Whiten, A., & Byrne, R. W. (1988). The Machiavellian intelligence hypotheses: Editorial. In R. W. Byrne & A. Whiten (Eds.), *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes, and humans* (p. 1–9). Clarendon Press/Oxford University Press.

Whiten, A., & van Schaik, C. P. (2007). The evolution of animal 'cultures' and social intelligence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1480), 603-620.

Williams, B. K., Nichols, J. D., & Conroy, M. J. (2002). *Analysis and management of animal populations*. Academic Press.

Williams, B. L., Holtfreter, R. W., Ditchkoff, S. S., & Grand, J. B. (2011). Trap style influences wild pig behavior and trapping success. *The Journal of Wildlife Management*, *75*(2), 432-436.

Wright, T. F., Eberhard, J. R., Hobson, E. A., Avery, M. L., & Russello, M. A. (2010). Behavioral flexibility and species invasions: the adaptive flexibility hypothesis. *Ethology Ecology & Evolution*, *22*(4), 393-404.

Wrogemann, D., Radespiel, U., & Zimmermann, E. (2001). Comparison of reproductive characteristics and changes in body weight between captive populations of rufous and gray mouse lemurs. *International Journal of Primatology*, *22*, 91-108.