THE CONTEXTS OF SOCIAL LEARNING IN WILD VERVET MONKEYS

CHRISTINA MARIE NORD
Behavior Analysis, MS, University of North Texas, 2014

A thesis submitted
in partial fulfilment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

EVOLUTION AND BEHAVIOUR

Department of Psychology
University of Lethbridge
LETHBRIDGE, ALBERTA, CANADA

THE CONTEXTS OF SOCIAL LEARNING IN WILD VERVET MONKEYS

CHRISTINA MARIE NORD

Date of defense: July 28, 2021

Dr. L. Barrett	Professor	Ph.D.
Dr. S. Henzi	Professor	Ph.D.
Thesis Co-Supervisors		
Dr. J. Leca	Associate Professor	Ph.D.
Thesis Examination Committee Member		
Dr. U. Kothe	Full Professor	Ph.D.
Internal External Examiner Department of Chemistry & Biochemistry Faculty of Arts and Science		
Dr. P. Izar	Associate Professor	Ph.D.
External Examiner University of São Paulo São Paulo, Brazil		
Dr. D. Logue	Associate Professor	Ph.D.
Chair, Thesis Examination Committee		

DEDICATION

“I think, at a child's birth, if a mother could ask a fairy godmother to endow it with the most useful gift, that gift should be curiosity.”

— Eleanor Roosevelt

For my mother, Peggy, the only sister among six to graduate high school, but was taken from this earth shortly after I was accepted into my doctoral program.

For my godmother, Rebecca, who fulfilled her spiritual duties by keeping me in science books, kits, and conversations.

For my sister, also Rebecca, who engendered my first interest in social learning during our childhood when I insisted that she do everything I did the way I did it, but now, in adulthood, embodies the etymology of “sister” by being “one’s own woman” to me.

And for all of the little girls who love reading books and catching lighting bugs and poking at mushrooms—never question the validity of your own curiosity, and your right to speak what you know.

ABSTRACT

Using both observational and experimental methods, I explored the conditions under which wild vervet monkeys (*Chlorocebus pygerythrus*) learned from one another during 12 months of field study. I paid particular attention to the contextual nature of social learning, applying a behavior analytic approach that focused on behavior—the relationship between organism and environment—rather than on individual attributes, in order to understand which behavioral transmission pathways were available to the vervets, as well as how social dynamics and individual differences influenced learning. Overall, my findings demonstrate that by taking a behavior analytic approach, we can expand the unit of analysis for cognition beyond individual animals to one that situates the organism within its environment. Doing so allows us to realize that cognition can be distributed across the environment to include not only the behavior of individual animals, but also their interactions with one another and their environments.

ACKNOWLEDGEMENTS

Science is a social practice, and I like to think that my practice began early in life as I followed my dad around while he patiently answered every single question I could think to ask. He also taught me that for every rule there is a reasonable exception when he interrupted a very strict bedtime schedule, waking me in the dead of night, to see the Hale-Bop comet.

The Barrett-Henzi Lab and Samara Vervet Monkey Project fully embraces the social practice of science, and I can confidently say that this thesis is wholly the product of the supportive conditions our lab maintains. From the beginning of my studies, I was not only welcomed in, but welcomed with open arms—rare for a radical behaviorist poking her nose in a field beyond her own. Thank you to every member of the lab and project, who number almost as many as the monkeys, but luckily, are more willing to recount the latest episode of Bake-off or dance to Queen on a hot Karoo night. I cannot list each of you, for you are more than the sum of individuals--but if you're reading this, know for certain that you were a critical component to the most formative experience of my scientific career, and I am forever grateful.

Thanks especially to Richie and Kitty Viljoen, who provided a home, a braai, a (mostly stable) dance floor, and most importantly, reminded us all to stop and appreciate the majesty around us (but also that life is too short for nonsense). The University of Lethbridge supported my work by awarding me with a Dean's Award. Thanks to Delaney Roth for helping me run experiments while in the field, the Animal Behavior Society for supporting me with a student research grant that allowed me the most spectacular

research assistant, Madison Clarke, and the Natural Sciences and Engineering Research Council for support through Louise Barrett to also hire Sam Booth, an equally spectacular research assistant. Kyla Funk and Stephanie Varsanyi also contributed immensely through independent study projects.

Chris and Miri Young and Rose Blersch trained me when I came the field, and Rose patiently and endlessly re-described every monkey ID on RST during the day until I dreamed about their faces at night. Colin Dubreuil provided immeasurable emotional and academic support (explaining every ecological and primate behavior theory) while we were in the field together, and Tatiana Bortolato, Lucy Twitcher, Delaney Roth, Maria Vollmar, Steven Bekker, Stephen Morris, comprised not only a team of incredible field assistants, but also the best international group of dance party dancers and singers that would give Eurovision a run for its money. Sophie Collier and Chrissy Grebe, the babooners, rounded out our primate dance party team, and provided a couch and (all the) gin in the greatest time of need.

Deanna Forrester hosted me, a complete stranger, for a month while I visited the lab, and gave me the confidence to officially inquire whether PhD positions were available (telling me in no uncertain terms that if I didn't ask, she would), and Mark Artibise let me live in his spare room and kept me in fresh sourdough bread while I figured out my American re-entry plan. Jon Jarrett, Jessica Parker, and Miranda Lucas ushered me into all things BanziLab, and have provided unwavering friendship throughout. Anne Jones and Chloé Vilette have been my paranymphs, (virtually) working alongside me in (mostly) silent solidarity over the past six months. I truly would not have

been able to finish without your camaraderie.

Thank you to my committee members Tyler Bonnell and Jean-Baptiste Leca, who encouraged and challenged me. I owe a special thanks to Tyler, whose humility and enthusiasm made this thesis a thousand steps beyond what I could have ever imagined as a behaviorist only cursorily aware of statistical techniques. Tyler endlessly deals with the emotional labor of a bushel of graduate students who are desperately trying to do good, slow science in a world where p-values and confidence intervals still reign. Furthermore, thanks to Matt Hasenjager, who answered my frantic emails about network-based diffusion analysis, making the bulk of these findings possible.

Thanks to my supervisors, Louise Barrett and Peter Henzi, for taking me on despite having zero field experience, a penchant for burying the lead, and reporting my results to the 10th decimal place. Your feedback has had an immeasurable impact on my scientific practice, and your influence will forever paint my scientific life. Additionally, my life is now complete by the ability to make an excellent pork shoulder.

Thank you to my family—Dad and Becky, who believed me every time I said I was “almost done"; Becky kept my cats for a year while I was in the field, which included an emergency surgery and is clearly the best aunt furry nephews could ask for. Fred, George, and Hastings always reminded me of the importance of taking a break to go outside or to spend an evening knitting instead of making endless plots. And to Mom, who didn’t get to see any of this, but would have loved to hear about every single monkey.

Thank you to Stephen, my own Marty Ginsberg, who waited with no complaint as

I left the US for my dream doctoral position, followed the monkeys with me for a year, left Los Angeles for Lethbridge, and gave me the space to voice my fears, but banished them with his complete support and punny humor.

And finally, thanks to Louise—this is all because you graciously accepted an overly excited biologist-turned-behaviorist who crashed a conference dinner, dreaming that she might actually be able to study wild animals from a behaviorist perspective. Coming to work with you was the first time I was free to do what I wanted to do, rather than concede my particular scientific interests for whatever was available. Thank you for ensuring that I said what I wanted to say in these pages, and challenging me in a way that made me find my voice. I hope I was able to draw a few hands like bananas in the end. But, if I didn't, I take comfort in knowing that nothing is ever wasted.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1: GENERAL INTRODUCTION

1.1 What is Social Learning?

All animals need information in order to flexibly respond to environmental change, and sometimes this information is acquired socially. The ability to learn from others is pervasive across animal taxa, from insects to mammals (Brown & Laland, 2003; Danchin et al., 2018; Galef & Giraldeau, 2001; Leadbeater & Chittka, 2007), but the process by which behaviors are transmitted between individuals that sometimes results in group-wide traditions is still open to investigation. More formally, social learning is defined as learning that is mediated by another individual though the observation of or direct interaction with another individual and/or their behavioral products (Heyes, 1994; Hoppitt & Laland, 2013). Vervet monkeys (*Chlorocebus pygerythrus*), like most diurnal primates, are social foragers, and thus virtually every decision they make has a social component (Garber, 2000). Given their high sociality and tolerance, and that they live in highly variable environments and seek social information during foraging (Nord et al., 2021), vervets are an excellent species in which to investigate social learning.

1.2 Towards a Behavior Analytic Approach to Social Learning

In this Introduction, I offer a behavior analytic view of social learning, one that considers behavior as part of a three-term contingency and that pays greater attention to environmental context. I take this approach because, as I will show, social learning research often refers to context, not as the circumstances under which behavior occurs, but rather, as the attributes of individual animals. As a result, social learning is rarely about behavior, despite it being presented as such. In what follows, I will expand on these ideas and explain why a behavior analytic approach is needed.

Behavior analysis is focused on the science of behavior change, i.e., learning (Morris, 1992). The analytical framework of behavior analysis is the three-term contingency, which describes the stimulus contexts in which behavior occurs, the behavior itself, and the consequences that maintain it (Sidman, 1988, Skinner, 1938). Behavior analysis has been widely misunderstood (Barrett, 2012); it is not the S-R behaviorism of Hull and Spence (see Lee, 1988), not positivist, and it is not mechanistic (Morris, 1993a; Morris, 1993b). Rather, behavior analysis is contextual (Morris, 1988) and selectionist (Skinner, 1981), and views behavior as the product of contingent consequences; as such, behavior emerges from the relation between an organism and its current context. These contexts, or “discriminative stimuli," “signal” the availability of various consequences that have been previously experienced in similar or equivalent environments. For example, to understand why an animal may approach another and sniff its mouth, a behavior analyst would look to previous consequences of that behavior, such as being able to investigate what the other animal is foraging (Nord et al., 2021).

Because behavior is the product of learning histories and local contingencies, behavior analysis has long recognized that there is wide variation in how similar behaviors (i.e., its topography, outcome, or both) can emerge. This is why behavior analysis uses single subject design to investigate how an organisms’ behavior changes through time (Scruggs & Mastropieri, 1998). Consequently, behavior analysis does not rely on statistical techniques designed for group-level analyses to test hypotheses (e.g., the hypothetico-deductive model, Skinner, 1984), but instead uses within-subject replication (i.e., reversible control methods: Bernard, 2012; Marr, 1985; Sidman, 1988; Thompson, 1984) with the aim of behavioral "prediction and control" (Skinner, 1931). To achieve prediction and control, behavior analysts specify learning scenarios in detail, including antecedent stimuli (e.g., discriminative stimuli), the learner's behavioral repertoire (including its learning history), and the values of the available consequences (Bouton & Balleine, 2019; Lind et al., 2019). Behavior analysis is also an applied science (Baer et al., 1968), and must generalize its laboratory and clinical findings to the "real world" (where the relevant antecedent and consequent conditions cannot be easily manipulated by an experimenter). Going from the lab or clinic, where situations are controlled and behavior can be recorded automatically, to the uncontrolled and non-automated "real world," requires being able to confirm or deny predictions directly from the observation of the behavior in the environment of interest. Due to its focus on translating basic research to applied settings (which is also reflective of the field's pragmatist roots; Moxley 2001), behavior analysis has been very successful wherever it has been applied, most notably in the treatment of autism (Baer et al., 1968; Baer et al., 1987; Foxx, 2008; Peters-Scheffer et al., 2011).

In my view, social learning research is too concerned with looking inside organisms for the sources of social behavior, and has neglected context. For example, the main program of social learning research today, selective social learning (Kendal et al., 2018; Laland, 2004), assumes that individuals choose to learn on their own or from others using a wide range of available strategies (e.g., copy when asocial learning is costly, copy the majority, etc.), but never explains exactly how animals choose a strategy. With the discovery that not all animals appear able to use social learning despite having both opportunity and ability (Lorenz et al., 2011; Racine et al., 2012), social learning researchers have proposed that individuals are somehow constrained from doing so (e.g., Carter et al., 2016). Thus, social learning research often looks to individual attributes, such as age or sex, to explain failures to learn socially, but does not often consider that variation may reflect environmental contingencies or varying learning histories.

The selective social learning hypothesis is an example of this individual attribute approach to social learning. According to this hypothesis, "context-based" social learning strategies refers to rules that govern when social learning should be used by animals (Laland, 2004; Kendal et al., 2018). These contexts, however, are not the contexts of behavior. Rather, they describe either (1) the state of the learner (e.g., "copy if uncertain," "copy if asocial learning is costly," "copy depending on age or sex", "copy if personal information is outdated"), (2) the frequency of the target behavior in the group as a whole (e.g., "copy if rare," "copy the majority", i.e., strategies that do not make clear how individuals acquire such information) (3) or the identity of the demonstrator (e.g., attribute-based rules such as copy animals of certain rank or sex classes, copy based on the demonstrator's knowledge, etc.). All of these so-called "context" based strategies take the viewpoint of the learner and neglect the conditions under which the social learning happens.

As an example, Canteloup et al. (2020) found that animals were more likely to solve novel foraging task after watching higher-ranked animals complete it. In contrast, Botting et al. (2018) found no evidence of a rank bias when using a similar novel foraging task in the same population as Canteloup et al. (2020). This was surprising to me because the language of selective social learning heavily implies that strategies correspond to specific individual attributes; if vervets use social learning based on a rank-based strategy, then that strategy should be available and active for all individuals given that attribute (Heyes & Pearce, 2015).

How does the selective social learning hypothesis account for such contradictory findings? A more context-based approach focused on the conditions under which vervets do and do not preferentially attend to higher ranked animals could help. Using a framework that treats behavior as emerging from animals with certain attributes, rather than as the interaction between animals and their environments (Truskanov & Lotem, 2017), discounts the possibility that changes in the environment, or the context of the experimental setup, could explain when learning biases do and do not emerge. Indeed, in accounting for such discrepancies, Canteloup et al. (2020) point to the contingencies of the experiment as a possible influence on their results: their experiment used an open diffusion method with untrained demonstrators, whereas Botting et al. (2018) trained demonstrators of specific dominance ranks. Rather than providing post-hoc explanations for unexpected findings, my behavior analytic approach expects behavioral variation due to different experimental arrangements.

What is missing, then, from the dominant frameworks of social learning theory is an interest in how animals go about learning the behaviors in which they engage (see also Heyes, 2012; Heyes, 2018). For example, suggesting that humans have robust cultural learning because we can imitate, and that we can imitate because we have special cognitive powers (e.g., that we can learn about behavior, unlike animals; Tomasello, 1996) leaves more to be explain than it manages to explain in the first place. Claiming that we possess certain cognitive processes does not actually explain anything—the problem has only been moved up a level (Skinner, 1977). What kind of explanation of the cognitive processes responsible for social learning has been achieved if the cognitive process is only inferred from the behavior and not by explaining how the behavior occurs?

To be clear, I am not arguing that social learning research should become wholly behavior analytic, as I understand the necessity of group-level analyses for explanations in terms of evolutionary function because evolution occurs in populations. But I do think that by adopting a more behavior analytic framework, including its precise vocabulary to describe the conditions under which behavior occurs and its focus on identifying the controlling conditions in the environment, social learning research can make progress in explaining precisely how animals learn from one another. Social learning research already has the methods to achieve this, but a more behavior analytic approach can adjust our focus from organisms to behavior, and, in turn, illuminate the behavioral mechanisms that are available to selection (Fawcett et al., 2012).

1.3 The Selective Social Learning Hypothesis

Research on social learning in vervet monkeys has been dominated by the selective social learning approach, which aims to understand how animals trade-off social and asocial learning (c.f., Enquist et al., 2007). Understanding these trade-offs is of interest because fitness outcomes of social learning are dependent on the costs and benefits associated with being either a producer of information or a recipient of social information. Asocial learners produce information by learning directly from the environment. For example, Li et al. (2021) found that vervets who spent more time in the front-outer position of a moving group were better able to produce information because they arrived at novel food patches early. Once asocial learners have discovered something newly available in the environment, social learners can then scrounge, or exploit what the asocial learners have produced, avoiding any costs associated with learning directly from the environment. In the same experiment, Li et al. (2021) found that scrounging vervets benefited mostly by being socially tolerated, able to approach the food patches producers has discovered and forage alongside them.

The benefits of learning socially are predicated on social information being up to date. Thus, there is a trade-off between being a social learner versus an asocial learner: A population of exclusively social learners would quickly become extinct in a changing environment, and a population of exclusively asocial learners could not capitalize on the benefits of learning socially. However, as long as the environment varies, a social learner in a population of asocial learners could incur benefits while also avoiding the costs of learning on its own, similar to the benefits for an asocial learner in a population of social learners. In sum, the fitness benefits associated with social learning are dependent upon the frequency of social learners in the population, resulting in the hypothesis that populations exhibit asocial and social learning as part of a mixed evolutionary stable strategy (Hoppitt & Laland, 2013; Rendell et al., 2010; Rogers, 1988). Explained another way, animals behave *as if* they decide between using asocial or social learning in accordance with the costs and benefits of each within a given environment.

Thus, the selective social learning hypothesis posits that social learning is shaped by various biases, referred to as social learning strategies ("SLSs"), which animals flexibly choose between when faced with a learning scenario (Hoppitt & Laland, 2013; Kendal et al., 2018; Laland, 2004; Rendell et al., 2011). SLSs describe specific heuristics that specify either when animals use social learning, who they learn from, or what they should learn. For example, dominant females have often been used as demonstrators in vervet social learning tasks probing whether they are capable of copying and imitating, and whether they are sensitive to conformity biases. The emphasis on dominant females began after a 2018 finding that dominant females were copied more often than dominant males (Bono et al., 2018). Realizing the importance of sex biases, Renevey et al. (2013) investigated whether these biases were also present during typical foraging (as opposed to novel foraging experiments) and found that group members preferentially attended to adult females over adult males under natural foraging conditions. Thus, Renevey et al. (2013) hypothesized that vervets selectively attended to females because females are philopatric and are likely to know more about local resources than do males (van de Waal et al., 2010).

Other possible strategies, as outlined by Kendal et al. (2018), include those that are: (a) unbiased or random, (b) context dependent, including state-based copying (e.g., copy if uncertain, copy depending on age, copy if asocial learning is costly, etc.), frequency-dependent copying (e.g., copy rare behavior, copy dependent upon the number of demonstrators, conformist biases, etc.), and model-based copying (e.g., age-based, sexbases, prestige-based, etc.), (c) content-dependent (e.g., biases for social information, biases derived from emotional reactions, etc.), and (d) mediated by guided variation, i.e., unbiased transmission of behavior resulting from trial-and-error learning.

Using this hypothesis that animals have SLSs, social learning researchers have generated a number of testable predictions, and have been enormously successful in identifying animals that do and do not deploy certain strategies (Kendal et al., 2018). For example, the state-based social learning strategy "copy when asocial information is costly" is one of the best supported SLSs, able to account for how animals learn anti-predator responses (Chivers & Smith, 1995; Curio, 1988; Kelley et al., 2003; Krause, 1993; Mineka & Cook, 1988; Suboski & Templeton, 1989), to navigate routes in guppies (*Poecilia reticulata;* Laland & Williams, 1998), dogs (*Canis lupus familiaris*; Pongrácz et al., 2003), and humans (*Homo sapiens;* Reader et al., 2008), and to solve tasks of various difficulty in bumblebees (*Bombus terrestris*; Baracchi et al., 2017; Saleh et al., 2006; Wray et al., 2012), fish (Laland et al., 2011; Webster & Laland, 2008), monkeys (species of callitrichids; Kendal et al., 2009) and humans (Baron et al., 1996; Morgan et al., 2012). Conformity, a frequency-dependent copying strategy, has been found in fruit flies (*Drosophila melanogaster*; Danchin et al., 2018), fish (Munson et al., 2021; Pike & Laland, 2010), birds (Aplin et al., 2015a; though see van Leeuwen et al., 2015 and Aplin et al., 2015b), monkeys (van de Waal & Whiten, 2012), and humans (Morgan et al., 2012).

The SLS approach is the dominant approach in social learning research. Importantly, the selective social learning hypothesis is ultimately concerned with the functional nature, i.e., evolutionary adaptiveness, of social learning, rather than the proximate mechanisms that explain how it occurs. In the SLS approach, animals are predicted to engage in various strategies “as if” they are choosing among them, and SLSs are not, for now, concerned with identifying the exact mechanism by which animals behave “as if.” This “mock anthropomorphism” approach to animal behavior has been very successful in investigating adaptive behavior, because natural selection has produced animals with behavior that we can successfully describe in this metaphorical way (Barrett, 2011; Kennedy, 1992). Outside of SLS, mock anthropomorphism is widely used. For example, social learning research in general refers to animals as “passing” (or transmitting) “information” “through networks”. In using this language, researchers don’t literally mean that animals are sharing information like we share articles on social media, but that one animal learns a behavior, followed by another learning the same behavior, and this learning covaries with their social relationship.

However, we need to exercise caution when using mock anthropomorphism, not only because it can easily turn into actual anthropomorphism, but also because at some point, understanding complex traits, like behavior, requires an understanding its proximate mechanisms (Barrett, 2011). To explain behavior, it is not enough to predict it, to say that animals will behave “as if” they are choosing from strategies. We also need to understand just how they go about using these strategies, and directly address the “interpretive gap” between predicting how they will behave and explaining how they go about doing so; that is, focusing on behavior rather than functional strategies. Assuming that animals will behave as if they have a humanlike cognition can limit the range of hypotheses we can test, as the possibility of animals having unique, non-humanlike cognition is ignored.

Rejecting the Gambit and Jumping into the Gap

I am not the first to call on social learning research to be a little less mock anthropomorphic and a little more proximate. In the SLS literature, the phenotypic gambit (or behavioral gambit) is often evoked in order to explain there are no constraints on what selection can achieve, so the precise mechanism of selection can be safely ignored as natural selection will somehow find a way. However, some have called on social learning researchers to abandon the gambit. For example, Mesoudi et al. (2016) argued that there is now abundant evidence that understanding once-ignored sources of individual variation are critical to understanding variation in social learning expression, and that investigating this individual variation is essential to understanding the evolution of social learning on the whole. Such evidence, for example, is that individuals within species vary in their tendency to use different social learning strategies and mechanisms (Mesoudi et al., 2016). Heyes and Pearce (2015) have also argued that it is time to move beyond the phenotypic gambit, and that social learning research should focus more on causes as well as the consequences of selectivity in social learning. Heyes and Pearce (2015, pp. 6-7) explain that, despite researchers claiming that SLSs are not committed to any proposition concerning mechanism, current SLS practice uses “language that implies strong commitment to certain mechanisms, while suggesting that functions can be studied without concern for mechanisms” and that SLS research "is now in danger of leading the field astray.”

SLS researchers have responded to this criticism by relying on a claim of neutrality to mechanism, arguing that SLSs offer a functional account of behavior and are not a substitute for "the thorough analysis of mechanism" (Kendal et al., 2018, p. 8). However, Fawcett et al. (2012) have pointed out that using the phenotypic gambit for questions of behavior requires an additional assumption that goes unacknowledged ("that the psychological mechanisms underlying flexible decision making do not constrain the expression of adaptive behavior and allow animals to reach the optimal solution to a given problem" which they refer to as "the behavioral gambit", Fawcett et al., 2012, p. 2), sometimes resulting in unsupported predictions about the evolutionary function of behavior. This is because individual brains are assumed to be endowed with the "calculating power of evolution" (Hammerstein, 1998, p. 5 as cited in Fawcett et al., 2012, p. 12). Behavior is often not as "optimal" or "rational" as predicted in a functional account, but this "sub-optimality" and "irrationality" can be accounted for when the mechanisms of behavior are considered as the target of selection, rather than behavioral outcomes. For example, pigeons have been found to behave sub-optimally in a signaled choice procedure whereas rats do not, and Zentall et al. (2019) showed that how animals react depends on how conditioned stimuli conform to the animals' evolutionary niche (i.e., its functional behavior system, see Timberlake, 1993).

1.4 A Research Program

This thesis is an endeavor to understand the social learning abilities of another species by jumping headfirst into the interpretive gap, using a behavior analytic approach to explain (or, as may be more comfortable for behavior analysts, "describe"; see Marr, 2003), and not just predict, how a species can use social learning to cope with varying environments (Barrett, 2011). There are three areas in social learning research that are ripe for a behavior analytic approach. These are (1) the pathways available to behavioral transmission, (2) understanding how social dynamics influence the contexts of social learning, and (3) exploring the relationship between individual differences and how animals learn from one another. In what follows, I explain how context has been more or less ignored within these three areas, and how adopting a more behavior analytic framework can lead to greater progress in social learning research.

1.5 What Transmission Pathways are Available?

One method of studying social learning is to observe the spread, or diffusion, of a novel behavior. One of the first recorded instances of social learning came from Imo, a juvenile female Japanese macaque (*Macaca fuscata*), who was found washing provisioned potatoes in the sea (Kawai, 1965). This potato-washing behavior then spread via lines of social affiliation and, at the time, was considered to be the first documented cases of imitation in non-human animals. Today, potato washing is considered to have occurred not by imitation but via more general social processes that facilitated asocial learning of the washing process (e.g., social facilitation, local enhancement; Galef, 1992).

Diffusion research has progressed since the observations of Imo and her groupmates. One way has been to quantify social structure using social network analysis (Croft et al., 2008). A variety of connections including affiliative (e.g., grooming and proximity) and agonistic (i.e., aggressive) interactions can be used to determine whether animals that frequently interact are more likely to learn from one another (Coussi-Korbel

& Fragaszy, 1995; Hasenjager et al., 2020a; Hoppitt & Laland, 2013). For example, using network-based diffusion analysis (NBDA), Carter et al. (2016) revealed that the spread of a behavior—learning the location of a novel food patch—followed close affiliations (i.e., spatial proximity and grooming networks) in a group of wild chacma baboons (*Papio ursinus*).

Diffusion is the first area where I propose that social learning research could benefit from focusing more on context. For example, the original formulation of NBDA makes a large assumption common in social learning research: that animals who frequently interact in affiliative contexts like grooming should learn from one another (Hasenjager et al., 2020a; Hoppitt et al., 2010). However, there is a disconnect between the behavior being transmitted and these network measures. Early diffusion analyses could only confirm that transmission of a novel behavior followed close affiliations, but exactly how the behavior passes from one animal to another was not considered (Hoppitt et al., 2010). For example, it is not clear how a novel foraging behavior could spread via a grooming network, and, as such, affiliation networks are only proxies of actual transmission pathways.

How might behavior actually spread between individuals? One possible mechanism is simply observing another engage in novel behavior. Cambefort (1981) found that while chacma baboons can visually discriminate aversive visual foraging cues provided by other troop members, vervets could not. According to Cambefort (1981) vervets have weak hierarchies and weak cohesion compared to baboons and mandrills (*Mandrillus sphinx*), as well as an “acentric” and floating attention structure nonconducive to the collective transmission of feeding discrimination and fast culture propagation. However, Lycett and Henzi (1992) described the possible role of olfaction in information transfer among vervets. Lycett and Henzi (1992) argued that vervets might use muzzle-muzzle contact to discriminate cues from conspecifics and that the failure to learn the aversive stimulus was a consequence of its being odorless. Odor cues have long been hypothesized as a possible route of information acquisition. For example, three species of cercopithecines (*Mandrillus sphinx, Mandrillus leucophaeus,* and *Papio anubis*) often seek olfactory cues when foraging, including from the mouths of others, and Tonkean macaques (*Macaca tonkeana*) can locate food sites and discriminate food availability and quality after sniffing the mouths of conspecifics (Chauvin & Thierry, 2005; Drapier et al., 2002; Laidre, 2009). Thus, Lycett and Henzi's (1992) account suggests a route of information transmission available to vervets via muzzle-muzzle contact: a question I explore in Chapter 4.

NBDA became a bit more contextual with the inclusion of "observation networks" just as I was exploring whether muzzle contact was a possible route of vervet information transmission. Hobaiter et al. (2014) quantified when chimpanzees (*Pan troglodytes*) observed others engaging in a novel tool use behavior and found that tool use spread via dynamic observation pathways (Hasenjager et al., 2020a). This so-called "dynamic observation network" approach was used by researchers to identify social transmission through observation networks in guppies, honeybees (*Apis mellifera*), and vervets (Canteloup et al., 2020; Hasenjager et al., 2020a; Hasenjager et al., 2020b; Hasenjager et al., 2020c). Using NBDA with observation networks assumes that if a behavior is socially transmitted, those who observe the behavior at high rates should learn the behavior faster than those who observe it at lower rates. Testing different observation opportunities can reveal which observational contexts afford social transmission. Observation networks, then, are only informative of the first aim of NBDA—to assess the strength of evidence that social transmission is operating within the innovation of interest. However, it does address its main assumption, that information should follow close affiliations. The success of the original formulation of NBDA in detecting social transmission between affiliates across a wide range of taxa (e.g., grooming and proximity affiliates in baboons, proximity affiliates in fish, birds, and otters: Aplin et al., 2015a; Carter et al., 2016; Ladds et al., 2017; Saliveros et al., 2020; Webster et al., 2013) makes clear that social relationships can play a role in social transmission. However, recent research using observation network NBDA has not tested whether social transmission corresponds with affiliations and thus cannot say whether social relationships influence information flow (Canteloup et al., 2020; Hasenjager et al., 2020c; Hobaiter et al., 2014). By comparing observation network(s) to established association networks, researchers can determine if the two network types correlate in some way, and ultimately, begin to understand the relative importance of established associations in information transmission. I explore this question in Chapter 5.

Identifying the relevant transmission pathways can also aid in understanding other complexities that may underly social information transmission, such as the role of network position. There are many ways to measure an individual's network position or centrality (Croft et al., 2008). For example, degree centrality measures the number of partners an individual has, strength centrality measures the frequency an individual interacts with others, and eigenvector centrality incorporates strength centrality with the strengths of the individual's partners (Croft et al., 2008). These measures can in turn be used to test various predictions concerning social learning. For example, Kulahci et al. (2018) found that ring-tailed lemurs (*Lemur catta*) that solved a novel foraging task became more central in networks, i.e., had higher degree centrality.

Also concerned with context, Brent (2015) emphasized that social behavior almost always occurs in the context of polyadic, or "indirect" network ties, as opposed to the dyadic ties more-often used in social network analysis. Indirect connections are the connections of an individual to the partners of their social partners (i.e., "friends of friends"). Brent (2015) explains that social transmission often depends not on how many partners an individual may have, but on how those partners are connected. For example, individuals with high betweenness centrality (or the total number of shortest paths from one individual to another) can influence how information transfers through a network because they connect individuals that would otherwise be unconnected. Indeed, Aplin et al. (2012) found that betweenness centrality predicted feeder discovery in species of tits (family Paridae). I explore the role of direct and indirect connections in Chapters 5 and 6.

1.6 How do Social Dynamics Influence the Context of Social Learning?

The second area I propose where social learning can benefit from a contextual approach is social dynamics. In a seminal paper, Coussi-Korbel and Fragaszy (1995) argued that variation in social coordination influences the kinds of information that individuals can share and that differences in social learning are due to the ability of animals to coordinate in time and space, i.e., social dynamics. In Coussi-Korbel and Fragaszy's (1995) treatment, social dynamics occur at the group or species level and are described by "combining sets of interactions into gross categories of relationships" (Barrett et al., 1999, p. 670), i.e., describing groups as either "egalitarian," "despotic," or an intermediary between the two. Thus, more egalitarian societies are predicted to be better able to gather social information from one another because they have more frequent close proximity among their members compared to despotic societies. The role of social dynamics in directing and organizing social learning is crucial to understanding when and how social learning occurs (Galef & Laland, 2005).

1.6.1 Phenotypic Constraint

A major difficulty in social learning research has been to account for why social learning reflects social dynamics in one context but not others (e.g., Botting et al., 2018; Canteloup et al., 2020; Renevey et al., 2013), or why some animals, having successfully gathered social information, fail to use it (Leadbeater & Florent, 2014; Lorenz et al., 2011; McLachlan et al., 2019; Nord et al., 2021; Racine et al., 2012; Truskanov et al., 2018). Researchers investigating phenotypic constraint answer the question of variation in information use by hypothesizing that certain phenotypes can prevent social information from transferring between individuals. Because it is focused on how behavior can vary across individuals by measuring various behaviors predicted to encompass the social learning process, the phenotypic constraint hypothesis has the potential to refocus the attention of social learning research to investigating sources of variation. However, it is bounded by the same limitation as social learning research writ large in that it searches for the causes of variation in social learning as sitting within individuals, rather than in the contexts of their behavior. With the example of “ecological” phenotypes (resource availability), the “cognitive,” “social,” “behavioral,” and “demographic” phenotypes referred to by the phenotypic constraint hypothesis are still individual attributes, for they refer to individual SLSs (“cognitive” phenotypes), dominance ranks (“social” phenotypes), personality traits (“behavioral” phenotypes), and age/sex categories, including parity and residence time (“demographic” phenotypes). Thus, sources of variation are found within individuals, and rarely context.

The focus on individuals as sources of variation may be due to the study system of Carter et al. (2016)—adult male baboons, overall, outrank adult females (Henzi & Barrett, 2003). Thus, adult females who are constrained by the presence of adult males at one point in the social learning process are likely constrained throughout. However, less-rigid social systems could have social phenotypes that are not as restrictive, as social phenotypes are dynamic, moment-to-moment processes. Vervet monkeys lack the stark sex dimorphism of baboons (Cords, 2012), have male/female co-dominance hierarchies (Young et al., 2017), and do not show the restricted rank-related social behavior of baboons, at least in large groups (Henzi et al., 2013). Given this, vervets may not be as socially constrained as chacma baboons in their ability to use social information, and their particular social dynamics may allow them to mitigate constraints of social information use at various stages during social learning, resulting in variation in social information use dependent on the social dynamics of the social learning scenario. I explore this possibility in Chapter 5.

Thus, while the phenotypic constraint hypothesis presents an analytical framework in which to explore how social learning emerges, it is still focused on the sources of variation as being the product of individual attributes. Furthermore, the language of constraint can be rather confusing. For example, a finding that females looked at demonstrators at higher rates during a novel foraging task, and that they then use social learning at higher rates than males to solve the task, is interpreted as males being constrained from social transmission. To avoid confusion, I will not use the constraint language of the sequential phenotypic constraint hypothesis when I use its analytical framework in Chapters 5 and 6.

1.6.2 Social Tolerance

A promising area of research concerns the role of social tolerance and social proximity in social learning (van Schaik et al., 2003). Indeed, "…all else being equal, both tolerance of knowledgeable individuals for the presence of others and proximity seeking by the naive should affect the probability that the naive will acquire the behavior of the knowledgeable" (Galef & Laland, 2005, p. 490). Social tolerance has been found to influence a range of aspects relevant to social learning, including access to shared feeding and watering sites (Kummer, 1978; Li et al., 2021; Seyfarth & Cheney, 1984), the ability to gain information about food (Nord et al., 2021) and to learn how to exploit novel food sources (van de Waal et al., 2012). Animals can also trade biological commodities, like grooming, for increased tolerance. For example, Borgeaud and Bshary (2015) found that recent grooming dyads predicted tolerance at experimental feeding sites (Borgeaud & Bshary, 2015), and Li et al. (2021) found that tolerance allowed vervets to scrounge, i.e., use social information, in experimental feeding patches.

Research into orangutan (*Pongo*) juvenile foraging independence has investigated the kinds of social learning social tolerance affords and illustrates a contextual approach to the interaction between social learning and social tolerance. Orangutans spend their first two years of life in almost in permanent physical contact with their mothers (van Noordwijk & van Schaik, 2005) and learn the particularities of their very specific diet via “peering,” or “close attentive close range watching,” as well as selective practice, or engaging in behavior within the affording context (Schuppli et al., 2016).

Recently, Li et al. (2021) found that vervets can benefit from a novel food patch by either being a producer (i.e., relying on personal information) and arriving early, or by being a scrounger (i.e., using social information) and being tolerated. Although not investigating social learning in particular, Li et al. (2021) illustrate the ability of social dynamics, and social tolerance in particular, to mediate the solving of novel foraging problems. I consider social tolerance throughout this thesis, and in Chapter 4 in particular.

1.6.3 Social Facilitation

Furthermore, the *mere presence*[1] of other individuals, as in group-living species, has been found to affect learning. Social facilitation (also referred to as social enhancement: Galef, 1988; Zentall, 1996) describes circumstances in which the presence of another animal increases or decreases the probability of occurrence of the behavior for another it is not directly interacting with. (This is the definition I prefer and will use

---

[1] It is difficult to arrange experimental conditions, or observe wild behavior, that controls for effects of social interaction, cueing, or distraction, and thus “mere presence” may never be an isolatable variable. For a discussion of this issue, see p. 123 of Guerin, 1993.

throughout this thesis. Alternative definitions restrict social facilitation to instances when animals perform the same class of behaviors already established in their repertoires, referred to as “response facilitation" or “contagion”: Clayton, 1978; Hoppitt & Laland, 2013; Visalberghi & Addessi, 2000).

In a review of the effects of social facilitation on social learning, Visalberghi and Fragaszy (1996) found that “simple social tendencies,” such as social facilitation, can explain how capuchin monkeys (*Cebus apella*) deal with novel or difficult foods. In observing that monkeys ate a wider variety, and larger amount, of novel foods in social contexts compared to solitary contexts, Visalberghi and Fragaszy’s (1996) findings are similar to others (e.g., Forkman, 1991), and support the hypothesis that social facilitation reduces costs associated with increasing dietary breadth, such as identifying palatable foods (Galef Jr, 1993).

Historically, social facilitation effects are rarely explicitly tested (Dindo et al., 2009; Guerin, 1993), and social learning research has mainly viewed social facilitation as something to be ruled out in order to be able to conclude that social transmission has occurred (Hoppitt & Laland, 2013). This might be due to an interpretation of Zajonc’s (1965) theory of social facilitation that views it as preventing the acquisition of novel responses (Zentall, 1988). However, interpreting Zajonc’s theory can be nuanced (Guerin, 1993, pp. 32-45), and there are alternative theories of social facilitation which can be used in social learning research. For example, Visalberghi and Fragaszy (1996, p. 80) argued that, along with ecological characteristics, social dynamics and emotional signaling (their proposed mechanism of social facilitation) is “more likely to predict important characteristics of social learning in a given species than taxonomic status." In addition, isolating social facilitation from social transmission may obscure the social learning process, as doing so prevents the possibility that it may be a mechanism of social learning (akin to the problems with isolating imitation from associative learning, see Truskanov & Lotem, 2017).

It is my view that social facilitation is rarely emphasized as a relevant social learning mechanisms because its explanation is almost entirely contextual, simply requiring the mere presence of others and an environment that supports the behavior being facilitated, rather than some sort of enhanced cognition. Because, as mentioned previously, social learning research is often concerned with identifying special cognitive powers, as well as transmission *between* individuals (see section 1.5), explanation-by-social facilitation offers a quite boring account compared to those that claim that social learning requires special cognitive capacities (e.g., Tomasello, 1996). Thus, social facilitation research is a prime example of the need for context, for without it, social facilitation effects could go undetected. For example, some animals eat more in social contexts (e.g., chicks), but others less (e.g., rats; Guerin, 1993)—if "feeding rate" is the only measure used, it may seem that the feeding behavior of chicks, but not rats, is socially facilitated. However, including context reveals social facilitation—"If the whole context or social ecology is measured, then the contradictions disappear: The rats use their time together to groom and play and therefore stop eating, whereas the chicks reduce their fear activities when in groups and spend the extra time eating" (Guerin, 2010, p. 1). Understanding social facilitation, then, is another way to incorporate context into social learning research. I consider the role of social facilitation in social transmission in Chapter 6.

1.7 How Are Individual Differences Relevant?

The final area where I propose that social learning can benefit from a more contextual approach is by incorporating environment into analyses of individual differences. There is already a large body of literature that discuss the role of interindividual differences in behavior. For example, Mesoudi et al. (2016) have underlined the role of individual differences in social learning abilities (as discussed above), emphasizing the importance of interindividual differences in behavior or, as it is now known, animal personality.

Personality has yet to be incorporated into vervet social learning research but has been broadly explored in the laboratory (Fairbanks, 2001; Fairbanks et al., 2004; McGuire et al., 1994) and field (Blaszczyk, 2017). Other work, mostly in fish and birds, has explored the role of personality in using personal and social information when learning (reviewed in Hasenjager et al., 2020b). Often, animal personalities are quantified as animals that are "bold" or "shy" towards some novel stimulus (Blaszczyk, 2017), as "fast" versus "slow" explorers in novel foraging contexts (Vágási et al., 2021), or "anxious" versus "nonanxious" in predatory contexts (Carter et al., 2012). Shy/slow animals are proposed to be more attracted (Aplin et al., 2014; Jolles et al., 2015; Michelena et al., 2010; Ward et al., 2004) and responsive (Harcourt et al., 2009; van Oers et al., 2005) towards other group members compared to animals that are bold/fast, and thus shy animals are often predicted to use social learning more than asocial learning

(Kurvers et al., 2010; Smit & van Oers, 2019). For example, Kurvers et al. (2010) found social information use decreased with increasing boldness measures for barnacle geese (*Branta leucopsis*), and Smit and van Oers (2019) found that bold great tits (*Parus major*) ignored available social information when foraging.

It might seem counterintuitive that shy animals are predicted to use social learning more so than bold animals, but it is important to remember that “shy” and “bold” in animal personality research refers to responses towards novelty, not conspecifics. Thus, shy animals avoid approaching novelty, whereas bold animals are attracted to it, allowing bold animals to provide important sources of information for shy animals. In other works, because bold/fast individuals are thought to use asocial learning more than shy/slow individuals (Dyer et al., 2009; Kurvers et al., 2011; Smit & van Oers, 2019; Trompf & Brown, 2014), they are predicted to learn directly from the changing environment (Aplin et al., 2014; Dyer et al., 2009; Webster & Ward, 2011) and thus should be more likely to transmit novel information to other group members (Aplin et al., 2014; Dyer et al., 2009; Harcourt et al., 2009). For example, Dyer et al. (2009) found that shy guppies benefit from foraging near bold individuals because shy animals can capitalize on the information produced by bold animals.

These examples show that while interindividual differences in behavior has been incorporated into social learning research, it is often presented as yet another individual attribute, like sex, age, and dominance rank. However, interindividual differences in behavior, like all behavior, occurs in a context. Recently, the behavioral reaction norm approach (BRN) has presented a means by which researchers can investigate the possible relationship between interindividual differences and environment (Dingemanse et al., 2010). Context is key in the BRN approach, because it is primarily concerned with how behavior varies across environments, or “environmental gradients” (e.g., drought, intergroup-encounters, time, etc.). BRNs envision behavioral variation in a 3D parameter space: The axes represent degree of between-individual variation (or “personality”, “I”) in some behavioral trait, the degree of individual consistency (or “plasticity”, “E”) in that behavioral trait, and the interaction between these two parameters (IxE). Lines connect individual behavioral measures through the gradient, where slope indicates an individual’s behavioral plasticity, and the elevation, or y-intercept, indicates whether repeatable differences exist in the population, i.e., personality. Thus, BRNs identify the form of the relation between the reaction norm (the covariance between personality and plasticity) and environmental conditions (Dingemanse et al., 2010). BRNs also consider behavioral plasticity, or circumstances where individuals vary their behavioral expression across environmental grades and therefore investigate the interaction between personality and behavioral plasticity. Rather than peg plasticity and consistency against one another, as is common in functional-oriented explanations of behavior (Dall et al., 2004; Dingemanse & Wolf, 2010), BRNs reveal that personality does not preclude plasticity. For example, imagine that individual foraging rates are measured in a group of animals at two points in time. In this example, time serves as the environmental gradient. If individuals consistently differ in their foraging rates at both points in time, the group can be said to have a foraging rate personality. Furthermore, if individuals have higher foraging rates at the first point in time, but lower rates at the second point in time (reflecting resource availability, for example), this indicates that individuals are plastic in their foraging rates. Thus, in this example, the group has a foraging rate personality, while individuals exhibit plasticity in their foraging rates.

Furthermore, the reaction norm approach demonstrates that personality and plasticity could be the emergent properties of a selection process to afford behavioral variation in response to environmental change (Dingemanse et al., 2010). As such, personality and plasticity, Dingemanse et al. (2010) argue, cannot be understood in isolation if they are to be understood adaptively. Indeed, covariance between personality and plasticity does not have to be consistent, and understanding the conditions under which covariance is and is not maintained can illuminate what would otherwise be unknown selection targets.

Although there isn't much social learning research that explicitly uses the BRN approach, there are some specific findings that demonstrate the value of considering context alongside personality (Burkart et al., 2017; Dyer et al., 2009; Harcourt et al., 2009; Hasenjager et al., 2020b; Kurvers et al., 2011; Webster et al., 2007). For example, Kurvers et al. (2011) found that the personality effects on information use in barnacle geese co-varied with group size, as personality-related differences in information use was only present for pairs but not larger groups. More recently, Hasenjager et al. (2020b) found that the boldness of demonstrators and observers influenced social transmission dependent on the personality composition of the group—guppies that were bold learned socially in groups dominated by bold individuals, whereas bold demonstrators transmitted information in groups dominated by shy individuals. This finding coincides with the recent hypothesis that social groups can benefit from being composed of a range of personality types (Vágási et al., 2021).

1.8 Outline of this Thesis

In this thesis, I report the findings of study combining observational and experimental research in an effort to understand the social learning dynamics of wild primates. In order to understand how information is acquired by these animals, I observed three troops of vervet monkeys and characterized their social phenotypes, local ecologies, and group structures. I also presented a novel foraging task to three different troops to test whether certain ecological and social conditions promote the spread of relevant food information between animals.

Vervet monkeys are an excellent model in which to explore questions regarding social learning given their high sociality, spatial tolerance, and ease of observation compared to other primate species that are less social (e.g., orangutans), more spatially spread (e.g., baboons), or more arboreal (e.g., capuchins). Chapter 2 presents an overview of the study species and population, and the general methods of my study. I provide more detailed reports of specific methods and analyses in the relevant chapter.

Chapter 3 presents findings from an observational study of muzzle-muzzle contact behavior, which has been claimed to function as a mechanism of information transfer in many primate species (Chauvin & Thierry, 2005; Drapier et al., 2002; Laidre, 2009; Lycett & Henzi, 1992). By observing muzzle-muzzle contact dyads and the contingencies in which this behavior is embedded, I answer questions surrounding the structure and function of muzzle-muzzle contact behavior and determine whether it is a targeted means of information acquisition and an available pathway of information transfer.

Chapter 4 presents the methods and results from repeated tests of individual responses to novel foods, tests I used to generate a measure of personality that I use throughout this thesis.

Chapter 5 presents a targeted experimental analysis of social learning. I presented a novel water patch to our three study troops as a test of Carter et al.'s (2016) phenotypic constraint hypothesis to determine if and how information acquisition is constrained in vervet monkeys and whether or not it can be mitigated by social dynamics. Using various individual level variables including dominance ranking, age, sex, network position, and personality, I determined whether an animal's phenotype influenced its ability to gain and use information successfully. I also determined if ecological conditions influenced the tendency to gain information, and directly examined various paths of information transfer using association networks (grooming, spatial proximity) and observation networks measured in situ during the experiment (e.g., looking and muzzle contact network). As with Carter et al. (2016), this experiment provided me the opportunity to test whether or not information about the water patch diffused through one, or multiple, interaction networks.

Chapter 6 is a more targeted analysis of information acquisition, focusing on foraging information. I presented a novel foraging device to the vervets (that required the skills seen in their natural ecology when foraging for acacia gum), to ask questions regarding task difficulty and the extent to which social dynamics could overcome social constraints. The novel gum box allowed me to focus attention on the learning mechanisms responsible acquisition of the novel foraging behavior by providing multiple response alternatives in order to determine if animals paid attention to the behavior of individuals accessing gum.

Chapter 7 forms a general discussion of my findings, and allows me to use my findings to extend the current social learning research paradigm to one more focused on behavior, rather than organisms. I also frame my findings in light of their limitations, and discuss where we should go from here.

CHAPTER 2: GENERAL METHODOLOGY

In what follows I present a general overview of my study species, study site, and general methodology. More specific methodological and analytical details are presented in the relevant chapters.

2.1 Study Species

2.1.1 Taxonomy and Distribution

Vervet monkeys (genus *Chlorocebus*; hereafter "vervets") are the second-most most widespread and abundant species of the Cercopithecidae family, sister taxon to guenons (*Cercopithecus;* Mertz et al., 2019). Vervets are semi-terrestrial and are widely distributed across sub-Saharan Africa, including West Africa, northern Kenya and Ethiopia, and the South African temperate regions (Turner et al., 2019b). Six species compose this genus, five of which are widely distributed (Groves, 2001). My study species, *Chlorocebus pygerythrus*, has the most extensive latitudinal distribution of the genus and has been well studied in the wild (Turner et al., 2019a).

2.1.2 Ecology

Vervets are semi-terrestrial opportunistic omnivores (Struhsaker, 1967). They will eat leaves, grass, fruits, flowers, fungi, insects, succulents, roots, and gum exudate (Pasternak et al., 2013), and eggs and chicks when found (Struhsaker, 1967). Vervets adjust their diets seasonally (Fedigan & Fedigan, 1988; Tournier et al., 2014), but in our study population, *Acacia karroo* leaves, seeds, and flowers are a primary and critical food source (see Figure 1; Pasternak et al., 2013). Additionally, in our study population, vervets spend significant time foraging for succulents and digging up roots (particularly

Figure 2.1

(a) a Juvenile Feeds on the Leaves of an Acacia karoo *Tree (b) an Adult Female (and Infant Ventral) with Dirt on its Face After Digging Up* Asparagus africanus *From Under a Shrub*

(a) (b)

Asparagus africanus; see Figure 2.1b) during the dry season when water is scarce or even absent (Pasternak et al., 2013).

2.1.3 Physical Characteristics

Adults

Adult vervets have a silver-grey coat with white fur surrounding a black face, and black feet and hands. Males have brightly colored genitalia, with a red penis and blue scrotum. Adults are mildly sexually dimorphic, as males are larger and heavier than females, weighing on average 5.7 kg (range: 3.9-8.0 kg), and have an average body length of 41 cm (Turner et al., 2019c). Females are approximately two-thirds the size of males, averaging 4.1 kg (range: 3.4-5.3 kg) with an average body length of 37 cm (Turner et al., 2019c). Males experience an adolescent growth spurt, reaching adult weight at six years of age, but can reach sexual maturity at five years (Turner et al., 1997). Females reach

Figure 2.2

An Adult Female Holds a Newly Born Infant, Illustrating an Infant With its Natal Pelt and Pink Face Compared to the Grey Pelt and Black Face of an Adult

Note. Photo, S. Morris.

sexual maturity between three to five years of age, experience menstrual cycles throughout the year, and have varied, concealed ovarian cycles during the non-breeding season. Mating is seasonal, with the breeding occurring mostly during the dry months of the austral fall, and the birth season occurring during the rainy months of the austral spring (Butynski, 1988). Females give birth to a single offspring and have interbirth intervals of one to two years, largely dependent upon whether or not offspring survived from the previous breeding season (Sashaw, 2012; Varsanyi, 2021). Gestation lasts 165 to 165 days (Eley et al., 1989). Infanticide has not been observed, likely due to the lack of male reproductive coercion (Seyfarth, 1980).

Juveniles and Infants

Infants have black natal coats with pink faces (Figure 2.2). The black coat gives way to the grey adult pelage at approximately 3 months of age, coinciding with the appearance of black faces (Lee, 1984). Infants are weaned and begin to forage independently between eight and 12 months of age depending on the availability of high-quality foods (Lee, 1987), a time that marks the beginning of the juvenile period. Females cease growth between the ages of 20-24 months, and males cease growth between the ages of 20-40 months (Turner et al., 2019c).

Age

Subjects were categorized as either juvenile (birth to less than ~3.5 years for females or less than 5 years for males) or adult (~3.5 years for females; ~3.5 years for females; Jarrett et al., 2018; Wrangham et al., 1999).

2.1.4 Social Organization

Unusually for guenons, where social groups typically contain a single adult male, vervets live in multimale, multifemale troops, ranging in size between five to 76 individuals (Horrocks, 1986; Pasternak et al., 2013). Vervets are female philopatric, with males dispersing from their natal group around sexual maturity. Males move to new troops every 2.5 to 3 years (Henzi & Lucas, 1980) after original dispersal, dependent upon their rank and integration into the female network (Young et al., 2019b). Because vervets mostly inhabit riverine woodlands, migration is usually constrained by linear territories along rivers (Isbell et al., 2004). Females in small troops inherent maternal rank, maintaining stable matrilineal dominance hierarchies (Mertz et al., 2019). Males are co-dominant with smaller females, and have more variable dominance ranks over time

(Mertz et al., 2019; Young et al., 2017).

The troops in our study population are much larger than the species' average (Pasternak et al., 2013). It is possible that group fission is constrained because there is a large contrast in food productivity between the acacia woodland along the river within which the study troops inhabit, and the considerably lower productivity away from the river (Pasternak et al., 2013). This increased troop size likely has a large impact on the social dynamics of the study troops (Henzi et al., 2013).

2.2 Study site

Data were collected at the Samara Private Game Reserve in the Karoo, Eastern Cape, South Africa (32°22'S, 24°52'E), an approximately 10,000 ha. protected area where the Samara Vervet Monkey Project has been located since 2008. The long-term study area is within a semi-arid karoo biome characterized by riparian woodland and centered on the Milk River, the only source of water for the study animals. Sympatric species include many large mammals such as kudu (*Tragelaphus strepsiceros*), eland (*Taurotragus oryx*), red hartebeest (*Alcelaphus buselaphus*), gemsbok (*Oryx gazella gazella*), springbok (*Antidorcas marsupialis*), and duiker (*Sylvicapra grimmia*), cape buffalo (*Syncerus caffer*), white (*Ceratotherium simum)* and black (*Diceros bicornis*) rhinoceros, warthog (*Phacochoerus africanus*), aardvark (*Orycteropus afer),* cape zebra (*Equus zebra zebra)*, introduced cape giraffe (*Giraffa camelopardalis giraffa*), cape porcupine (*Hystrix africaeaustralis*), bat-eared fox (*Otocyon megalotis*), and chacma baboon (*Papio ursinus*). The site also includes three species of territorial predators, including the black-backed jackal (*Canis mesomelas*), caracal (*Caracal caracal*), and reintroduced cheetah (*Acinonyx jubatus*), as well as two aerial predators: Verroux's eagle (*Aquila verreauxii*) and Verroux's eagle-owl (*Bubo lacteus*). The site has three species of venomous snakes: puff adder (*Bitis arietans*), cape cobra (*Naja nivea*), and boomslang (*Dispholidus typus*). Although puff adder and cape cobra have known to kill monkeys at the site, they are not vervet predators as such. Additionally, while baboons are known predators of vervets at other field sites (Enstam & Isbell, 2002), the vervets in our study population are not known to predated by resident chacma baboons and do not alarm when baboons are near (see Figure 2.3).

Figure 2.3
Vervet Monkeys (Chlorocebus pygerythrus) and Chacma Baboons (Papio ursinus) at the Field Site

2.2.1 Climate.

Daily ambient temperatures and rainfall were recorded at an onsite weather station. The field site's wet season lasts from October to March, and the dry season lasts from April to September. Temperatures can range from diurnal ambient temperatures of 46 °C in December and January, to nocturnal temperatures well below 0 °C in July (McFarland et al., 2015).

2.2.2 Differential Resource Availability

I used the Normalized Difference Vegetation Index (NDVI) to model changes in resource availability experienced by the three troops, as this has been shown to be a strong correlate of food available to wild vervets (Willems et al., 2009). NDVI estimates were obtained using MODIS NDVI data downloaded from NASA's *Reverb|ECHO* site (Didan, 2015). The Earth Observing System (EOS) satellites Terra (EOS AM-1) and Aqua (EOS PM-1) collect MODIS data with a return-to-site periodicity of 16 days (Didan, 2015). We then used *ArcGIS* version 1.6.1 to overlay the MODIS data onto the three territories, with each territory represented as a regular series of points 10-m apart. NDVI values were then extracted from the MODIS rasters at each point. Area-weighted averages for each territory were generated for consecutive 33-day windows (16 days post and prior to the date of each MODIS raster) by averaging all NDVI values for points falling within the territory's 95% isopleth and weighted by the troop's differential usage of its territory during that period.

2.2.3 Water Availability

Our study site's primary source of water is the Melk River, which flows intermittently. We collected information each day regarding localized water availability by recording whether or not each troop had access to water during that day, either from the flowing river or in pools forming after rainfall (Freeman et al., 2012; Young et al., 2019a). Thus, for a measure of water availability, I calculated the number of days since a troop had access to water. For example, if a troop had access to water on day 1, but not days 2, 3, but again on day 4, they were assigned 0, 1, 2, and 0 for number of days since water, respectively. This detailed measure captures more variability than a broad measure such as rainfall, as this does not reflect a troop's daily access to standing water.

Table 2.1

Composition of the Study Troops Throughout the Two Study Periods

Age/Sex	Study Period 1		Study Period 2	
	Range	Mean	Range	Mean
RST Adult Females	9-13	11	8-8	8
RST Adult Males	8-10	9	7-8	8
RST Juvenile Females	14-14	14	16-16	16
RST Juvenile Males	10-11	10	4-10	7
PT Adult Females	9-9	9	8-9	8
PT Adult Males	7-9	7	5-5	5
PT Juvenile Females	8-9	9	10-10	10
PT Juvenile Males	15-15	15	13-16	15
RBM Adult Females	7-10	8	5-7	6
RBM Adult Males	4-5	5	5-6	6
RBM Juvenile Females	15-5	15	14-14	14
RBM Juvenile Males	11-13	12	10-12	11

2.3 Study Troops and Study Period

I collected data from three troops ("PT," "RST," and "RBM") of vervet monkeys (*Chlorocebus pygerythrus*) that occupy adjacent and overlapping territories. These troops have been studied continuously since 2008 (RST, RBM), and 2012 (PT) as part of the on-going Samara Vervet Monkey Project. All individuals are uniquely identifiable from natural markings and have been followed 10 hours a day, 5 days a week for 10 years. Data were collected during two field seasons. My first field season ("study period 1") was a 9-

month period lasting between September 2016 to May 2017. The second field season ("study period 2") was a 3-month period lasting between March and May 2018. Group composition varied throughout the study periods and across the three troops and are described in Table 2.1.

2.4 Behavioral Data Collection

2.4.1 Scan Sampling

Data were collected for 10 hours a day, five days a week (Monday-Friday) across all three troops throughout the two study periods. Each day began either at sunrise and lasted for 10 hr, or began 10 hr before sunset in order to account for seasonal day length variation, and start times were counterbalanced across weeks, allowing assistants to sample during all times when animals were active. Data were collected via scan sampling (Altmann, 1974) using electronic data loggers with proprietary software (Pendragon Forms). Each adult scan sample was collected every 30-min, and lasted for either a 10 min window (study period 1) or 15 min window (study period 2). Juvenile scan samples were conducted in the same way, but were collected only once per hour in study period 1. In study period 2, adults and juveniles were scanned at the same time.

During an adult scan (study period 1), research assistants recorded the identities of all observable adults, along with their behavior (see Table 2.2). The identities of all social partners were recorded, as were the identities of the nearest adult male, adult female and juvenile within a 5 m radius. Juvenile scans (study period 1) were conducted the same as adult scans, except that *all* animals within 3-m were recorded as spatial partners (rather

Table 2.2

Behavioral Categories and Their Corresponding Activities for Each Scan Sample Collected

Behavior Category	Activities	Additionally Collected Information
Moving	Walking, running, or climbing	Substrate location: (e.g., ground, tree, or shrub)
Foraging	Feeding or searching for food	Food target
Resting	Laying, sitting, standing, and auto-grooming	Substrate location
Social	Initiating or receiving grooming, playing, copulating, initiating or receiving aggression	Activity partners

than just nearest neighbors). During study period 2, when juvenile and adult scans sampling periods were combined, juveniles were sampled in the same way as adults in study period 1—the nearest adult male, adult female, and juvenile were recorded as spatial partners (rather than all individuals within 3-m).

2.4.2 Agonistic Interactions and Dominance Rankings

Agonistic interactions between all animals were recorded using behavior sampling (see Martin et al., 1986). Agonistic interactions were defined as interactions during which one animal either emitted a threat (e.g., eye flash, vocal threat) toward another, or caused another to give up a resource (e.g., space, food, social partner) by approaching (and sometimes coming into physical contact with). For agonistic interactions, the identities of the aggressor (the animal that initiated the aggressive interaction), and the victim (the animal that received the aggressive interaction) were recorded. I included agonistic interactions between all animals in the calculation of each troop's dominance hierarchy (see Vilette et al., 2020).

Dominance hierarchies were determined from decided, dyadic agonistic interactions (N_{RBM} = 5,061; N_{RST} = 5,914; N_{PT} = 5,619) for all troop members. Individual dominance ranks were estimated using the Elo-rating method and the "EloRating" package (Albers & Vries, 2001; Neumann et al., 2011; Vilette et al., 2020) in R 3.5.2 (R Core Team, 2018) and a 5-month burn-in period. The Elo-rating method allows individual rankings to be updated through time, appropriate for our population given that previous research has shown that rank was dynamic during this period (Nord et al., 2021).

2.4.3 Maternal Relatedness

The identity of mothers, their offspring, and maternal siblings have been collected since 2013 as part of the Samara Vervet Monkey Project's ongoing baseline data collection, providing maternal relatedness measures.

2.4.4 Association Networks and Network Measures

Association Networks

I constructed three main association networks: a grooming network, a spatial proximity network, and a muzzle contact network. Dyad sample sizes and sampling time windows are dependent on the questions of interest and are further explained within respective chapters.

Network Measures

Betweenness centrality (hereafter "betweenness") and strength centrality (hereafter "strength") are both predicted to correlate with social learning (Croft et al., 2008). I first determined whether these measures were dynamic throughout the study period in each network. Using the "check.windowsize" function of the "netTS" (Bonnell & Vilette,

2020) package in “R," I estimated the convergence of ties in both the grooming and spatial proximity networks using bootstrapped samples of the dyads in each network for each animal (i.e., "nodes"; Bonnell and Vilette, 2020). The “check.windowsize” function also allowed me to measure the sensitivity of this subsampling. After finding that both networks changed through time using various window sizes (Appendix A.1) but were stable (i.e., converged) and robust (i.e., least sensitive to subsampling) using a 90-day window (Appendix A.2), I updated network measures for each animal every 90 days.

CHAPTER 3: MUZZLE CONTACT AND INFORMATION TRANSFER

This data chapter has been published in the *Journal of Comparative Psychology* (22 February 2021), under the title "Tolerance of Muzzle Contact Underpins the Acquisition of Foraging Information in Vervet Monkeys (*Chlorocebus pygerythrus*)." The authorship list for the published version is as below. Since this publication, I changed how I calculate dominance ranks. Here, I used David Scores, as this was the method best available to me at the time.
URL: https://psycnet.apa.org/record/2021-19654-001

Christina M. Nord[1,2], Tyler R. Bonnell[1,2], Marcus J. Dostie1[,2,3], S. Peter Henzi[1,2], and Louise Barrett[1,2]

[1]Department of Psychology, University of Lethbridge, Lethbridge, Canada

[2]Applied Behavioural Ecology and Ecosystems Research Unit, University of South Africa, Pretoria, South Africa

[3]Department of Geography, University of Lethbridge, Lethbridge, Canada

3.1 Abstract

Muzzle contact, where one animal brings its muzzle into close proximity to that of another, has often been hypothesized as a straight-forward means of socially mediated food investigation. Using 2,707 observations of muzzle contact occurring across three troops of wild vervet monkeys (*Chlorocebus pygerythrus*), we tested this social learning hypothesis. We first explored the social structuring of muzzle contact by analyzing the characteristics of initiators and receivers of muzzle contact. Similar to previous research, juveniles initiated contact at higher rates than adults, particularly towards adult females and animals with lower dominance rankings. The highest number of contacts occurred between kin compared to contacts between nonkin. However, on the whole, contacts occurred at low rates, even among kin dyads. We next determined whether muzzle contact was used as a means to learn socially, specifically by animals seeking foraging

information. We found that initiators did not overwhelmingly target foragers, meaning animals do not appear to directly seek information about food during muzzle contact. However, animals that contacted foragers were more likely to forage themselves in comparison to those that contacted nonforagers, suggesting that foragers do provide food information. These findings indicate that both kin and low-ranking animals serve as discriminative stimuli for social tolerance, and that foraging animals serve as discriminative stimuli for food availability. We conclude that broad social tolerance, rather than the recipient's knowledge, is the most likely antecedent to muzzle contact, and that animals engage in this behavior as a low-cost means of maintaining a baseline level of information about their environment.

3.2 Introduction

All foraging animals need to locate food, obtain a balance of necessary nutrients, and avoid toxins (King, 1994b). Many taxa use olfaction to investigate potential food stuffs, and, for gregarious animals, such investigation can be socially mediated (Hoppitt & Laland, 2013). Social contact during foraging allows animals to acquire information about novel foods and to avoid consuming those that are harmful (Hoppitt & Laland, 2013). For example, Galef Jr and Wigmore (1983) notably demonstrated that rat food preferences can depend on odor cues found on the breath of conspecifics, an advantageous mechanism given that rats lack emesis abilities and are subsequently more at risk of poisoning if they ingest toxic substances. Similar socially mediated food preferences via olfaction have been found in mice (Valsecchi & Galef, Jr., 1989), bats (O'Mara et al., 2014), and even in invertebrates, most famously among the social insects

(Farina et al., 2012; Hasenjager et al., 2020; Provecho & Josens, 2009).

Primates can also use olfaction to identify foods, and some primates have particularly developed olfactory systems which are useful for foraging (strepsirrhines) or social communication (platyrrhines: Barton et al., 1995; Heymann, 2006; Zschoke & Thomsen, 2014). For example, Laidre (2009) found that three species of cercopithecines (*Mandrillus sphinx, Mandrillus leucophaeus,* and *Papio anubis*) often seek olfactory cues when foraging, including from the mouths of others, and Tonkean macaques (*Macaca tonkeana*) can locate food sites and discriminate food availability and quality after sniffing the mouths of conspecifics (Chauvin & Thierry, 2005; Drapier et al., 2002). Furthermore, muzzle-muzzle contact (hereafter *muzzle contact*; see Figure 3.1) has been proposed as a mechanism by which infant vervet monkeys (Lycett & Henzi, 1992) and

Figure 3.1
A Juvenile Male Muzzle Contacts Its Mother

Note. Photo, S. Morris.

yellow baboons (*Papio cynocephalus*; King, 1994b) can gather information about food, principally from their mothers. Gaining information about food is an essential steppingstone to foraging independence throughout primate ontogeny (King, 1994a), and muzzle contact could possibly afford such information acquisition (Lycett & Henzi, 1992). The prevalence of muzzle contact is likely to reflect species-relevant sensory modalities. For example, Lycett and Henzi (1992) suggested that olfactory information was more salient than visual information for vervet monkeys, given Cambefort's (1981) finding that vervets did not discriminate aversive visual foraging cues provided by other troop members. Lycett and Henzi (1992) therefore suggested that muzzle contact might act to allow vervets to gain information efficiently from other troop members, particularly infants from their mothers.

Primates have been suggested to possess particularly skillful social learning abilities, but such abilities could also be a byproduct of their social organization (Coussi-Korbel & Fragaszy, 1995; Heyes, 2012; King, 1994b; Shettleworth, 2010; Tomasello, 1996; Visalberghi & Fragaszy, 1990; Visalberghi & Fragaszy, 1996). Certain behavioral features and ecological characteristics of vervets might help tease apart whether the social learning features of primates are particular to the primate order, or can instead be explained by more straight-forward social tendencies. For example, vervets are omnivorous generalists, and generalist species have been hypothesized to benefit more from public information concerning foods because the large variation in generalist diets potentially increases the probability of encountering something toxic (Galef & Giraldeau, 2001). Additionally, vervet mothers are tolerant of infants while foraging (and sometimes allow infants to take food from their mouths (Hauser, 1993; Hauser, 1994), and vervets are capable of socially transmitting arbitrary food preferences (van de Waal et al., 2013).

Here, we test the idea that muzzle contact has functional consequences for vervet monkeys (Lycett & Henzi, 1992). We begin by determining whether it is mediated by demographic and/or social characteristics (referred to as "phenotypes" by Carter et al., 2016). There is some prior work that allowed us to make a few specific predictions regarding the structure of muzzle contact. Additionally, we conducted exploratory analyses regarding the phenotypic characteristics of initiators and receivers (whether contacts differentiated by age, sex, rank, or kinship) alongside the tests of our direct predictions (Gelman, 2003). Based on previous work, we predicted (a) that juveniles would initiate muzzle contact more often than adults (Grampp et al., 2019; King, 1994b; Lycett & Henzi, 1992); (b) that the initiators of muzzle contact would be less likely to direct muzzle contact to higher-ranking animals, given that muzzle contact requires close proximity and increases the risk of being bitten; and (c) that animals of all ages would target adult females, given that philopatric females are the focus of social attention and might also be expected to have experienced the range of local foods (King, 1994b; Renevey et al., 2013). We also predicted that (d) the majority of muzzle contact would be directed towards kin, and that (e) related dyads would have a higher number of muzzle contacts between them, as previous work on vervets has shown both that muzzle contacts are most frequent between infants and mothers (Lycett & Henzi, 1992) and that infants acquire foraging behavioral variants from their mothers (van de Waal et al., 2014).

We then answer our key question of whether muzzle contact affords information acquisition. If animals do indeed initiate muzzle contact to acquire foraging information, and initiators are faced with the choice to target either foragers or nonforagers, then (f) initiators should disproportionately target foragers more than what is expected by chance (i.e., greater than 50% of the time; King, 1994b). To the extent that initiators do target foragers, we predicted that (g) initiators would forage immediately after contact. We make this prediction in accordance with three lines of evidence. The first is that by foraging immediately after contacting a forager, initiators and receivers can engage in simultaneous foraging behaviors, which is a form of behavioral matching. Behavioral matching has been proposed as an important mechanism in novel foraging information acquisition in vervets (van de Waal et al., 2012). The second is that foraging immediately after contact affords selective practice, or the engagement in novel behaviors within an affording context (particularly useful to unskilled animals; Schuppli et al., 2016). Finally, foraging after contact allows animals to immediately capitalize on the benefits of social learning and reduce its potential costs (learning socially can be costly to an animal if the acquired information is outdated, but this cost can be reduced if the learner applies acquired information quickly, e.g., in the presence of the relevant food item: Dunlap & Stephens, 2016).

To the extent that animals forage themselves immediately after contacting foragers, we predicted that (h) initiators would be more likely to do so after contacting foragers that are eating rarely encountered foods because new information should be sought more often from foods that are rarely encountered (Barrett et al., 2017). As overall food availability is likely to be implicated in all predictions, we controlled for this in our analyses, although we could not specify the direction of any effects. That is, animals may well turn to olfactory cues when food is generally scarce and there is the strong possibility of missing a valuable or rare food but, equally, they may also do so when food availability is high and new dietary items are appearing in the home range.

3.3 Methods

3.3.1 Study Site and Subjects

We collected data between 2016 and 2018 at the Samara Private Game Reserve, Eastern Cape, South Africa from three troops (“PT," “RST," and “RBM”) of vervet monkeys that occupy adjacent and overlapping territories in semi-arid riparian woodland (Pasternak et al., 2013). These troops have been continuously studied since 2008 (RST, RBM) and 2012 (PT), and all animals are uniquely identifiable from natural markings. Group composition varied throughout the study period (Table 3.1).

Table 3.1

Composition of Study Troops Throughout the Study Period

Age/Sex	Range (n)	Mean (n)
RST Adult Females	8-13	9
RST Adult Males	6-10	8
RST Juvenile Females	14-16	15
RST Juvenile Males	4-11	10
PT Adult Females	8-9	9
PT Adult Males	5-9	6
PT Juvenile Females	8-10	9
PT Juvenile Males	13-16	15
RBM Adult Females	5-10	7
RBM Adult Males	4-7	6
RBM Juvenile Females	14-16	15
RBM Juvenile Males	10-13	12

3.3.2 Behavioral Data Collection

CN and three assistants used electronic data loggers to conduct behavior sampling (explained below) of agonistic interactions and muzzle contacts across a 9-month period from September 2016 to May 2017, and again during a 3-month period between March and May 2018. In all, 16,594 observations of decided agonistic interactions (N_{RBM} = 5,061; N_{RST} = 5,914; N_{PT} = 5,619) and 2,707 muzzle contact observations were collected across 1,107 observer days (N_{RBM}= 339; N_{RST} = 441; N_{PT} = 327).

Observers were trained to identify individual animals, relevant behaviors, vegetation, and how to record occurrences and outcomes of agonistic interactions by experienced field assistants as part of training to collect baseline data (Young et al., 2017). Muzzle contacts were not part of the baseline data collection, and as such, CN trained field assistants to identify muzzle contact and its duration. Consistency and accuracy were ensured by inter-observer reliability checks in the field on a regular basis, to ensure inter-observer agreement on particular cases. Given that we collect data for 10 hours a day, five days a week, there is some time during which animals are not observed. As such, we describe our behavioral data collection as behavior sampling (sensu Martin et al., 1986) rather than "all-occurrence sampling," as behavior sampling describes the recording of each instance of a behavior during a set observation period.

Observers also recorded agonistic interactions and muzzle contacts while performing other data collection duties (e.g., scan sampling, fecal sample collection) that required them to search for every individual every half hour. Given this, and that our study site is characterized by generally high visibility and animals are well-habituated, we are confident that data were collected data without systematic bias.

Agonistic interactions included lunges, charges, chases, displacements, and supplants (Young et al., 2017). We defined muzzle contact as a directed dyadic behavior that began when one animal (the initiator) brought its muzzle to within 1 cm of another animal (the receiver), and ended when the dyad members' muzzles were more than 2-cm apart (Figure 3.1). We recorded dyad member identities and date and time of muzzle contact, along with approximate duration, bracketed as 1-3 s, 3-5 s, 5-10 s, or 10+s. We also recorded whether or not dyad members foraged in the 5 seconds before muzzle contact began, and/or in the 5 seconds after muzzle contact ended. Foraging was defined as actively gathering (e.g., pulling grass, pulling leaves), searching for (digging through dirt or grass, chasing insects), and ingesting food (putting food in the mouth, biting food, or chewing food). If animals did forage, we also recorded the food type. As our study troops' territories overlapped, we also observed and recorded muzzle contacts between members of different groups.

3.3.3 Age

Subjects were categorized as either juvenile or adult in relation to sexual maturity (Jarrett et al. 2018; birth to less than ~3.5 years for females; or less than 5 years for males).

3.3.4 Relatedness

The identity of mothers, their offspring, and maternal siblings have been collected since 2013 as part of the Samara Vervet Monkey Project's ongoing baseline data collection. We included only muzzle contacts initiated by juvenile animals in our relatedness analyses because, while the relatedness between all juvenile-juvenile and juvenile-adult dyads for the current study is known, relatedness between adults born before 2013 is largely unknown.

3.3.5 Dominance Rankings and Dominance Rank Differences

These analyses focus on the structure and function of muzzle contact between all group members, so we calculated dominance ranks across all members of each troop rather than within specific age- and sex classes, allowing us to compare muzzle contact and agonistic interactions directly.

We generated dominance hierarchies from decided agonistic dyadic interactions for all troop members. We first determined if rank changed by dividing the 12-month study period into four 3-month blocks and calculated rank as standardized (allowing comparison across troops), normalized David's Scores using the R package "compete" (Curley et al., 2015) in R 3.5.2 (R Core Team, 2018). The divisions ensured adequate sample sizes with which to estimate ranks. After confirming that rank varied within animals (we measured variation by calculating the standard deviation (SD) of each animal's ranks throughout the study period; $\text{mean}_{SD} = .116$, $\text{range}_{SD} = 0\text{-}.385$), we used these dynamic rank estimates (i.e., our 3-month block estimates) in our analyses.

For all models exploring dyadic relationships, we used differences in dominance rank (initiator - receiver), where positive values indicate that the initiator was higher-ranking than the receiver. Dominance ranks were averaged across the study period for all Poisson models. Sometimes, muzzle contacts occurred across troops. For muzzle contacts that occurred across troops, differences in dominance rank were relative to each dyad members' within-troop rankings, as dominance rankings were only calculated from within-troop agonistic interactions.

3.3.6 Relative Frequencies of Food Types

The relative frequency with which animals encountered different foods was derived from the foods that recipients were eating prior to muzzle contact.

3.3.7 Troop-Level Estimates of Resource Availability

We used the Normalized Difference Vegetation Index (NDVI) to model differential resource availability experienced by the three troops, as this has been shown to be a strong correlate of food availability to wild vervets (Willems et al., 2009). NDVI estimates were obtained using MODIS NDVI data downloaded from NASA's "Reverb| ECHO" site (Didan, 2015). The Earth Observing System (EOS) satellites Terra (EOS AM-1) and Aqua (EOS PM-1) collect MODIS data with a return-to-site periodicity of 16 days (Didan, 2015). We then used "ArcGIS" version 1.6.1 to overlay the MODIS data onto the three territories, with each territory represented as a regular series of points 10-m apart. NDVI values were then extracted from the MODIS rasters at each point. Area-weighted averages for each territory were generated every 16 days by averaging all NDVI values for points falling within the territory's 95% isopleth and weighted by the troop's differential usage of its territory during that period.

3.3.8 Statistical Analyses

We constructed multilevel regression models within a Bayesian framework (Gelman & Shalizi, 2012) using the package "brms" (Bürkner, 2017) in R (R Core Team, 2018). Sample sizes of observed muzzle contacts varied with respect to the variables included in each tested model. We specified four chains and 3,500 iterations for all models. All models included weakly informative priors (mean = 0, *SD*=1). We used $\hat{r}$s ("r.hats") to confirm model convergence (see Gelman & Shirley, 2011). Using the "DHARMa" package in R (Hartig, 2017), we tested residual assumptions for each dataset. All datasets met model assumptions except for our model investigating muzzle contact interaction indices between related dyads (see below). Additionally, we used directed dyads because we were interested in whether or not specific animals were being targeted for contact and, given cross-troop contact, we included initiator and/or receiver troop membership as random effects in all models.

We explored whether specific social and demographic phenotypes influenced muzzle contact (predictions a-c) by constructing two Poisson models, one modeling the characteristics of initiators, and the other the characteristics of receivers. For both models, age-sex categories and rank served as predictor variables, while the number of times an animal acted as an initiator served as the response variable in the initiator model, and the number of times an animal acted as a receiver served as the response variable in the receiver model. We entered ID and troop membership as random effects, as well as an offset variable accounting for the number of days each animal was present during the sample period.

We then assessed the relationship between relatedness and muzzle contact (prediction d). Because relatedness between adults was largely unknown, we explored this question for only juvenile-initiated dyads by constructing a Bernoulli model to determine how often juveniles contacted kin as compared to nonkin. For this model, whether or not the receiver was related to the juvenile initiator (yes/no) served as the response variable, and differences in dominance rank, receiver sex, and initiator age at the time of contact (calculated by adding days since birth to the time of muzzle contact; these values were centered and scaled, resulting in ages represented as standard deviations above and below the mean value) were entered as predictor variables, with receiver ID, initiator troop membership, and receiver troop membership as crossed random effects.

We were also interested in the effect of relatedness on muzzle contact interaction rates, i.e., the total number of contacts per the study duration, between specific dyads initiated by juveniles (prediction e), so we constructed a Poisson model to determine the rates of juvenile-initiated muzzle contacts. Using rates allowed us to calculate muzzle contact interaction indices and determine if certain dyads made contact at higher rates than others. Given that our response variable for this model was dyadic, so too were all of our fixed effects (e.g., the fixed effect "sex" included the sexes of both dyad members, either male-male, male-female, female-male, or female-female). Thus, we specified the identities of each dyad as our response variable, and included sexes of the dyad, dominance differences between the dyad, average age of the initiator during the study period, and whether or not the dyad was related (yes/no) as fixed effects. Initiator ID, receiver ID, and troop memberships of the initiator and the receiver were entered as crossed random effects. Our analysis of residuals for this model (which used a Poisson distribution) revealed underdispersion in the data—the model did not account for many of the dyads that interacted only one time. Running this model using a hurdle Poisson distribution (Hilbe, 2017) removed the underdispersion and revealed the same relative estimates as our original, underdispersed Poisson version of the model. Given this, we present the results from the simpler Poisson model below and provide results from the hurdle Poisson version of the model in Appendix B.

We then explored whether muzzle contact affords information acquisition by constructing three Bernoulli models (predictions f-h). We first determined if initiators targeted foragers significantly more than nonforagers (prediction f) by creating a model with whether or not receivers foraged (yes/no) as the response variable, NDVI as the predictor variable, and initiator ID, receiver ID, and troop memberships of the initiator and receiver as crossed random effects. We next determined how often initiators foraged after contacting a forager (prediction g) by constructing a model in which foraging post-contact (y/n) was entered as our response variable, whether receivers foraged prior to contact (yes/no), age-sex, and differences in dominance rank as predictor variables, and receiver ID, initiator troop membership, and receiver troop membership as crossed random effects. Finally, to determine if rarely encountered foods increased initiator post-contact foraging (prediction h), we specified whether initiators foraged post-contact (y/n) as our response variable, relative food type frequency, age-sex, and differences in dominance rank as predictor variables, and receiver ID, initiator troop membership, and receiver troop membership as crossed random effects. We included NDVI in all information acquisition models to account for local ecological conditions, and duration of contact as a statistical control for the probability that information could be adequately transmitted during contact.

Model main effects are presented as summary statistics for posterior means, standard errors (SE), and 95% credible intervals (CI), along with group-level variation in our response variables.

3.3.9 Ethical Note

All protocols were noninvasive and adhered to the laws and guidelines of South Africa and Canada. Procedures were approved by the University of Lethbridge Animal Welfare Committee (Protocols 0702 and 1505). This study also adheres to the ASAB/ ABS Guidelines for the Use of Animals in Research.

3.4 Results

We found that once initiators brought their muzzles within 1 cm of the receivers' muzzle, initiators were never refused or rejected, and we observed no agonistic interactions during muzzle contacts. It could be the case that potential receivers refused contact prior to what we have defined as initiation. However, such refusals would have occurred outside of our definition of muzzle contact, as they would have occurred before the 1 cm threshold.

Predictions, variables, and findings are summarized in Table 3.2.

Table 3.2

Summary of the Predictions Made, Variables Included, and the Subsequent Findings

Prediction	Response variable	Predictor variables (Grouping variables)	Covariates	Finding
(a) juveniles initiate muzzle contact more often than adults	Count of contacts initiated	initiator age/sex, initiator average rank (initiator ID, initiator troop)	N/A	Juvenile females had the highest rate of initiating muzzle contacts per the study period (Table 2a, Figure 2a)
(b) initiators direct less muzzle contact to higher-ranking animals	Count of contacts received	receiver age/sex, average receiver rank (receiver ID, receiver troop)	N/A	Lower-ranking animals received more muzzle contacts than did higher-ranking animals (Table 2b, Figure 2b)

c) animals target adult females	Count of contacts received	receiver age/sex, average receiver rank (receiver ID, receiver troop)	N/A	Adult females received muzzle contact at the highest rates, and females overall received muzzle contacts at higher rates than did males (Table 2b, Figure 2b)
(d) the majority of contact is directed towards kin	Kin and nonkin dyads	initiator sex, receiver sex, initiator age (initiator ID, receiver ID, initiator troop, receiver troop)	NDVI	9.6% of contacts occurring between kin (Table 3a)
(e) related dyads have more contacts between them	Counts of kin and nonkin dyads	initiator sex/receiver sex, dyad relatedness, average dyad rank difference, initiator age (initiator ID, receiver ID, initiator troop, receiver troop)	N/A	Kin-based muzzle contacts occurred at the highest rates per the study period compared to nonkin-based muzzle contacts (Table 3b, Figure 3)
(f) initiators target foragers greater than 50% of the time	Contacts to foragers vs nonforagers	N/A (initiator ID, receiver ID, initiator troop, receiver troop)	NDVI	Initiators targeted foragers 46.7% of the time (Table 4)
(g) initiators forage immediately after contact	Initiators foraged post contact (yes/no)	foraging receiver (yes/no), initiator age/sex, dyad rank difference (initiator ID, receiver ID, initiator troop, receiver troop)	Approximate duration, NDVI	There was a higher probability that an initiator would forage immediately following contact with a forager than with a non-forager (Table 5a, Figure 4)
(h) initiators forage immediately after contact more so after contacting foragers who are eating rarely encountered foods	Initiators foraged post contact (yes/no)	initiator age/sex, dyad rank difference, receiver food type frequency (initiator ID, receiver ID, initiator troop, receiver troop)	Approximate duration, NDVI	No clear effect of rarely encountered foods (Table 4b)

3.4.1 Initiator and Receiver Characteristics

Juvenile females had the highest rate of initiating muzzle contacts per the study period, while adult males initiated muzzle contact at the lowest rates pre age/sex class (Table 3.3, Figure 3.2a). Dominance rank had little effect on the number of contacts initiated (Table 3.3). Adult females received muzzle contact at the highest rates per the

Table 3.3

Posterior Estimates of Muzzle Contact Initiation Rate

Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept (Adult Females)	-2.797	0.142	-3.077	-2.485
	Juvenile Females	0.536	0.130	0.289	0.796
	Adult Males	-0.674	0.153	-0.979	-0.372
	Juvenile Males	0.159	0.129	-0.096	0.412
	Average Rank	0.326	0.182	-0.025	0.688
Group-Level Effects	sd(ID)	0.454	0.042	0.379	0.543
	sd(Troop)	0.141	0.192	0.003	0.657

Note. Age-sex is relative to adult females. Estimates are on the log scale; CI = credible interval. N = 145. R^2 marginal = .427; R^2 conditional = .903.

Table 3.4

Posterior Estimates of Muzzle Contact Receiving Rate

Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept (Adult Females)	-1.890	0.136	-2.164	-1.600
	Juvenile Females	-0.804	0.130	-1.053	-0.552
	Adult Males	-1.565	0.155	-1.873	-1.264
	Juvenile Males	-1.462	0.132	-1.721	-1.202
	Average Rank	-0.425	0.183	-0.778	-0.059
Group-Level Effects	sd(ID)	0.479	0.042	0.403	0.567
	sd(Troop)	0.150	0.202	0.003	0.742

Note. Age-sex is relative to adult females. Estimates are on the log scale; CI = credible interval. N = 145. R^2 marginal = .515; R^2 conditional = .945.

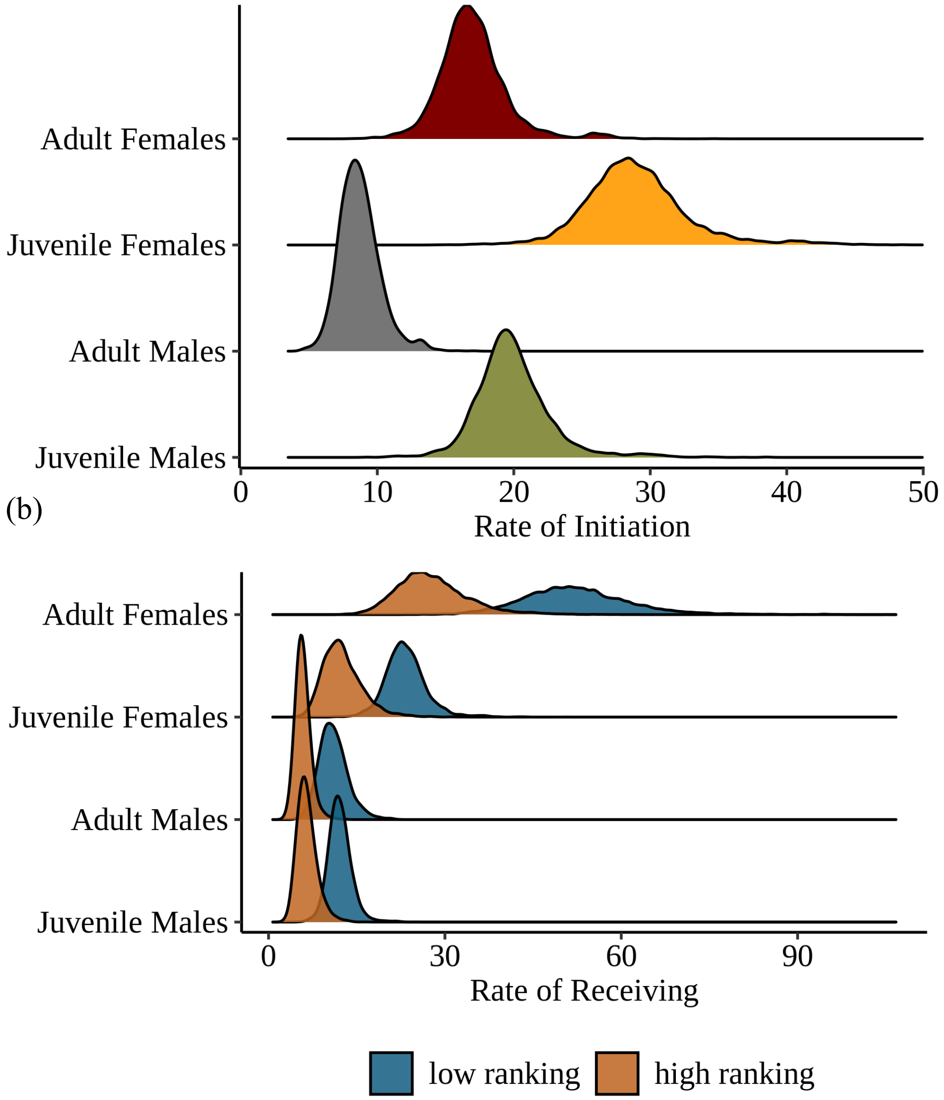
study period, and females overall received muzzle contacts at higher rates per the study period than did males (Table 3.4). In addition, lower-ranking animals received more muzzle contacts than did higher-ranking animals (Figure 3.2b). The difference between the marginal and conditional R^2 values reveal that there remains unexplained variation (beyond our predictor variables) in our grouping variables, particularly between individual animals (as opposed to between observations within animals Nakagawa &

Schielzeth, 2012), but not between troops (Tables 3.3 and 3.4).

Figure 3.2:

Rates of Muzzle Contact (a) Initiation and (b) Receiving by Age-Sex Category

(a)



Note. Density plots present the range of rates predicted by the model, with the height of the density curve indicating the probability of the predicted rate, and the spread of the curve indicating its uncertainty (Tables 3.3 and 3.4). Rates are backtransformed from the log scale into the original scale. In this context, rate refers to the number of contacts initiated (a) and received (b) per the study duration.

Table 3.5

Posterior Estimates of Whether Juveniles Contacted Kin (y/n)

Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept (Juvenile Females)	-2.359	1.195	-5.011	0.062
	Rank Difference	-0.785	0.326	-1.413	-0.151
	Male Initiators	0.451	0.229	0.012	0.917
	Male Receivers	-1.422	0.325	-2.076	-0.788
	Initiator Age	-0.875	0.130	-1.129	-0.617
Group-Level Effects	sd(Initiator)	0.702	0.144	0.436	1.000
	sd(Initiator troop)	0.984	1.452	0.021	5.112
	sd(Receiver)	1.252	0.173	0.946	1.626
	sd(Receiver troop)	1.041	1.533	0.018	5.281

Note. Sex is relative to (a) females and (b) female–female dyads. All initiators are juveniles. Estimates are on the logit scale; CI = credible interval. N = 1,964. R^2 marginal = .092; R^2 conditional = .314.

Table 3.6

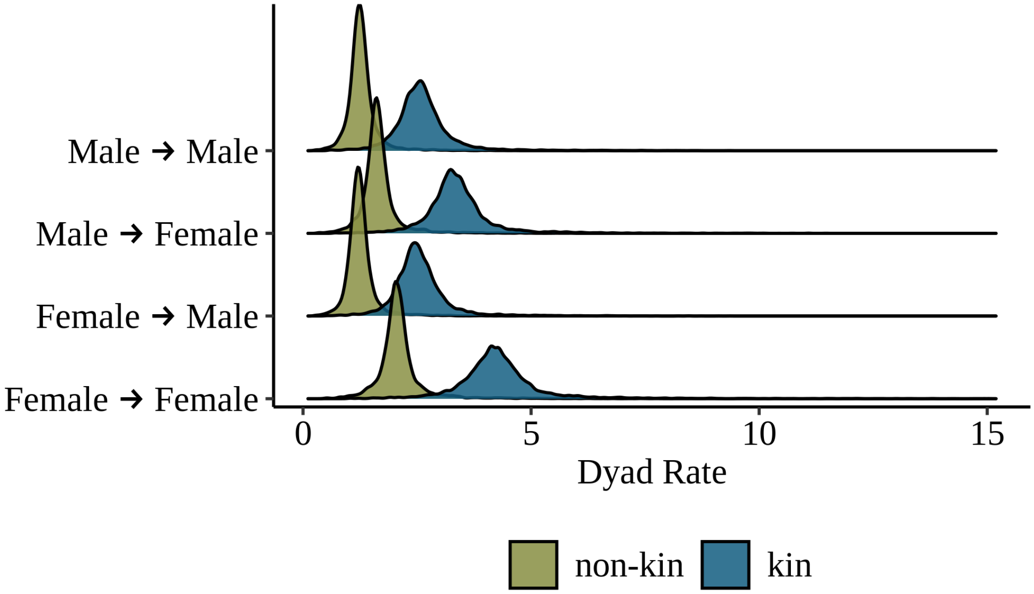
Posterior Estimates of Dyad Association Indices

Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept (F-F Dyads)	-4.896	0.225	-5.372	-4.401
	Average Rank Difference	0.014	0.090	-0.164	0.191
	Relatedness	0.718	0.062	0.592	0.837
	Female-Male Dyads	-0.520	0.090	-0.696	-0.348
	Male-Female Dyads	-0.236	0.062	-0.357	-0.114
	Male-Male Dyads	-0.499	0.096	-0.688	-0.313
	Average Initiator Age	0.026	0.040	-0.051	0.103
Group-Level Effects	sd(Initiator)	0.119	0.040	0.034	0.194
	sd(Initiator troop)	0.199	0.331	0.003	1.063
	sd(Receiver)	0.222	0.031	0.164	0.286
	sd(Receiver troop)	0.189	0.303	0.003	1.005

Note. Sex is relative to (a) females and (b) female–female dyads. All initiators are juveniles. Estimates are on the logit scale; CI = credible interval. N = 1,105. R^2 marginal = .199; R^2 conditional = .305.

Figure 3.3

Muzzle Contact Rates as Predicted by the Model for Nonkin and Kin Dyads



Note. Density plots present the range of rates predicted by the model, with the height of the density curve indicating the probability of the predicted rate, and the spread of the curve indicating its uncertainty (see Table 3.6). Rates are backtransformed from the log scale into the original scale. In this context, rate refers to the number of contacts per the study duration.

3.4.2 Is There a Kin Basis to Muzzle Contact?

How Often Do Juveniles Contact Kin?

Our model testing whether related juveniles were more likely to contact kin compared to nonkin found little evidence that this was the case, with only 9.2% of contacts occurring between kin (Table 3.5; we calculated percentages using model marginal means and backtransformed this value into the original scale. For a comparison of expected contacts to kin given kin availability, see Appendices B.13 and B.14). There were, however, age and sex differences in kin-based contacts: Younger juveniles and juvenile males were more likely to direct contacts towards kin compared to nonkin, and juvenile males were less likely to be contacted by relatives. Comparison of marginal and conditional R^2 values reveals that overall model performance was, to a large degree, driven by unexplained variation in our grouping variables, including initiator and receiver identities, as well as initiator troop membership (Table 3.5).

Are Dyad Rates Influenced by Kinship?

Our model investigating the rates of contact per dyad found that most dyads occurred at low rates (Table 3.6). We also found that kin-based muzzle contacts occurred at the highest rates per the study period compared to nonkin-based muzzle contacts (Table 3.6, Figure 3.3). We found no effect of average initiator age between related dyads on this rate (Table 3.6). Comparison of marginal and conditional R^2 values reveals that unexplained variation remains among initiator and receiver identities (Tables 3.6).

3.4.3 How Often Do Initiators Contact Foragers?

There was little evidence that initiators contacted foragers more frequently than nonforagers, doing so only 46.7% of the time (and therefore contacted nonforagers 53.7% of the time, Table 3.7; we calculated percentages using model marginal means and backtransformed this value into the original scale). We found little evidence that initiators were more likely to contact foragers during times of low resource availability (Table 3.7). This model accounted for minimal variance in the response variable, as indicated by the marginal R^2 and conditional R^2 values.

3.4.4 Do Initiators Forage After Contacting a Forager?

There was a higher probability that an initiator would forage immediately following contact with a forager than with a non-forager (Table 3.8), with female

Table 3.7

Posterior Estimates of Whether Initiators Contacted Foragers (y/n)

Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept	0.179	0.623	-1.060	1.563
	NDVI	-0.800	0.485	-1.797	0.131
Group-Level Effects	sd(Initiator)	0.315	0.070	0.178	0.455
	sd(Initiator troop)	0.495	0.779	0.008	2.781
	sd(Receiver)	0.506	0.075	0.361	0.657
	sd(Receiver troop)	0.471	0.766	0.009	2.611

Note. Estimates are on the logit scale; CI = credible interval. N = 2,707. R^2 marginal = .001; R^2 conditional = .069.

Table 3.8

Posterior Estimates of Initiators Foraging After Contacting Foragers

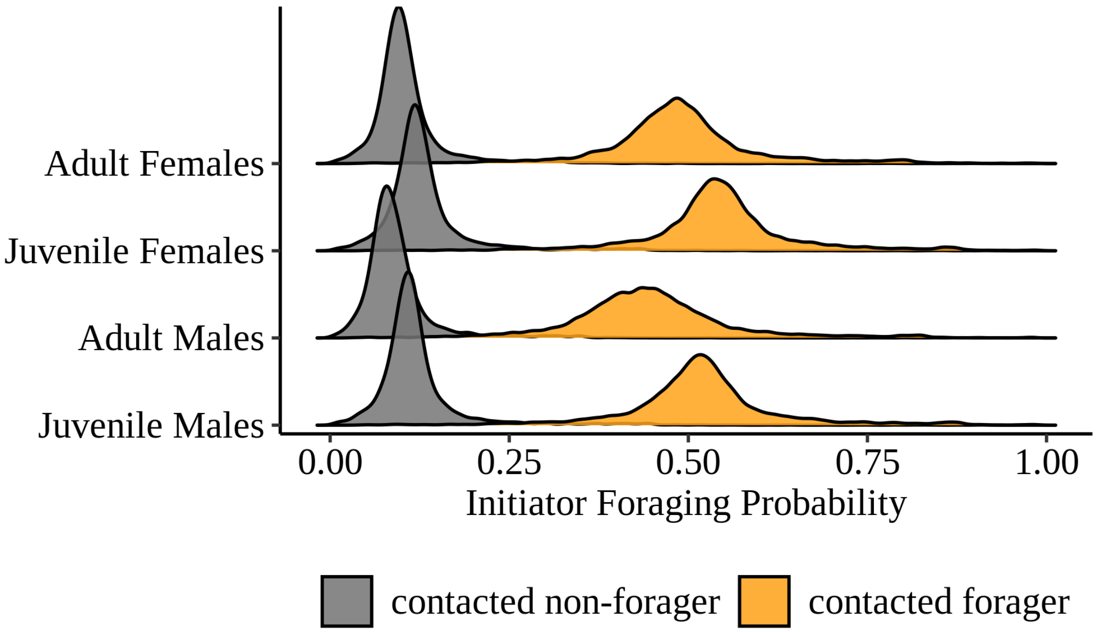
Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept (Adult Females)	-2.218	0.563	-3.300	-0.907
	Foraging Receiver	2.148	0.105	1.947	2.355
	Juvenile Females	0.232	0.138	-0.035	0.499
	Adult Males	-0.177	0.210	-0.600	0.215
	Juvenile Males	0.128	0.147	-0.151	0.428
	Approximate Duration	0.018	0.042	-0.065	0.101
	NDVI	-0.010	0.532	-1.059	1.048
	Rank Difference	-0.051	0.139	-0.324	0.228
Group-Level Effects	sd(Initiator)	0.102	0.073	0.004	0.270
	sd(Initiator troop)	0.406	0.627	0.008	2.232
	sd(Receiver)	0.138	0.086	0.007	0.320
	sd(Receiver troop)	0.426	0.641	0.006	2.392

Note. Age-sex is relative to adult females. Estimates are on the logit scale; CI = credible interval. N = 2,655. R^2 marginal = .189; R^2 conditional = .201.

juveniles being slightly more likely to do so compared to all other age-sex classes (Figure 3.4). Duration of muzzle contact, NDVI, and difference in dominance rank had little impact on the probability of subsequent foraging. The overall model explained

Figure 3.4

Probabilities of Initiators Themselves Foraging After Contacting Foragers and Nonforagers by Age-Sex Categories



Note. Density plots present the range of probabilities predicted by the model, with the height of the density curve indicating the likelihood of the probability, and the spread of the curve indicating its uncertainty (Table 3.7). Probabilities are backtransformed from the logit scale into a probability scale.

approximately 20% of the variance, and comparison of marginal and conditional R^2 values indicated little contribution of grouping-level differences in either individual or troop identities, indicating that most observed variation was between observations rather than among particular grouping variables (Table 3.8).

3.4.5 Do Rarely Encountered Foods Affect Foraging After Contact?

We cannot be certain of any effect for rarely encountered foods, as the right tail of the CI for the estimate contains zero. However, the density of the CI could point towards a possible effect of rarely encountered foods, as most of the density lies within the negative range, indicating that the rarer the food foraged by the receiver, the more likely the initiator was to forage post contact. However, any effect of rare foods is uncertain. We found no effect of duration of contact, food availability, or age/sex class on the frequency of foraging post contact. We did find a small effect of rank difference on whether or not initiators foraged post contact given they had contacted a forager. However, comparing the conditional and marginal R^2 values indicate that our model accounts for minimal variance and reveals few differences among either individual or troop identities, again indicating that most observed variation was between observations rather than between particular grouping variables (Table 3.9).

Table 3.9

Posterior Estimates of Initiators Foraging After Contacting Foragers Dependent Upon the Food Item Eaten by the Receiver

Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept (Adult Females)	-0.108	0.804	-1.886	1.646
	Juvenile Females	0.258	0.160	-0.056	0.577
	Adult Males	0.008	0.249	-0.484	0.479
	Juvenile Males	0.115	0.168	-0.211	0.456
	Receiver Food Type Frequency	-1.248	0.771	-2.759	0.277
	Approximate Duration	0.010	0.048	-0.083	0.106
	NDVI	0.415	0.591	-0.727	1.562
	Rank Difference	-0.343	0.168	-0.668	-0.004
Group-Level Effects	sd(Initiator)	0.108	0.078	0.004	0.289
	sd(Initiator troop)	0.547	0.851	0.010	2.928
	sd(Receiver)	0.129	0.087	0.006	0.326
	sd(Receiver troop)	0.722	1.348	0.009	5.300

Note. Age-sex is relative to adult females. Estimates are on the logit scale; CI = credible interval. N = 1,305. R^2 marginal = .012; R^2 conditional = .024.

3.5 Discussion

Our results confirm that muzzle contact is afforded and constrained by social structure, and directed towards tolerant animals. Additionally, we found that muzzle contact has the potential to afford foraging information. As predicted, muzzle contact was influenced by both demographic and social phenotypes. Juveniles initiated contact more so than adults, and contact was directed disproportionately towards adult females, replicating Lycett and Henzi's (1992) findings. Additionally, dyads that had the largest number of muzzle contacts were more likely to be kin. Most dyads, however, did not interact very often, and these lower levels of interaction were not disproportionately kin-based.

In sum, we found evidence that muzzle contact had functional consequences for our monkeys: Animals were more likely to forage themselves after contacting foragers. This suggests that foragers provide salient information about local food availability. Given this, it seems reasonable to infer that muzzle contact may afford social learning for foraging (Hoppitt & Laland, 2013). Against this, initiators did not appear to target foraging animals specifically for muzzle contact, nor did they clearly adapt their behavior post-contact in relation to the type of food eaten by receivers[2]. Thus, although muzzle contact is a potential means of information transfer, it appears that our animals did not always seek such information from others, nor did they vary their behavior with respect to the information they obtained.

Perhaps a more reasonable interpretation of our results is that foragers serve as

---

[2] As pointed out by reviewers, an alternative null from which we could interpret these findings is that initiators do not always have equal access to foragers and nonforagers, and we could conclude that initiators are targeting foragers if they do so more than 27.0% of the time, as this is the proportion of animals foraging at any given time (Appendix B.13, Appendix B.14). The authors thank the editor and three anonymous reviewers for their comments and suggestions here and elsewhere, which greatly improved the manuscript.

discriminative stimuli for food availability, and kin and low-ranking animals serve as discriminative stimuli for social tolerance. That is, animals may have learned that by approaching foragers (i.e., coming within close proximity) they will often find food, and that by approaching kin and low-ranking animals, they will often either gain access to social reinforcement (e.g., grooming partners; positive reinforcement) or avoid social punishment (e.g., displacement; negative reinforcement). Any muzzle contacts that occur in these contexts could then be reinforced by either accessing food or gaining/avoiding social reinforcement. Thus, given our findings, it is likely that muzzle contact is multiply determined (Video S1).

With respect to relatedness, our findings speak to an ongoing debate in the social learning literature: Do some animals fail to benefit from social learning because they lack certain adaptive strategies (e.g., Kendal et al., 2018), or because they are constrained by various phenotypic traits (e.g., Carter et al., 2016)? Our data suggest that, at least for our animals, this question cannot be answered in a binary fashion. Our findings do not follow from either the adaptation or constraint hypotheses. For example, while dyads with higher interaction counts were more likely to be related (which could be interpreted as a kin-biased adaptive learning strategy and thus consistent with the adaptation hypothesis), most dyads had low numbers of interaction, meaning that the large majority of contacts were between nonkin. Additionally, because muzzle contact occurred mostly between nonkin, relatedness did not necessarily restrict any information potentially gained from muzzle contact, contradicting an interpretation that follows the phenotypic-constraint hypothesis.

Given this pattern of results, our hypothesis is that these animals use muzzle contact as a low-cost means of targeting socially tolerant conspecifics in order to quickly and effectively update their knowledge of current resource availability, rather than to seek specific foraging information. The tolerance levels of recipients, rather than the quality of the “knowledge” they possess, thus serves as the impetus for muzzle contact. Our observation that juveniles engage in muzzle contact more than adults supports this interpretation: With less-established learning histories than adults, they will need to update their information more frequently.

Furthermore, muzzle contact might also have additional functions. As close facial contact is a significant pathway of pathogen transfer, muzzle contact could potentially transmit microbes in addition to transmitting foraging information. Tung et al. (2015) found that after controlling for diet, kinship, and shared environments, variation in the gut microbiomes of yellow baboons can be explained by social relationships. This finding underscores the significance of direct physical contact between social partners in gut microbial species transmission, which could in turn be consequential in the evolution of sociality. Additionally, the patterns of juvenile engagement we found also suggest that muzzle contact might serve a social function, as a way to signal and assess inter-individual tolerance, much as play signals do (c.f., Bergman & Sheehan, 2013; Cordoni et al., 2018; Palagi et al., 2015). Older juveniles were less likely to contact kin than younger juveniles, suggesting that juveniles may use muzzle contact to learn that they can contact without adverse consequences as they grow older. This, in turn, might form part of a larger juvenile strategy to integrate themselves into networks beyond their kin-groups as they age, possibly affording the development of affiliative relationships beyond the broad social tolerance we find here (Jarrett et al., 2018). In this regard, it will be interesting to discover if factors beyond those associated with individual dyads (e.g., the structure of the network itself, which can be investigated via triadic relationships: Faust, 2010; Ilany et al., 2013; Wey et al., 2019) could help identify possible social affiliative functions of muzzle contact. A social affiliation component to muzzle contact would help explain why hypotheses related to information acquisition cannot fully account for the patterns we observe, and add to our findings of broad social tolerance.

CHAPTER 4: MODELING FOOD NEOPHILIA AS A TEST OF PERSONALITY

4.1 Introduction

Interindividual differences in behavior can inform our understanding of how animals learn socially. For example, Aplin et al. (2013) identified a correlation between social learning and individual differences in innovative problem solving among blue tits (*Cyanistes caeruleus*), and Carter et al. (2014) found that bolder chacma baboons improved their task-solving after observing a demonstrator. In this chapter, I present data on responses by vervets to the presentation of novel foods. This provides a measure of inter-individual differences in a behavior relevant to the social learning tasks presented in Chapters 5 and 6.

Many researchers choose to investigate individual-level variation by developing specific tests that are designed to measure responses to controlled, novel stimuli. Understanding how animals respond to novelty is a major element in innovation research, as one definition of innovation includes the ability to exploit a new resource (Greenberg, 2003). Devising and conducting such animal personality tests (Réale et al., 2007) offers all the benefits of controlled experimental designs, including confidence in the novelty of stimuli, measurement accuracy, and the ability to observe the entirety of the behavior in question. As animal performance is contingent not only on cognitive capacity, but also on the motor, perceptual, and motivational aspects of the tasks that are used, tests are often designed to narrow possible sources of variation (Morand-Ferron et al., 2016). For example, testing animals alone was the norm in early, lab-based primate cognition research (Cronin et al., 2017) in an effort to minimize contextual (e.g., feeding motivation), ecological (e.g., food availability), and social (e.g., social interaction) variability (Morand-Ferron et al., 2016). Field-based researchers have also attempted to standardize testing environments by, for example, testing animals when they are isolated from the social group, either by capturing them (e.g., Vágási et al., 2021) or by waiting until they are alone (e.g., when conspecifics were more than 2.5 m away; see Carter et al., 2013).

More recent work has begun to challenge the ecological validity of the results from such tests, especially when it comes to social context, as it is deemed important to consider the effect of ongoing environmental variation on cognitive performance (Cauchoix et al., 2020; Cronin et al., 2017). For example, tightly controlled testing conditions might create an environment that represents only one of many possible environments (e.g., isolating gregarious species), or could even result in a situation that is out of the range of the natural environment (Cauchoix et al., 2020; Niemelä & Dingemanse, 2014). Morand-Ferron et al. (2016, p. 372) therefore argued that, rather than removing the effects of possible confounding factors during testing conditions, "studying multiple confounding factors simultaneously might ultimately be a more effective and realistic way of investigating any target cognitive trait." Furthermore, such "realized cognitive ability" assessed under natural conditions offers a more accurate measure of the variability on which natural selection acts (Morand-Ferron et al., 2016; Niemelä & Dingemanse, 2014).

The possibility that an animal's behavior may be influenced by conspecifics is in itself an interesting line of inquiry that cannot be explored if animals are tested in isolation. For example, Visalberghi and Fragaszy (1995) found that capuchins were more likely to investigate novel foods when others were around. If such forms of social facilitation are dependent on the specific conspecifics engaging in behavior, then it is referred to as "response facilitation." Social facilitation has been argued to play a large role in the ontogeny of foraging (Galef Jr, 1993) and social learning, as when Visalberghi and Fragaszy (1996) argued that social facilitation might be more predictive of social learning than a species' taxonomic status.

Finally, there are two further considerations that are important when using novelty as a test of interindividual differences. The first is that responses to novelty can depend on the type and form of novelty that is presented. For example, Heyser and Chemero (2012) found that mouse responses towards objects depended not only on their novelty, but also on also the object's affordances (in this case, whenever mice could climb on the object). The second is that, while neophobia (spontaneous aversion towards novelty) and neophilia (spontaneous attraction towards novelty), can be grouped as responses to novelty (i.e., "neotic" responses) there is good evidence to suggest that they result from different selection pressures. Neophobia is hypothesized to result from selection for responses that allow animals to avoid danger, whereas neophilia is a consequence of selection for responses that produce rewards. For example, corvids and psittacines are both neophilic and neophobic, as they must often explore novel situations in order to gain access to resources, but do so with high levels of fear and arousal that can protect them from unknown dangers (Greenberg, 2003).

The second consideration is deciding how to estimate variation in individual performance. For example, Blaszczyk (2017) developed a composite score of individual responses to novel objects in vervet monkeys, including both the latency to respond and inspection duration, which was successfully used to predict individual differences in the response to snakes. In contrast, Carter et al. (2012b) used a principal components analysis on three measures—latency, inspection time, and handling time— of baboon responses to novel food and found no correlation with subsequent responses to the presentation of model snakes. Finally, random regression models allow the detection of individual differences using a reaction norm approach (Dingemanse et al., 2010; Dingemanse & Dochtermann, 2013; Nussey et al., 2007). Random regression models are a type of mixed effects model that allows individual functions of continuous covariates to be fitted as random effects; in other words, they allow each observation of the phenomenon under assessment to vary in its parameter estimates as opposed to forcing each observation to have the same variation. For example, in studies that include multiple observations of the same individuals, individuals might well vary in different ways from observation to observation. Random regression models can account for such individual-level variation by allowing predictions to vary in accordance with each observation of the individual.

As my social learning experiments included both novel components and tested foraging behaviors, I developed a test of how vervets responded towards novel foods, bearing in mind the considerations listed above. My primary concern was with the validity of my test, i.e., its ability to predict similar responses during my experiments (Carter et al., 2012a). I was also concerned with test reliability, that is, if repeated tests of the same nature yielded similar results (Carter et al., 2012a; Carter, 2013) within and across environmental contexts (e.g., time, breeding season, etc.; also known as "environmental gradients")— in other words, whether responses were repeatable (Dingemanse et al., 2010). I therefore conducted multiple trials for each individual, using a different food for each trial, and ensured it was novel for each tested animal. I used a random regression model to derive individual differences, as a modeling approach also allowed me to account for variation in individual attributes that may have contributed to responses towards the novel food (e.g., age, dominance rank). In addition, this modeling approach allowed me to account for variation in within-trial events, such as the presence of another animal, that I could not control during the tests themselves. Finally, because I found a partner effect (animals were more likely to eat the novel food item when a conspecific was present; see 4.3 Results), I modeled whether this was dependent on the behavior of the partner, thereby testing for response versus social facilitation.

4.2 Methods

To begin a novel food test, either myself or a research assistant presented a novel food item to the focal animal (i.e., the animal being tested) by placing the item in the animal's path while it was either traveling or foraging. To do so, we turned our backs to the intended focal animal and placed the food item between our boots so as to block the item from view and to prevent the possibility that animals could associate us with food. On occasion, we placed our backpacks on the ground to further block any view from the animals. Every effort was made to test animals when they were alone (i.e., had no conspecifics within 5 m), but this wasn't always possible (see “Partner Presence” below). In an effort to increase the food item’s salience, we placed it on a bare piece of ground whenever possible, and we used artificial food coloring to dye many of the food items. Novel food items included 2 cm^3 pieces of potato (blue or pink), marrow (yellow), eggplant (blue), green bean (red or not dyed), pumpkin, baby corn, apple (pink), or a sliced grape. Any non-focal animals that witnessed a focal animal engaging with one food item were subsequently tested using a different item in order to ensure novelty (e.g., Figure 4.1; however, see "Exposure" below). Food tests were repeated, using different food items, for as many animals as possible, both within and across field seasons (see Appendix C.1 for a description of all trials across all focal animals). All trials were video recorded using a Canon PowerShot ELPH 100 HS camera while observers stood at least

Figure 4.1

Animals During the Novel Food Tests, Demonstrating Exposure (Top), the Alone Condition (Bottom Left) and Partner Presence (Bottom Right)

10 m away.

All video trials were coded in the lab by one of two observers using Behavioural Observation Research Interactive Software (BORIS version 7.7.3, Friard & Gamba, 2016). We scored whether the focal animal came within 0.5 m the food item, and whether it engaged in any of our target behaviors (“ignore,” “gaze,” “sniff,” “handle,” “mouth," and “eat,”). All behaviors were scored as mutually exclusive, and varied in whether they were recorded as point events (occurred or not) or state events (with a beginning and end), as explained below. Focal subjects were considered to be participants in the trial if they clearly directed their gaze at the novel food for ≥ 1 second or walked within touching distance of the food item. If an animal only walked to within touching distance of the food item but did not engage in any other target behaviors, the trial was coded as “ignore.” Trials were excluded if the focal animal was within touching distance of the food item for less than 1 s (e.g., was running past).

Focal animals were recorded as having looked (yes/no) at the food item if they oriented their gaze towards it while within 1 m of the food item for greater than or equal to 1s. Focal animals were recorded as having sniffed the food item if it brought its muzzle within 2 cm of the food item and ended when the focal animal moved its muzzle more than 2 cm away from the food item. Focal animals were recorded as having handled the food item if there was any contact between its hands and the food item, and ended either if the focal animal removed its hands from the food item or began either to sniff or mouth it. Mouthing the food item was recorded if the focal animal brought its mouth, including tongue, into contact with it (including holding the food item while doing so) and ended when the focal animal removed its mouth from the food item. Durations of sniffing, handling, and mouthing the food item were also recorded, as well as whether the focal animal was seen to eat the food item, which was defined as bringing the food item into contact with its teeth (yes/no).

4.2.1 Partner Presence and Partner Behavior

I coded trials as “partner present” if there was a non-focal animal or animals present within 2 m of the focal animal during the trial. The number of partners present, and whether or not they foraged (y/n) before the focal animal ate the novel food (“partner behavior”), was also recorded. If the focal did not eat the novel food, I recorded whether or not the partner foraged at all during the trial.

Although a previous study used a 1 m threshold for partner presence (Blaszczyk, 2017), we have found 2 m to be a relevant social distance for these animals (Young et al., 2017). However, as the 2 m threshold may present an important difference between my study and previous work, I also conducted all analyses using a 1 m threshold and found essentially identical results (see Results; Appendix C.2). I compared the models using leave-one-out-cross-validation (Vehtari et al., 2017) with the “loo_compare” function of “brms” and found that the model using 2 m received more support (see Results). I therefore present results using the 2 m threshold in the main text.

4.2.2 Stimulus Exposure

If focal animals interacted with a food item they had witnessed previously, I recorded the trial as “food item exposed.”

4.2.3 Trial Interruption

Trials were recorded as “interrupted” if a non-focal animal contacted the focal animal and/or food item once the trial began, or if the focal animal and non-focal animal engaged in aggression during the trial.

4.2.4 Statistical Analyses

To ensure consistency with other research on interindividual differences, I first calculated inter-rater reliability and repeatability using the standard frequentist approaches, explained below. After determining that observations were reliable and therefore repeatable, I then used a Bayesian approach to calculate my own measure of interindividual differences, and to determine whether the partner effect I found could be attributed to either response or social facilitation (see Results). It should be noted, however, that the assumptions of Bayesian credible intervals are not completely compatible with frequentist confidence intervals. A Bayesian approach is valuable because, unlike a frequentist approach, it cannot only determine whether there was no evidence for the tested hypothesis, but also whether the lack of evidence constitutes evidence of no effect for the tested hypothesis (i.e., we can assess both absence of evidence and evidence of absence (Dienes & Mclatchie, 2018).

Inter-rater Reliability

All trials were filmed and coded post-hoc by CN. A research assistant (MC) blind to experimental predictions coded a subset of the trials (68 out of 281; 23.84%) in order to determine inter-rater reliability. I calculated frequency within interval agreement (Miltenberger, T. M, 2013) and used the “IRR” package (Gamer et al., 2019) in R to estimate Cohen’s kappa.

Repeatability

Repeatability is a measure of the behavioral variation in a population that is due to differences between individuals (Nakagawa & Schielzeth, 2010) and serves as a validity measure for tests of interindividual differences (Carter et al., 2012a). I estimated repeatability of the "eat" behavior (y/n) during the novel food test using the "rptR" package in R (Stoffel et al., 2017). I calculated repeatability for individuals across all novel food trials and both study periods, as well as by troop. Because I was only interested in repeatability as a measure of the validity of the "eat" behavior due to differences between individuals (as opposed to determining the mechanisms of individual differences or "intrinsic" repeatability; Wilson, 2018), I specified a binary GLMM in the 'rptR' calculation. The response variable was whether or not the focal animal ate the novel food, with focal animal ID and troop ID as grouping variables. I initially calculated repeatability without regard to any factors during testing. However, because I found an effect of dominance ranking and partner presence (see 4.3 Results), I also calculated repeatability accounting for rank and partner presence by including these variables as fixed effects in the model. I ran both models for 1,000 bootstraps and 1,000 iterations (Stoffel et al., 2018).

Responses Towards Novel Foods

In order to determine measures of individual differences using the novel food test, I focused on whether or not the focal subject ate the food item. First, this allowed me to determine whether certain demographic and social phenotypes, as well as factors present during testing (e.g., partner presence, trial interruption), influenced whether or not focal animals ate the food item during the novel food test trial. Second, I was able to extract individual means from this model to use as a measure of interindividual differences for future predictions and tests (Dingemanse & Dochtermann, 2013). To do so, I constructed a multilevel Bernoulli model within a Bayesian framework (Gelman & Shalizi, 2012) using the “brms" package (Bürkner, 2017) in R 3.5.2 (R Core Team, 2018) in order to predict whether or not animals ate the novel food. For this model, I specified four chains and 2,000 iterations and included weakly informative priors (mean = 0, *SD*=1). All $\hat{R}$s = 1.0, confirming model convergence (Gelman & Shirley, 2011).

I specified whether or not the focal animal ate the novel food (yes/no) as the response variable, with age/sex, rank, previous food item exposure (y/n), partner present (y/n), and trial interruption (y/n) as predictor variables. I controlled for the possible effects of repeated experience with the testing condition by including within-individual trial number as a fixed effect, and controlled for any effects of food item type, and troop-level NDVI, by including these variables as additional fixed effects. I entered troop ID, study period, observation, and focal animal ID as group-level effects

Rather than use the random intercepts to calculate interindividual differences, I used the model to estimate the probability that an individual would eat the novel food, thus acquiring a measure of interindividual variation (Allegue et al., 2017; Nakagawa & Schielzeth, 2010). My method differed from using random intercepts (Dingemanse & Dochtermann, 2013) in that I fixed the conditions (e.g., fixing the number of nearby social partners, food type, etc.) of each model predictor, and calculated the probability that an animal would eat the novel food given these fixed conditions. This allowed me to estimate the probability with which an animal would eat the novel food, while standardizing the circumstance of the trial. In other words, I calculated the probability that each animal would eat the novel food, accounting for their rank, age, troop-level NDVI, exposure, stimulus type, and so on, for each predictor included in the model. I then centered the probabilities on zero and divided them by the standard deviation, which created an individual measure for each animal.

This differs from using the estimated interindividual differences provided by random intercepts, which captures if individuals are consistently higher or lower than expected given the fixed effect variables in the model (e.g., rank, age, etc). For example, using random intercepts, I might know that a particular animal, on average, was less or more likely than others to eat the novel food given its rank and age, but not the probability that it would do so.

Social/Response Facilitation

To determine whether partner presence constituted either a response facilitation or social facilitation effect, I constructed an additional Bayesian multilevel Bernoulli model using the same framework, response variable, predictor variables, and grouping variables as for the novel food neophilia model above, with one exception: I included how many partners were foraging during the trial. By doing so, I accounted for the fact that partner behavior could only be meaningful if a partner was present (Gelman & Hill, 2007).

4.3 Results

4.3.1 Inter-Rater Reliability

In total, I conducted 276 trials with 116 different animals (Table 4.1). We achieved

Table 4.1

Description of the Novel Food Test Trials

Age/Sex	Participated	Ignored Trial	Ate Novel Food
Adult Females	60 (25)	17 (13)	8 (5)
Adult Males	31 (16)	20 (13)	0
Juvenile Females	102 (39)	12 (10)	43 (22)
Juvenile Males	83 (38)	5 (5)	28 (18)
	276 (118*)	**54 (41)**	**79 (45)**

Note. Parenthetical values indicate the total number of unique animals, as animals were tested multiple times. *Some animals aged up during the study period and are represented in the relevant age/sex category to which they belonged at the time of their trials. $N_{Individuals}$=116; N_{Trials}=276.

an agreement of 86.58%, and an unweighted Cohen's kappa of 0.654 (z = 21.5, p < 0.001), indicating "substantial" agreement (McHugh, 2012).

4.3.2 Repeatability

The first model used to calculate repeatability, which did not account for variance that might be due to partner presence or dominance ranking (see below), indicated a repeatability (R) of 0.205 (link scale; 95% confidence interval = 0.026-0.366, p = 0.002) of the "eat" response during the novel food tests for animal ID (i.e., there were systematic differences in responses to novel foods by individual animals). This model found no repeatability of the "eat" response due to differences in troop (i.e., troops did not differ systematically in their responses to novel foods; link scale R = 0.031, 95% confidence interval = 0.000-0.099, p = 0.075). The second model, which accounted for variance due to partner presence and dominance ranking, indicated an R of 0.267 (link scale; 95% confidence interval: 0.020-0.491, p = 0.002) for animal ID and no repeatability due to troop ID (link scale R = 0.040, 95% confidence interval = 0.000-0.117, p = 0.075),

Table 4.2

Posterior Estimates of Animals Eating the Novel Food

Effect	Parameter	Estimate	Est. Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept (Adult Female, Food: Baby Corn)	-2.990	1.779	-6.627	0.469
	Exposed (y/n)	0.104	0.488	-0.867	1.005
	Interrupted (y/n)	0.281	0.505	-0.668	1.301
	Food: Eggplant, blue	-0.984	0.754	-2.443	0.450
	Food: Green Bean	0.283	0.736	-1.098	1.723
	Food: Green Apple	-0.166	0.937	-1.940	1.634
	Food: Potato, pink	-0.618	0.605	-1.792	0.578
	Food: Pumpkin	-0.934	0.636	-2.180	0.309
	Food: Red Grape	1.173	0.651	-0.082	2.426
	Food: Green Bean, red	-0.075	0.897	-1.884	1.660
	Food: Marrow, yellow	-0.063	0.638	-1.301	1.229
	Food: Potato, blue	0.292	0.591	-0.835	1.459
	Partner Presence (y/n)	1.850	0.473	0.965	2.819
	Adult Males	-1.007	0.832	-2.705	0.627
	Juvenile Females	1.124	0.597	-0.041	2.273
	Juvenile Males	0.959	0.639	-0.287	2.182
	Total Trials	0.101	0.272	-0.411	0.679
	Dominance Rank	-1.237	0.700	-2.649	0.084
	Troop-Level Resource Availability	0.169	1.003	-1.800	2.146
Group-Level Effects	sd(Collector)	1.054	1.015	0.030	3.615
	sd(Study Period)	1.186	1.276	0.029	4.758
	sd(ID)	1.936	0.553	0.990	3.170
	sd(Troop)	1.392	1.060	0.130	4.148
	sd(Trial ID)	0.511	0.401	0.024	1.512

Note. Age-sex is relative to adult females, food type is relative to baby corn. Estimates are on the login scale; CI = credible interval, sd = standard deviation. N = 276. LOO-adjusted R^2=0.279.

indicating that animals differed in the probability of whether or not they ate the novel foods (Figure 4.2).

4.3.3 Responses Towards Novel Foods

I found that lower-ranking animals were slightly more likely to eat the novel food compared to higher-ranking animals (Table 4.2; Figure 4.3), and that animals were more

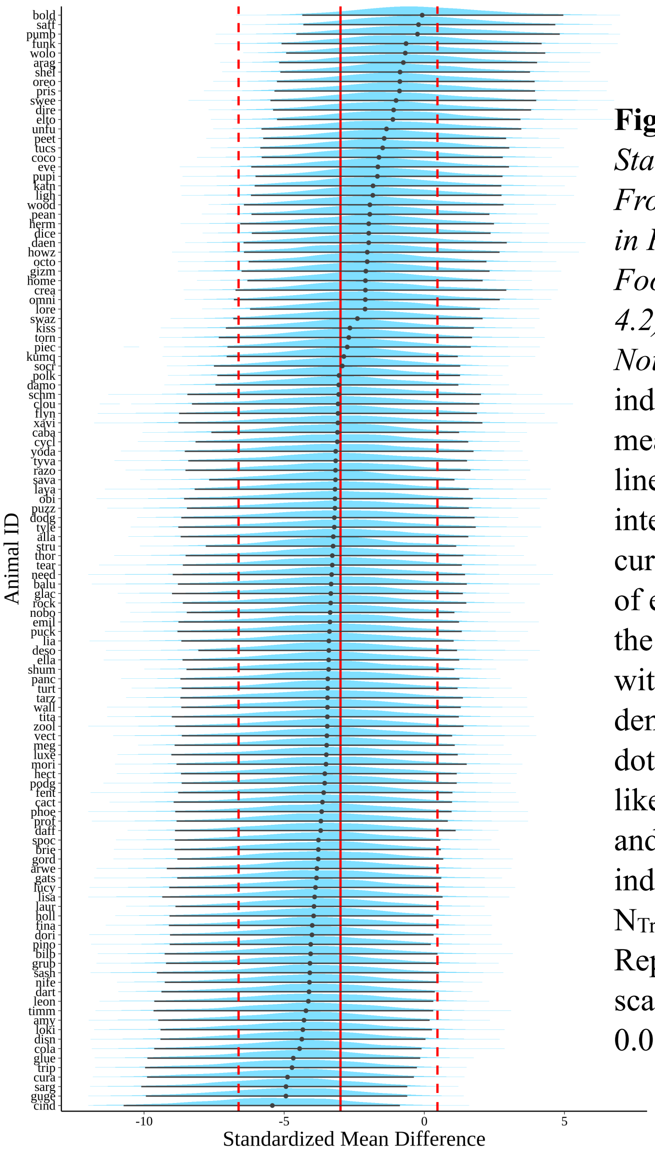


Figure 4.2

Standardized Difference From the Population Mean in Responses to Novel Foods by Animal ID (Table 4.2)

Note. The solid red line indicates the population mean, and the dotted red line its 95% credible intervals. Blue density curves represent the range of estimates predicted by the model for each animal, with the height of the density curve (and the black dot) indicating the likelihood of the estimate, and the spread of the curve indicating its uncertainty. N_{Trials}=276, $N_{Individuals}$=116. Repeatability = 0.321 (link scale; 95% CI: 0.076-0.623).

likely to eat the novel food if there was a partner present within 2 m (see also Appendix C.2) during the trial (Table 4.2; Figure 4.4). I also found that the model using 2 m as the threshold for partner presence received slightly more support than the model using 1 m (expected log pointwise predictive density “ELPD” of the 1 m model = -2.260, standard error = 1.308). The likelihood of focal subjects eating the novel food increased as the number of partners increased (Table 4.3; Figure 4.5). There was, however, no evidence of a response facilitation effect (Figure 4.6; Table 4.3).

Table 4.3

Posterior Estimates of Animals Eating the Novel Food with Partner Foraging Behavior

Effect	Parameter	Estimate	Est. Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept (Adult Female, Food: Baby Corn)	-3.205	1.896	-7.129	0.548
	Exposed (y/n)	-0.022	0.564	-1.109	1.065
	Interrupted (y/n)	-0.011	0.549	-1.058	1.040
	Food: Eggplant, blue	-1.047	0.785	-2.567	0.498
	Food: Green Bean	0.215	0.746	-1.266	1.669
	Food: Green Apple	-0.095	0.969	-2.003	1.800
	Food: Potato, pink	-0.505	0.676	-1.862	0.815
	Food: Pumpkin	-0.662	0.686	-1.989	0.731
	Food: Red Grape	1.180	0.739	-0.259	2.613
	Food: Green Bean, red	0.075	0.909	-1.662	1.846
	Food: Marrow, yellow	0.062	0.691	-1.284	1.444
	Food: Potato, blue	0.419	0.634	-0.835	1.643
	Count Partners	1.458	0.382	0.779	2.270
	Count Partners Foraging	-0.336	0.418	-1.173	0.480
	Adult Males	-0.816	0.878	-2.600	0.876
	Juvenile Females	1.028	0.653	-0.249	2.295
	Juvenile Males	0.731	0.671	-0.615	2.049
	Total Trials	0.089	0.295	-0.477	0.683
	Dominance Rank	-0.897	0.424	-1.793	-0.132
	Troop-Level Resource Availability	0.163	0.524	-0.843	1.254
Group-Level Effects	sd(Collector)	0.924	0.950	0.028	3.502
	sd(Study Period)	1.406	1.336	0.039	4.727
	sd(ID)	2.159	0.689	1.075	3.769
	sd(Troop)	1.686	1.241	0.251	4.974
	sd(Trial ID)	0.840	0.650	0.031	2.493

Note. Age-sex is relative to adult females, food type is relative to baby corn. Estimates are on the login scale; CI = credible interval, sd = standard deviation. N = 276. LOO-adjusted R^2=0.299.

I also found no effect of age/sex, previous food item exposure, trial interruption, repeated experience, food item type or NDVI in the model investigating responses towards novel foods. For both models, responses varied by animal ID, but there was little evidence that

Figure 4.3

Probabilities of Animals Eating the Novel Food Dependent on Dominance Rank

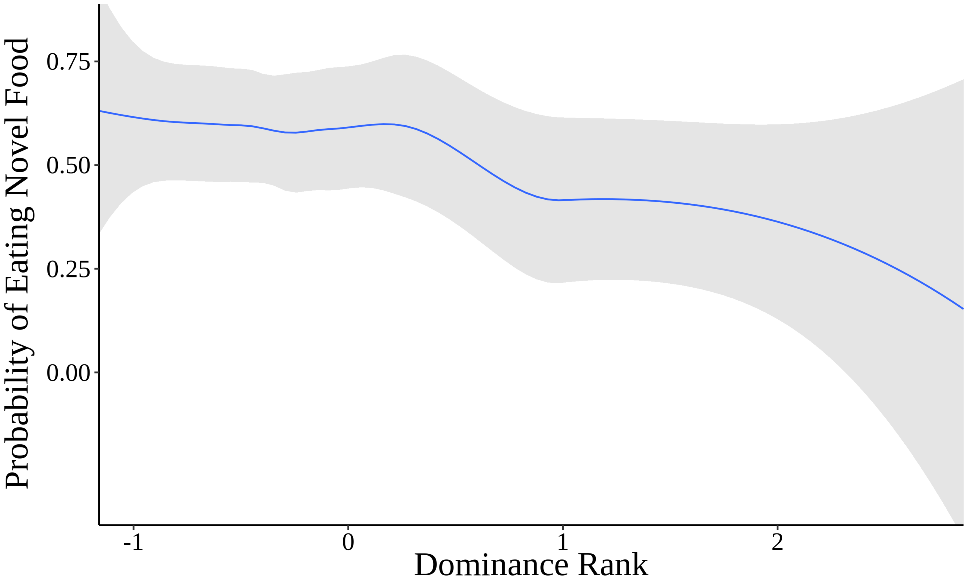
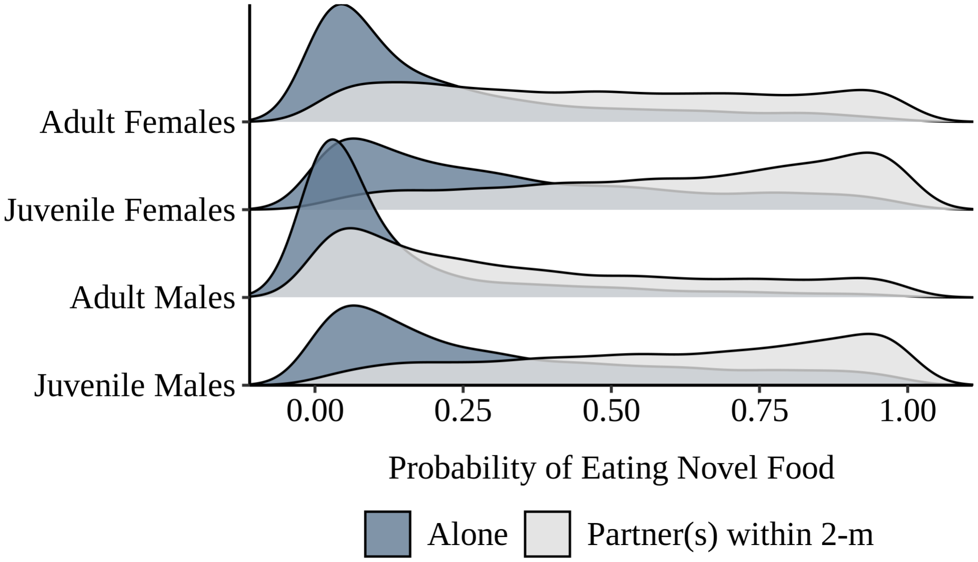


Figure 4.4

Probabilities of Animals Eating the Novel Food Given They Had at Least One Partner Present or Not During the Food Trial



Note. Density plots present the range of probabilities predicted by the model, with the height of the density curve indicating the likelihood of the probability, and the spread of the curve indicating its uncertainty (Table 4.2). Probabilities are backtransformed from the logit scale into a probability scale.

Figure 4.5

Probabilities of Animals Eating the Novel Food Dependent on the Number of Partners Present During the Trial

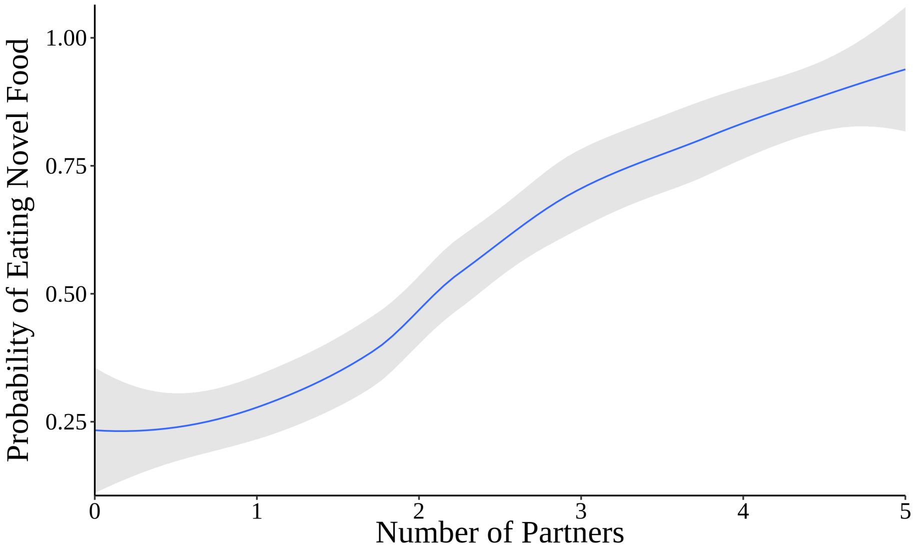
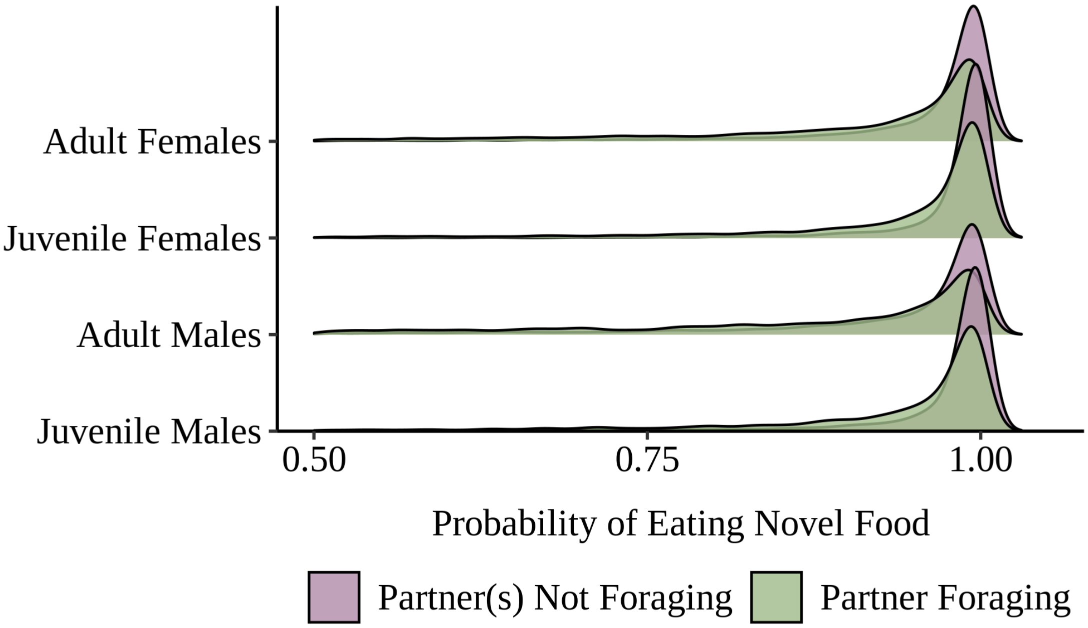


Figure 4.6

Probabilities of Animals Eating the Novel Food Dependent on the Partner Foraging or Not During the Food Trial



Note. Density plots present the range of probabilities predicted by the model, with the height of the density curve indicating the likelihood of the probability, and the spread of the curve indicating its uncertainty (Table 4.3). Probabilities are backtransformed from the logit scale into a probability scale.

they did so with regard to troop ID and trial ID, and no evidence that they did so with regard to study period, or observation, as indicated by the group-level effects (Table 4.2). Juvenile females were slightly more likely than adult females to eat the novel food, but only for the model investigating facilitation effects (Table 4.3).

4.4 Discussion

In this chapter, I have demonstrated that the vervets were consistently different in their probabilities of eating novel foods, and that the probability of doing changed slightly with dominance rank—lower ranking animals were slightly more likely than higher-ranking animals to eat the novel food. I also found that the probability of eating novel foods was socially facilitated, and that variation in an animal's probability of eating a novel food was repeatable. As I used novel foods in each test, and because responses were repeatable, I can therefore say that my measure indicated novel food neophilia (Carter, 2013).

My findings regarding rank disagree with previous work in vervets that found no effect of rank on personality (Blaszczyk, 2017) but fall in line with previous work that has hypothesized that higher-ranking animals should be more neophobic, given their better access to resources and thus gain lower potential payoffs associated with approaching novelty compared to lower-ranking animals (Greenberg, 2003; Laland & Reader, 1999; Wolf et al., 2007; though see Amici et al., 2020 and Drea, 1998). Despite my best efforts, I was not always able to test individuals when they were alone. This was not necessarily surprising given that I was dealing with a highly social species, and study animals were likely to be in the close vicinity of other members of their group (2-3 m on average, unpublished data). Unlike Blaszczyk (2017) who found no social context effect when a partner was present, I found that neophilia increased with partner presence and that this increased with the number of partners. However, while neophilia was socially facilitated, the fact that it did not depend on whether their partners were also foraging meant that there was no response facilitation effect. Despite this, and despite the fact that I used novel foods rather than novel objects, the repeatability measures for the two vervet populations were somewhat similar—0.37 for Blaszczyk (2017) and 0.27 here. This value is rather close to values found for other species (Bell et al., 2009; Wolak et al., 2011), and close to the values found by the only two other reports of primate "boldness" (Blaszczyk, 2019; 0.33 for baboons tested with novel foods by Carter et al. 2012b; 0.31 for mouse lemurs *Microcebus murinus* tested with novel objects in Dammhahn, 2012).

These findings raise a number of issues. First, the fact that neophilia changed with social context would never have come to light had I been successful in testing animals alone, as is standard for neotic tests. I also found that trial interruption had no effect on the probability of eating the novel food, meaning that the likelihood with which animals ate was not affected by another animal either interacting with the food before they did or after they had begun to do so. Given these findings, it is unclear why there is a preference to test animals singly. It may be because researchers are often interested in personality as unexplained variance in a particular behavior that is consistent across situations and time, thus accounting for any bias due to plasticity in accordance with such social aspects. For example, Westneat et al. (2011) argued that true personality can only be measured once the potential sources of plasticity are controlled for, such that personality represents consistent interindividual differences that are intrinsic to each animal. However, as I have shown, current analytical approaches are increasingly capable of incorporating multiple confounding factors simultaneously, reducing the need to standardize the testing conditions themselves.

Galhardo et al. (2012) have also questioned why animals, especially gregarious species, are tested alone, given that their responses in such situations may not reflect those given in more naturalistic social settings. This is especially relevant for social learning, as familiarity with conspecifics can promote its occurrence (Swaney et al., 2001). Indeed, Greenberg (2003) specifically emphasized the importance of understanding neophilia in relation to the spread of innovations, i.e., social transmission. In order for innovation to occur, animals must be willing to approach novel objects and situations, and this attraction must spread for social transmission of the innovation to take place. Thus, attending to others who are more neophilic can relax the need for individuals themselves to be exploratory, *and,* "by influencing the propensity to approach novel situations, social responses to novelty become a critical feature in the development of innovative [behavior]" (Greenberg, 2003, p. 179).

Given these considerations, along with my finding that previous food item exposure or trial interruption had no effect on subsequent behavior, the concern that confounding factors may influence or obscure measures of personality and/or responses to novelty may be misplaced. The Bayesian multilevel modeling approach used here not only allowed me to account for partner interruption, and previous exposure to the novel food, but also revealed a social facilitation effect that could have important implications for my social learning experiments. This might otherwise have gone undocumented had I been able to run my trials as planned. In addition, a Bayesian approach allowed me to demonstrate that there was *no* effect (rather than only absence of an effect) of interruption and previous exposure, while providing positive evidence of social facilitation—i.e., this approach provides good statistical control over potentially confounding variables, and to some degree obviates the need for the strict experimental conditions deemed necessary to obtain reliable and valid personality scores.

Finally, many animals ignored the trials, coming to within 0.5 m of the intended novel food, but did not engage in any behaviors towards it. We know that these animals are excellent at discriminating colorful objects, particularly at close range. Although I found that age/sex did not affect whether animals ate the food, it appears that some animals, particularly adults, actively avoided the novel food tests, which may foreshadow their participation (or lack thereof) in the social learning experiments. Thus, although animals may not differ in whether or not they ate the novel food depending on their age and sex, this may not be the case for whether or not they ignored the trial altogether.

In summary, these analyses achieved my goal: I found variation along a dimension — novel food neophilia—that I can use to inform my subsequent analyses on animals' performance in social learning tasks and thereby account for the effect of personality on such learning (Cauchoix et al., 2020). Furthermore, these results show that it is important to understand the extent to which cognitive performance may vary with the environment (i.e., be plastic), and such measures and conditions must be reported. As Cauchoix et al. (2020) have pointed out, doing so will enable more accurate measures of cognitive abilities, and determine which aspects of behavior are repeatable or plastic (Dingemanse et al., 2010).

CHAPTER 5: NOVEL WATER PATCH TEST

5.1 Introduction

My aim in this chapter is to determine the means by which animals learn from each other—if indeed they do—via a straightforward social learning experiment. Specifically, three groups of wild, non-provisioned vervet monkey were given the opportunity to learn to drink from a novel water patch. The behaviors required to “solve” this task—approaching a novel water source and drinking from it—were likely already in the animals’ repertoire. Consequently, this did not require the monkeys to use the kinds of complicated behavioral topographies necessary to solve puzzle boxes or engage in two-action tasks (e.g., pushing doors, pulling drawers, see Canteloup et al., 2020; Galef & Laland, 2005; van de Waal et al., 2013). Furthermore, as the habitat is drought-prone, and water is rarely abundant, I could be certain that animals would be sufficiently motivated to identify novel water sources. Additionally, because the dish was rather small and could easily be monopolized by one animal, I could observe how social dynamics interacted with learning to drink from a novel water source.

The first step to any behavior analysis is description, which involves a baseline analysis of the behavior(s) of interest. The next step is a functional analysis: identifying the conditions under which the behaviors are emitted, i.e., the contingencies of behavior. In my effort to apply a more behavior analytic approach to social learning, many of the questions here are investigated using the descriptive and exploratory approach of behavior analysis alongside the typical hypothetico-deductive approach used in social learning studies.

In order to determine whether animals used social learning to learn to drink from the novel water patch, I investigated potential behavioral transmission pathways, and how social dynamics and individual differences influenced learning. I used network-based diffusion analysis (NBDA) to determine whether the novel drinking behavior was socially transmitted. Specifically, I used NBDA to (i) assess the likelihood that a behavior was acquired via social as opposed to asocial learning, (ii) determine whether transmission followed specified social networks (either through observations of the novel behavior in vivo or during periods of association, such as grooming), (iii) identify the percentage of initial learning events (i.e., initial acquisition of drinking from the novel water patch) that were acquired via asocial or social learning, and finally, (iv) assess the relationship between individual level variables (ILVs; e.g., sex, rank, age, etc.) and learning (either social or asocial), thereby also accounting for possible spurious social transmission effects should an ILV be correlated with social association (i.e., homophily).

I first tested whether muzzle contact was a direct pathway through which social information could pass. Given that muzzle contact is a means of social information acquisition (Nord et al., 2021), I expected NBDA to identify social transmission in networks describing muzzle contacts between animals that drank from the novel dish (i.e., informed animals) and animals that had yet to do so (i.e., uninformed animals). I tested my muzzle contact prediction alongside two other possible observation networks, a looking network, which was constructed from data on animals that directly observed the target drinking behavior, and a co-presence network, which was based on the animals that came within 1-m of others drinking from the dish. Initially, I chose a looking network because rates of muzzle contact during the experiment were quite low, and it seemed likely that vervets, being diurnal catarrhines, could use also use vision to gain social information (Barton et al., 1995). However, looking proved quite difficult to observe from video, so I also included a co-presence network, which was more salient to code (see Methods). Additionally, using an exploratory approach, I also determined whether the diffusion followed general social affiliations, as measured by stable grooming and proximity relationships. Doing so allowed me to test the core assumption of NBDA—that animals that frequently interact are more likely to learn from one another (Coussi-Korbel & Fragaszy, 1995; Hasenjager et al., 2020). Additionally, if social transmission followed both observation and affiliation networks, I could compare them to better understand how frequent social interactions could have afford observational opportunities.

One of my main criticisms of social learning research is that it relies too much on individual attributes, and not enough on the context of the learning episode, to explain social learning. The validity of this criticism, however, rests on the extent to which age, sex, rank, and neophilia can explain learning. Therefore, I also tested the extent to which individual attributes co-varied with the diffusion of drinking from the patch. Given my prediction that social learning will follow muzzle contact, and given the findings of the previous chapter, I predicted that juveniles and females would use social learning more because they engaged in muzzle contact at higher rates than adults and males. I also found that rank did not predict rates of muzzle contact initiation, so I did not expect social learning to differ by rank. As my muzzle contact analyses did not test neophilia, my predictions regarding neophilia and diffusion come from findings regarding boldness and social learning. Bolder animals are hypothesized to rely more on personal information (Smit & van Oers, 2019; van Oers et al., 2005), so I predicted that more neophilic animals will use asocial learning more than social learning.

I was also interested in how animals learned to drink from the novel water patch. NBDA only measures the target behavior—drinking from the patch—but does not analyze *how* animals learn. To better understand the behaviors that occurred while animals learned to drink from the patch, and whether these behaviors correlated with social transmission, I tested (v) whether age, sex, rank, neophilia, and water availability were associated with whether animals visually observed others interacting with the patch, "entering" the patch, and drinking from it. These categories correspond to Carter et al.'s (2016) categories of acquiring, applying, and exploiting information. Although useful as a framework, the use of the word "constraint" can be rather confusing and underspecified (Antonovics & van Tienderen, 1991). As a result, while I employ the same sequential analytical approach, I do not use the same terminology.

5.2 Methods

5.2.1 Study Site and Subjects

During this study, our study site experienced a period of prolonged drought, limiting access to water. As the river rarely flowed during this time, water often only existed as pools in the river during and shortly after rainfall. Following periods of rainfall, additional small pools of water often appeared throughout the study site in patches of low vegetation, such as on field roads or in the dried riverbed. This meant that these animals were often water deprived, and were used to encountering small pools of water in various places. Such water sources lasted for varying lengths of time, from hours through to weeks, depending on the amount of rainfall. Taking advantage of this, I introduced a novel water source in order to determine whether and how information diffused through social networks.

5.2.2 Information Diffusion Experiment

The first experimental water patch was a 15 x 22 x 6 cm plastic dish. The size of this dish allowed multiple animals to access it simultaneously, but was small enough that one animal could monopolize it if it chose to do so. During trials, the dish was filled with approximately 230-mL of water, an amount that would not unduly benefit one animal should only one have access to it, but enough that would allow multiple animals to drink at the same time. Pilot trials revealed that many animals ignored the dish, which I attributed to its stark contrast to the appearance of water holes in the environment: Water was rarely clear, and always contained various particulates, including dirt, grass, and twigs. I then started adding a bit of surrounding vegetation to the water before each trial, after which animals began participating (Figure 5.1).

Approximately three weeks into the experiment, and during a particularly extreme period of drought (Figure 5.2), some animals became preoccupied with the plastic dish itself, scratching it once the water was depleted and tipping it over. Because of this, I switched to a 15.5x15.5x6-cm ceramic dish that also met the above criteria for the remainder of the trials (Figure 5.3).

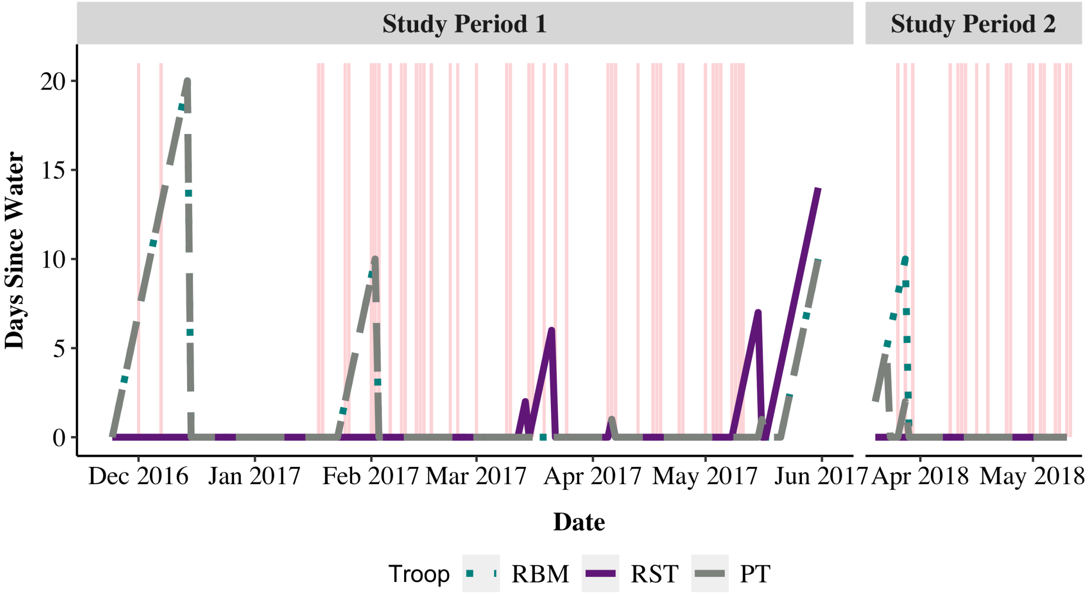
Before each trial, one of two observers traveled 15m-20m ahead of the group and

Figure 5.1

The First Water Patch With the Plastic Container

Figure 5.2

Water Availability and Trial Dates Across the Study Period



Note. Troops are indicated by line-type and color. Red bars indicate dates on which trials were run.

placed the water dish on the ground in its direction of travel, and filled it with water. In order to prevent the animals from associating observers with the patch, observers used

Figure 5.3

The Final Water Patch With the Ceramic Dish

Table 5.1

Description of the Participants and Trials Across the Two Study Periods

Troop	Study Period	Part.	Solvers	Success Trials	Unsuccessful Trials	Ignored Trials	Total Trials
RST	1	28	18	18	1	1	20
RST	2	8 (23)	5 (13)	8	0	1	9
RBM	1	29	13	15	2	0	17
RBM	2	8 (29)	9 (17)	10	0	1	11
PT	1	28	15	16	5	0	21
PT	2	11 (33)	5 (11)	14	1	0	15
	Total	**113 (170)**	**65 (87)**	**81**	**9**	**3**	**93**

Note. Parenthetical values indicate the total number of animals for that category in study period 2; counts of unique animals compared to study period 1 are presented before the parenthetical values. For example, RST had 23 total participants in study period 2, but only 8 had not previously participated in study period 1.

their bodies and backpacks to keep the placement of the patch from being seen by the animals. Observers then moved approximately 10 m away from the patch and filmed the trial, identifying all individuals who came within 5 m of the patch.

Not every trial resulted in animal participation, either because animals did not see the patch, or because they changed their direction of travel away from the patch. When this happened, the trial was ended and marked as unsuccessful. If conditions were suitable, another trial was attempted. Another possibility for non-participation was that animals ignored the patch; that is, they came within 5 m but did not interact with the patch. These trials were marked as “ignored,” and, where appropriate, another trial was attempted (Table 5.1).

All video trials were coded in the lab by one of two observers using Behavioural Observation Research Interactive Software (BORIS version 7.7.3, Friard & Gamba, 2016). We recorded all animals who came with 1-m of the patch (“trial participation”), looked at another animal who was within arm’s reach of the dish (“gaze”; recorded with a modifier of the recipient’s behavior to measure whether the recipient was interacting with the patch, coded as “looking”, or drinking from the patch, coded as “visual observation”), came within touching distance of the patch (“entering”), and drank from the patch (“drinking”). We also recorded all muzzle contacts and aggressions that occurred during trials.

Approximately 20% of trials were coded by a third observer for inter-rater reliability by calculating frequency within interval agreement (Miltenberger, T. M, 2013) and Cohen’s kappa (McHugh, 2012), which was 79.06% (Cohen’s kappa=0.59, z=23.9, p=0.00). Gaze was particularly difficult to code in the lab because vervet faces and eyes appeared very dark on video, making it difficult to determine gaze direction. Because of this, I also analyzed the agreement of each scored behavior, and found that only 49.75%

(Cohen's kappa=0.07, z = 1.53, p = 0.13) of gaze observations agreed. Agreements measures for all behaviors recorded during the experiment are included in Table 5.2.

Table 5.2

Reliability of Measured Behaviors

Behavior	Agreement (%)	Cohen's Kappa
Trial Presence	81.18	-0.05 (z = -0.85, p = 0.40)
Muzzle Contact	91.89	0.26 (z = 4.11, p = 0.00)
Gaze	49.75	0.07 (z = 1.53, p = 0.13)
Entering the Patch	86.17	0.72 (z = 13.6, p = 0.00)
Drinking from the Patch	86.31	0.54 (z = 13.8, p = 0.00)
Overall	79.06	0.59 (z=23.9, p=0.00)

Note. Gaze was used for both the looking network and visual observation, with the modifier of whether the gaze recipient was either drinking from the dish, or interacting with it (touching, sniffing) but not drinking.

Association Networks

Grooming and spatial proximity networks were generated as described in Chapter 2. Here I provide a brief overview of each network and how they were used for each hypothesis.

I first identified the stability and robustness of each network by measuring dyad weights (i.e., ties) across 30-, 60-, 90-, and 120-day timeframes in order to determine an appropriate window size across which to construct the association networks. I quantified network stability by determining whether the dyad weights converged within the timeframe using the "check.windowsize" function in the "netTS" package (Bonnell & Vilette, 2020) in R 3.5.2 (R Core Team, 2018). I quantified robustness by how sensitive the dyad weights were to subsampling using the same function. As a consequence, I used a 90-day window size to create all association networks (see Appendix A). Finally, because I was using these networks to test whether or not associations predicted information transmission, I constructed association networks using data from the 90 days prior to the date of the first trial on each troop for each study period.

Grooming. Grooming dyads were identified from instantaneous scan samples as in Chapter 4, yielding 4,529 directed grooming samples in study period 1 (N_{RBM}=1,367, N_{RST}=1,255, N_{PT} =1,907), and 2,263 directed grooming samples in study period 2 (N_{RBM}=834, N_{RST}=729, N_{PT}=700).

Spatial Proximity. Spatial proximity dyads were also collected from instantaneous scan samples, yielding 35,946 directed grooming samples in study period 1 (N_{RBM} =12,550, N_{RST} =8,540, N_{PT} =14,856), and 30,103 directed spatial proximity samples in study period 2 (N_{RBM} =11,129, N_{RST} =7,386, N_{PT} =11,588).

Observation Networks

Observation networks record the number of times a potential learner observes the target behavior being performed and can be considered to be the most direct means of both detecting social transmission, and quantifying it (Hasenjager et al., 2020). Observation networks are best used when researchers can be confident that they have recorded all instances of the target behavior, i.e., when the target behavior occurs in a limited space and can be monitored closely. Such conditions mostly occur for captive populations or, in wild populations, under experimental arrangements where availability of the target behavior is experimentally controlled (e.g., access to a novel foraging device. For an example using observation networks of a naturally derived novel behavior in a wild population, see Hobaiter et al., 2014). Importantly, observation networks need to be updated through time, i.e., they are dynamic (Hasenjager et al., 2020; Hoppitt & Laland, 2013). For this same reason, observation networks should be updated after each new acquisition of the target behavior (Hasenjager et al., 2020). If they are not, it is impossible to determine the order of events, and thus whether performing the behavior happened before or after witnessing it, preventing analysis of social transmission.

Additionally, although "observation" may imply the visual modality, this is not a necessity. For example, rats rely principally on olfaction to learn about novel foods (Galef Jr & Wigmore, 1983), and olfaction is a relevant sensory modality of information transfer in vervet monkeys (Lycett & Henzi, 1992; Nord et al., 2021). Here, I recorded three possible directed observation networks within which to test for social transmission of the novel water patch drinking behavior. These were a within-experiment muzzle contact network, a visual observation network, a co-presence network. Networks were dynamic, and updated after each learning event (learning events were relative to troop such that each troop had a unique number of learning events; Hasenjager et al., 2020).

Within-experiment muzzle contact. The within-experiment muzzle contact (hereafter, "muzzle contact") network was recorded in order to test whether animals that muzzle contacted drinkers learned to drink themselves. Within-experiment muzzle contact dyads were comprised of animals who muzzle contacted another during the experiment. Muzzle contact dyads totaled to 16 directed dyads in study period 1 ($N_{RBM} = 7$, $N_{RST} = 8$, $N_{PT} = 1$), and 3 directed dyads in study period 2 ($N_{RBM} = 0$, $N_{RST} = 3$, $N_{PT} = 0$).

Visual observing network. Visual network dyads were comprised of animals who gazed at another that was drinking from the provided water source. Visual observation was recorded if an animal directed its gaze toward a drinker for ≥ 2 secs. It was difficult to score visual observation when multiple animals were within the patch because animals could occlude one another. As such, visual observation was not recorded for animals when they were present in the patch, that is, when they were within arms-reach of the patch. I identified 357 directed visual observation dyads in study period 1 ($N_{RBM}=45$, $N_{RST}=231$, $N_{PT}=81$), and 69 directed dyads in study period 2 ($N_{RBM}=43$, $N_{RST}=20$, $N_{PT}=6$).

Co-presence network. The co-presence network allowed me to test whether proximity to the solver while the solver was actively solving the patch was required for social learning. The co-presence network was composed of dyads where one animal was present in the patch (i.e., within arms-length of the water vessel) at the same time as another was drinking. Co-presence dyads totaled to 434 directed dyads in study period 1 ($N_{RBM}=89$, $N_{RST}=308$, $N_{PT}=37$), and 112 directed dyads in study period 2 ($N_{RBM}=55$, $N_{RST}=41$, $N_{PT}=16$).

5.2.3 Statistical Analyses

In general, I have used a Bayesian approach (McElreath, 2020) in this thesis. However, NBDA is only publicly available within a frequentist framework (although see Boogert et al., 2014; Nightingale et al., 2015; Whalen & Hoppitt, 2016). Bayesian and frequentist approaches use different terminology to refer to the variation around an estimate—Bayesian approaches often use the term "credible intervals" whereas frequentist approaches often us "confidence intervals" (Hespanhol et al., 2019). Furthermore, the assumptions of Bayesian credible intervals are not completely compatible with frequentist confidence intervals, nor vice versa (e.g., if the majority of a Bayesian credible interval is positive, but the tail includes zero, researchers can still conclude that there is some evidence that the parameter is indeed positive; the same cannot be interpreted from frequentist confidence intervals). In what follows, all analyses are Bayesian, with the exception of NBDA.

Information Diffusion

I used NBDA to determine if learning to drink from the novel water patch was socially transmitted and if so, through which pathways and how individual attributes contributed to social transmission (questions i-iv). For my analyses, I was confident that we observed all possible occurrences of drinking from the patch, because we regulated its availability. Accordingly, I first used a continuous time of acquisition diffusion analysis (cTADA) to model the diffusions across troops (for details about NBDA, see Appendix A). However, outcomes of the cTADA were dependent on the shape of the baseline learning function (see Appendix A), so I then fit the models using order of acquisition of diffusion analysis (OADA) (Hasenjager et al., 2020). According to Hasenjager et al. (2020), it is best to compare networks that make similar assumptions with each other (namely, the two association networks to one another; the three observation networks to one another) rather than compare networks that make different assumptions. I therefore tested association and observation networks in separate OADA models. To test observation networks, I modeled OADA using muzzle-contact, visual observation, co-presence networks. To test the role of general association and information flow, I modeled OADA using established grooming and spatial proximity networks.

For both the association and observation OADAs, I made the following decisions. I modeled multiple diffusions because the experiment was conducted both across three independent troops and across two study periods (resulting in six total diffusions). Because nine months separated the two study periods, I decided to treat animals that had solved the patch in study period 1 as demonstrators (though they were not seeded) in study period 2. As I knew the rates of performance, I included transmission weights (calculated as that animal's number of drinks divided by the difference in the duration of the experiment and the time at which that animal first drank) for each animal within each diffusion. As I controlled access to the experimental apparatus, I accounted for exposure to the task to ensure that observations of the target behavior were reflective of transmission opportunities and not local enhancement (Hasenjager et al., 2020; Hobaiter et al., 2014). This was estimated by dividing the number of times each animal was patch-present over their latency to solve the task, as any exposure after solving the task could not have influenced that animal's initial solving (Hobaiter et al., 2014; for animals that did not solve the task, I divided the number of times each animal was patch-present over the duration of the experiment) for each animal. I included age, sex, rank, NFT score, and exposure as individual attributes.

Furthermore, I fit all individual attributes in an unconstrained fashion (i.e., the effects of individual attributes on asocial learning and/or social transmission were assumed to be independent: see Appendix A), as individual attributes may influence asocial and social learning differently (Hasenjager et al., 2020; Hoppitt & Laland, 2013). I used the Akaike Information Criterion (AIC) to determine support for social and asocial learning and, rather than determining the best model to interpret, calculated model-averaged estimates and 95% confidence intervals for each parameter included in the analyses (Hasenjager et al., 2020). As it is not always possible to determine upper 95% confidence intervals for the rate of social transmission (Hasenjager et al., 2020), I sometimes only report the lower 95% confidence interval. Additionally, as the rate of social transmission is relative to the association network used and the nature of the transmission episode (e.g., whether or not it was seeded), I also report the estimated percentage of events that occurred by social transmission for each network to allow for comparison across studies (Hasenjager et al., 2020).

Finally, it is possible that the tested networks interacted with one another. Possible interaction effects between networks were tested using the same method as Hasenjager et al. (2020). I first created interacting networks by multiplying the adjacency matrices of the networks of interest, and fit a model to it. I then compared AICs corrected for small sample sizes (AICc) of this model to the best-fit model without interacting networks.

Behaviors During Learning

In order explore rates of behaviors during learning (question v), I constructed three multilevel Poisson models, using a Bayesian framework using “brms” (Bürkner, 2017b) in R 3.5.2 (R Core Team, 2018). All models included weakly informative priors (mean = 0, SD=1), and the residual assumptions for each dataset were evaluated using the package “DHARMa” (Hartig, 2017). I included the same predictors in each model, despite not always having a specific prediction for each variable, as this analysis was exploratory. Therefore, I modeled whether age/sex, dominance ranking, novel food neophilia (hereafter “neophilia”; see Chapter 2.5.4), social network position, troop membership, and local troop ecologies influenced the number of times an animal looked at another individual interacting with the patch, entered the patch, or drank from it during a given trial.

I defined looking as gazing at another interacting with the patch (e.g., another animal sniffing, touching, or drinking), and thus looking was a different behavior than visual observation, as it did not require the animal being observed to be drinking from the patch. Additionally, I defined entering as being within arms-reach of the dish, and drinking as drinking from the dish. Specifically, counts of looking, entering, and drinking served as the response variable for each model, and age/sex category, rank, betweenness centrality in the grooming network, betweenness centrality in the proximity network, strength centrality in the grooming network, strength centrality in the proximity network, water availability, and neophilia rating served as predictor variables. ID, troop membership, study period, and trial ID were entered as group-level variables (i.e., random effects), and, to account differences in exposure to the experiment, the duration of each trial was entered as an offset variable.

The model exploring how often animals entered the patch revealed data underdispersion—the model did not predict well the animals that did not interact with the patch (the zeros) nor animals that only interacted once (the ones) per trial (Appendix D). I first tried to account for the underdispersion by running the model using a hurdle Poisson distribution (Hilbe, 2017). The hurdle Poisson model performed better than the Poisson (Appendix D.2), but did not solve the underdispersion. I then ran the model as a hurdle negative binomial (Hilbe, 2017), which removed the underdispersion (Appendix D.3) and revealed the similar relative estimates as the hurdle Poisson (Appendix D.4 and D.5). To determine which model to report in the main text. I compared the models using leave-one-out-cross-validation ("LOO"; Vehtari et al., 2017) with the "loo_compare" function of "brms" and found that the hurdle negative binomial model received more support (i.e., received the highest theoretical expected log pointwise predictive density, "ELPD") than the Poisson model, indicating that entering the patch was best modeled as two processes ($\text{ELPD}_{\text{hurdle negative binomial}}$ = 0.00, SE = 0.00; $\text{ELPD}_{\text{Poisson}}$ = -106.33, SE=16.88). I present the results from this hurdle negative binomial below, and provide the results from the Poisson and hurdle Poisson version of the model in Appendix D.

I ran all three models within a multivariate fashion (i.e., a model that specified identical predictor variables for the three different response variables) accounting for any correlated varying effects of animal ID (Bürkner, 2017a). Accounting for correlated varying effects of animal ID means that the model allowed animal ID to vary across the three response variables and thus allowed me to determine whether the animals that varied beyond the predictor variables in one response (e.g., entering the patch) were the same animals that varied in another response (e.g., drinking). Finally, I examined the scatterplots of the Markov Chain Monte Carlo draws from each model (Gabry et al., 2019) to confirm that network measures were not correlated (Webber et al., 2020).

Sample sizes varied with respect to the variables included in each analysis.

5.3 Results

I conducted 93 trials (study period 1: 58 trials; study period 2: 35 trials). Of these, 9 trials (study period 1: 8 trials; study period 2: 1 trial) were unsuccessful, and 3 trials (study period 1: 1 trial; study period 2: 2 trails) were ignored. There were 113 different participants across the two study periods, and 65 animals solved the task. Details by troop are provided in Table 5.1.

5.3.1 Information Diffusion

Social Transmission

I found overwhelming evidence that animals used social information to learn how to drink from the novel water patch. Over 99.9% of models in the observation (muzzle contact, visual observation, and co-presence; Table 5.3) network NBDA, and over 97.2% of models in the association (grooming and spatial proximity; Table 5.4) network NBDA found evidence for social learning.

The Pathways of Social Transmission

In the observation network NBDA, I found that transmission followed the co-presence network to the greatest extent, and minimal followed the visual observation network. I found no evidence that transmission followed the muzzle contact network (Table 5.3). On average, 25.99% (lower confidence interval: 22.25%) of learning events followed the co-presence network, and 1.71% (lower confidence interval: 0.001%) of learning events followed the visual observation network (Table 5.3). There was no evidence that observation networks interacted ($AICc_{best\text{-}model}=291.74$, $AICc_{interactive\ model}=294.7$).

The association network NBDA revealed that zero percent of the learning events followed the grooming and spatial proximity networks. Therefore, there was no evidence

Table 5.3

Diffusion Through The Observation Networks

Parameter	Model-Averaged Estimate (±95% CIs)	Backtransformed Effect (95% CIs)	Akaike Weight	Δ AIC
Visual Observation Network	0.202 (0.000, 1.215)	1.702 (1.00)*	0.072	1.683
Co-Presence Network	4.053 (0.085, 20.212)	25.938 (22.178)*	0.166	0.000
Muzzle Contact Network	0.001 (0.00, 0.927)	0.00 (0.00)*	0.041	2.811
ILVs Asocial Transmission				
Age (Adults)	-1.679 (-2.828, -0.614)	x0.186 (x0.059, x0.541)† *x5.362 (x1.848, x16.906)*	0.166	0.000
Sex (Females)	0.144 (-0.419, 0.932)		0.054	2.228
Dominance Rank	0.033 (-0.394, 0.553)		0.043	2.690
Neophilia Score	0.309 (0.0307, 0.688)	x1.362 (x1.031, x1.99)	0.166	0.000
Exposure	0.498 (0.296, 0.681)	x1.645 (x1.344, x1.976)	0.166	0.000
ILVs Social Transmission				
Age (Adults)	-0.917 (-3.72, 1.155)		0.166	0.000
Sex (Females)	3.529 (1.487, 6.871)	x34.090 (x4.424, x964.059)	0.166	0.000
Dominance Rank	2.364 (1.174, 3.857)	x10.630 (x3.235, x47.307)	0.166	0.000
Neophilia Score	0.821 (-1.23, 2.69)		0.166	0.000

Note. Shaded rows indicate variables that received at least 50% support. Age is relative to juveniles; sex is relative to males. Estimates are on the log scale; CI = certainty interval. MAEs and lower CIs for network estimates are conditioned on the models constrained to that network.

*Backtransformed effects for network estimates represent the percentages of events transmitted socially, with the minimum percentage in parentheses.

† This estimate is negative, indicating that adults used asocial transmission 0.186 times less on average compared juveniles. Italicized values give the effects relative to adults, e.g., juveniles were 5.362 times more likely to use asocial transmission on average.

that social learning followed general association (Table 5.4). There was also no evidence of an interaction between observation networks ($\text{AICc}_{\text{best model}}$=331.0, $\text{AICc}_{\text{interactive model}}$=368.9).

Table 5.4

Diffusion through the Association Networks

Parameter	Model-Averaged Estimate (95% CIs)	Backtransformed Effect (95% CIs)	Akaike Weight	ΔAIC
Grooming Network	0.000 (0.000, 0.507)	0.00 (0.00)*	0.091	0.000
Spatial Proximity Network	0.000 (0.000, 1.000)	0.00 (0.00)*	0.091	0.000
ILVs Asocial Transmission				
Age (Adults)	-1.714 (-2.786, -0.878)	x0.180 (x0.062, x0.416)† *x5.549 (x2.406, x16.211)*	0.091	0.000
Sex (Females)	0.515 (-0.025, 1.116)		0.091	0.000
Dominance Rank	0.207 (-0.159, 0.500)		0.091	0.000
Neophilia Score	0.162 (0.000, 0.600)	x1.176 (x1.000, x1.822)	0.091	0.000
Exposure	0.537 (0.400, 0.696)	x.1.710 (x1.492, x2.006)	0.091	0.000
ILVs Social Transmission				
Age (Adults)	0.000 (0.000, 0.000)		0.091	0.000
Sex (Females)	0.000 (0.000, 0.000)		0.024	2.699
Dominance Rank	0.000 (0.000, 0.000)		0.024	2.699
Neophilia Score	0.000 (0.000, 0.000)		0.091	0.000

Note. Shaded rows indicate variables that received at least 50% support. Age is relative to juveniles; sex is relative to males. Estimates are on the log scale; CI = certainty interval. MAEs and lower CIs for network estimates are conditioned on the models constrained to that network.

*Backtransformed effects for network estimates represent the percentages of events transmitted socially using the best performing model, with the average percentage of events from all models with that network in parentheses.

† The estimate for this variable is negative, indicating that adults used asocial transmission 0.186 times less on average compared juveniles. Italicized values give the effects relative to adults, e.g., juveniles were 5.549 times more likely to use asocial transmission on average.

Learning and Individual Attributes

Given that not all animals used social learning to acquire the novel water patch behavior (as approximately 27% of acquisitions followed the co-presence and looking networks combined), my results reflect the attributes of both social and asocial learners. For animals that solved the patch via social learning, there was an effect of sex and rank

(Table 5.3). Females were 34.1 times more likely to learn socially compared to males, and higher-ranking animals were 10.6 times more likely to learn socially compared to lower-ranking animals. I found no effect of age or neophilia on social transmission.

For animals that learned how to drink from the patch using personal (i.e., asocial) information, I found effects of age, neophilia, and exposure to the task (Table 5.3). Juveniles were 5.4 times more likely to learn the task asocially compared to adults. Animals that were more neophilic during the novel food tests were 1.4 times more likely to learn asocially compared to animals that were less neophilic, and animals that had more exposure to the task were 1.6 times more likely to learn asocially compared to animals with less exposure. I found no effect of sex or rank on asocial learning. Asocial individual attribute effects in the association networks (Table 5.4) were quantitatively similar to the observation network asocial individual attribute effects Table 5.3.

5.3.2 Behaviors During Learning

A total of 93 animals looked at others interacting with the patch (hereafter "looking"), 102 animals entered the patch (hereafter "entering"), and 69 animals drank from the dish (hereafter "drinking"). Animals were correlated in their rates of looking, entering and drinking; that is, animals that varied in rates of looking varied similarly in rates of entering, and animals that varied in rates of entering varied similarly in rates of drinking (Table 5.5a). Additionally, all models revealed variation with regard to group-level variables (Table 5.5b-d).

For rates of looking, there was variation across individual animal identities, trial

Table 5.5a

Correlated Varying Effects of Animal ID Across All Models

Models	Correlation	Estimate Error	Lower 95 CI	Upper 95 CI
Looking & Entering	0.471	0.253	-0.087	0.872
Looking & Exploit	-0.023	0.171	-0.344	0.328
Entering & Drinking	0.679	0.192	0.212	0.950

Note. CI = credible interval.

Table 5.5b

Posterior Estimates of Rates of Looking

Effect	Parameter	Estimate	Est. Error	Lower 95 CI	Upper 95 CI	pd (%)
Population-Level Effects	Intercept (Adult Females)	-0.712	1.021	-2.771	1.274	76.45
	Adult Males	-0.152	0.401	-0.935	0.637	65.50
	Juvenile Females	0.186	0.299	-0.398	0.774	72.83
	Juvenile Males	0.187	0.320	-0.413	0.830	71.30
	Novel Food Neophilia	-0.187	0.106	-0.410	0.012	96.60
	Dominance Rank	-0.297	0.095	-0.486	-0.114	99.90
	Water Availability	0.220	0.148	-0.068	0.515	92.88
	Grooming Degree Strength	0.069	0.182	-0.283	0.427	64.20
	Spatial Proximity Degree Strength	-0.151	0.161	-0.471	0.147	82.18
	Grooming Betweenness	0.102	0.124	-0.139	0.342	79.20
	Spatial Proximity Betweenness	0.067	0.094	-0.115	0.254	76.30
Group-Level Effects	sd(ID)	0.593	0.099	0.413	0.805	100.00
	sd(Troop)	1.449	1.874	0.058	7.031	100.00
	sd(Study Period)	5.381	2.940	0.691	12.206	100.00
	sd(Trial ID)	0.970	0.142	0.723	1.286	100.00

Note. Age-sex is relative to adult females. Estimates are on the log scale; CI = credible interval, SD = standard deviation, pd = probability of direction. N = 489. LOO-adjusted R^2=0.15.

ID, and study period, but not between troops. Rates of entering the patch varied by animal and trial ID, and rates of drinking varied with respect to study period, ID, trial ID, and troop. Entering the patch fit best using a hurdle negative binomial distribution, entering the patch, unlike looking and drinking, was best modeled as two processes—the first

Table 5.5c

Posterior Estimates of Probability and Rates of Entering

Effect	Parameter	Est.	Est. Error	Lower 95 CI	Upper 95 CI	pd (%)
Population-Level Effects	Intercept (Adult Females)	-1.025	1.094	-3.204	1.120	82.20
	Adult Males	-0.132	0.775	-1.695	1.350	55.23
	Juvenile Females	0.723	0.480	-0.224	1.669	93.68
	Juvenile Males	0.648	0.516	-0.374	1.637	89.53
	Novel Food Neophilia	0.068	0.138	-0.205	0.333	69.68
	Dominance Rank	0.082	0.155	-0.217	0.396	69.90
	Water Availability	0.217	0.142	-0.062	0.506	93.93
	Grooming Degree Strength	-0.021	0.261	-0.537	0.508	53.23
	Spatial Proximity Degree Strength	0.039	0.219	-0.413	0.466	58.30
	Grooming Betweenness	-0.148	0.233	-0.614	0.295	73.73
	Spatial Proximity Betweenness	-0.196	0.191	-0.581	0.160	84.60
	hu_Intercept (Adult Females)	-0.720	1.533	-3.706	2.387	72.25
	hu_Adult Males	2.059	1.231	-0.217	4.638	96.05
	hu_Juvenile Females	-2.096	0.937	-3.957	-0.311	99.00
	hu_Juvenile Males	-2.239	1.042	-4.364	-0.246	98.58
	hu_Novel Food Neophilia	-1.231	0.434	-2.125	-0.434	99.98
	hu_Dominance Rank	0.242	0.314	-0.364	0.902	78.40
	hu_Water Availability	0.354	0.283	-0.177	0.918	89.63
	hu_Grooming Degree Strength	-0.240	0.464	-1.144	0.696	70.55
	hu_Spatial Proximity Degree Strength	0.125	0.372	-0.614	0.850	62.75
	hu_Grooming Betweenness	0.162	0.333	-0.515	0.790	69.28
	hu_Spatial Proximity Betweenness	0.101	0.233	-0.344	0.580	67.00
Group-Level Effects	sd(ID)	0.548	0.174	0.217	0.911	100.00
	sd(Troop)	1.325	2.003	0.023	7.472	100.00
	sd(Study Period)	5.932	3.274	0.313	13.977	100.00
	sd(Trial ID)	0.728	0.187	0.388	1.115	100.00
	hu_sd(ID)	1.786	0.450	1.025	2.814	100.00
	hu_sd(Troop)	0.934	0.925	0.039	3.583	100.00
	hu_sd(Study Period)	1.144	1.288	0.031	4.603	100.00
	hu_sd(Trial ID)	1.513	0.423	0.769	2.437	100.00

Note. Age-sex is relative to adult females. Estimates are on the logit scale for the hurdle portion of the model (hu; probability of application) and log scale for the count portion of the model (rate of application); CI = credible interval, SD = standard deviation, pd = probability of direction. N = 489. LOO-adjusted R^2=0.21.

Table 5.5d

Posterior Estimates of Rates of Drinking

Effect	Parameter	Estimate	Est. Error	Lower 95 CI	Upper 95 CI	pd (%)
Population-Level Effects	Intercept (Adult Females)	-1.705	1.086	-3.789	0.476	94.20
	Adult Males	-0.827	0.665	-2.087	0.467	88.65
	Juvenile Females	1.773	0.460	0.887	2.664	100.00
	Juvenile Males	1.431	0.486	0.491	2.392	99.83
	Novel Food Neophilia	0.600	0.169	0.277	0.932	99.95
	Dominance Rank	0.000	0.137	-0.264	0.275	50.95
	Water Availability	0.347	0.127	0.093	0.602	99.70
	Grooming Degree Strength	-0.190	0.134	-0.461	0.070	92.10
	Spatial Proximity Degree Strength	0.628	0.104	0.425	0.832	100.00
	Grooming Betweenness	-0.072	0.118	-0.309	0.160	72.00
	Spatial Proximity Betweenness	0.195	0.111	-0.018	0.416	96.28
Group-Level Effects	sd(ID)	1.298	0.162	1.018	1.660	100.00
	sd(Troop)	1.781	1.971	0.096	7.387	100.00
	sd(Study Period)	5.483	2.929	0.842	12.526	100.00
	sd(Trial ID)	0.960	0.122	0.745	1.212	100.00

Note. Age-sex is relative to adult females. Estimates are on the log scale; CI = credible interval, SD = standard deviation, pd = probability of direction. N = 489. LOO-adjusted R^2=0.45.

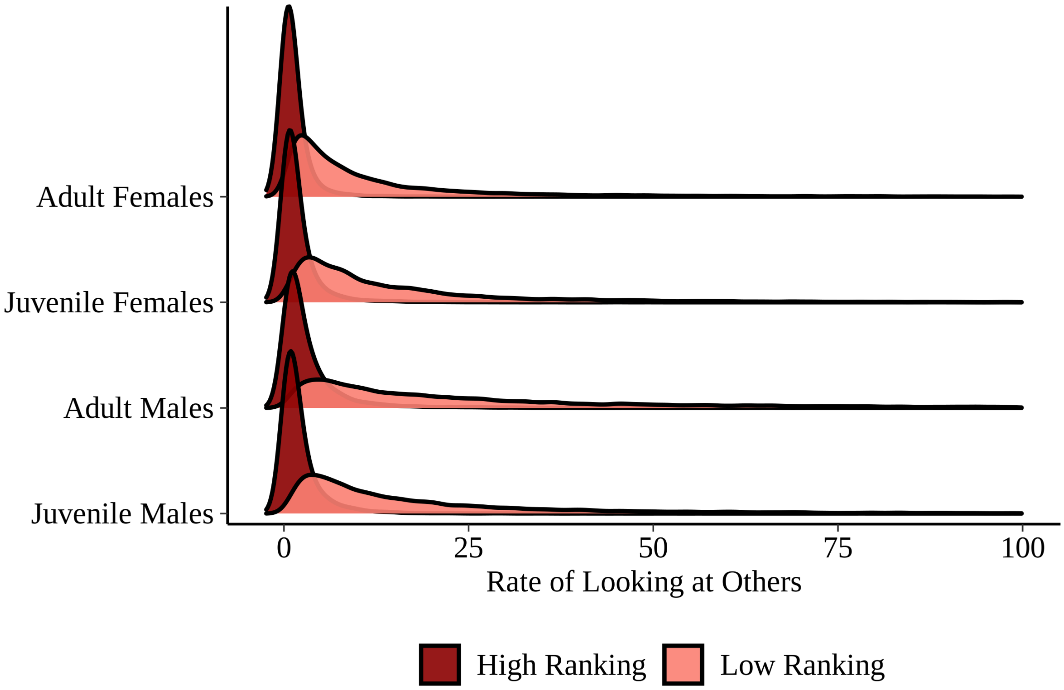
being whether or not an animal entered the patch (y/n; the “hurdle” of the hurdle negative binomial), and then by the rate at which it did so in each trial (i.e., the magnitude of entering). Given this, results for this model reflect these two processes (Table 5.5c).

Individual Attributes and Looking, Entering, and Drinking

Looking. Dominance rank was negatively correlated with looking. Specifically, higher-ranking animals were less likely to look at others who were interacting with the patch (Figure 5.4). There was weak evidence that more neophilic animals looked at higher rates (pd = 96.58%; Table 5.5b). There was no evidence that looking was influenced by age/sex, neophilia, or social network position (Table 5.5b).

Figure 5.4

Rates of Looking at Another by Rank

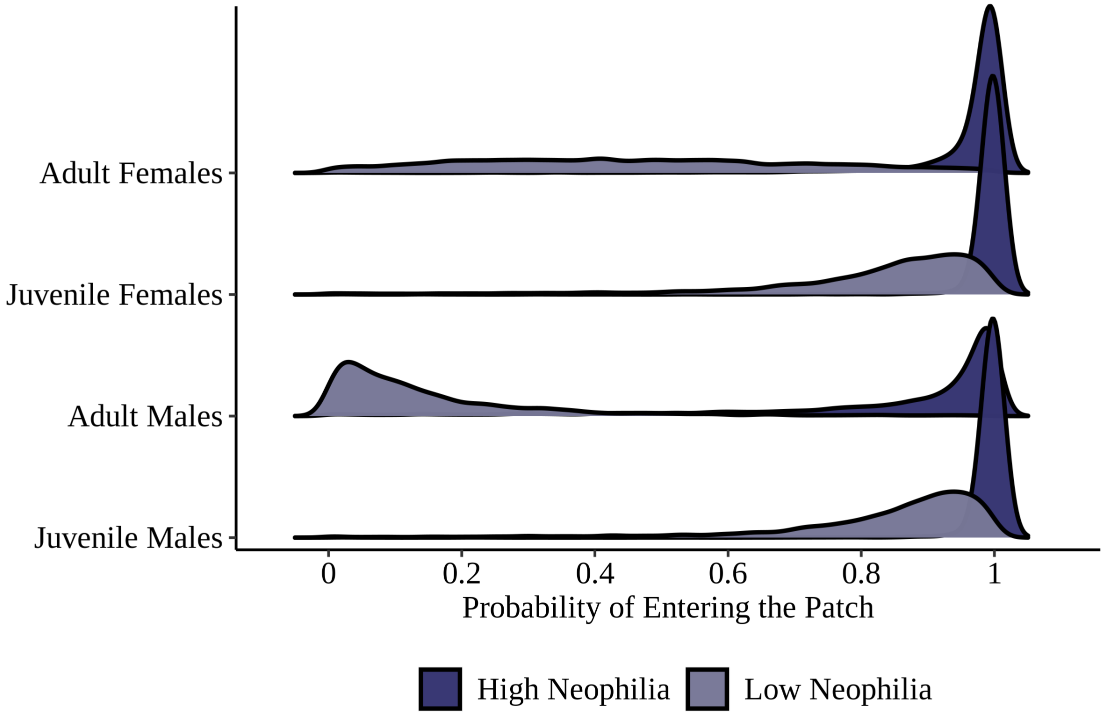


Note. Density plots present the range of rates predicted by the model, with the height of the density curve indicating the probability of the predicted rate, and the spread of the curve indicating its uncertainty (see Table 5.5b). Rates are backtransformed from the log scale into the original scale. In this context, rate refers to the average number of acquisitions per trial as determined by the model marginal means.

Entering. I found no evidence that entering the patch was influenced by rank. Age/sex class and neophilia influenced whether not animals entered the patch, but dominance rank did not (Table 5.5c). Compared to adult females, adult males were less likely to enter the patch, and both juvenile females and juvenile females were slightly more likely to do so. I also found that animals with higher neophilia scores were more likely to enter the patch (Figure 5.5). Rank, network position, and age/sex class did not affect *how often* an animal entered the patch during a trial (Table 5.5c).

Figure 5.5

Probabilities of Entering the Patch by Neophilia



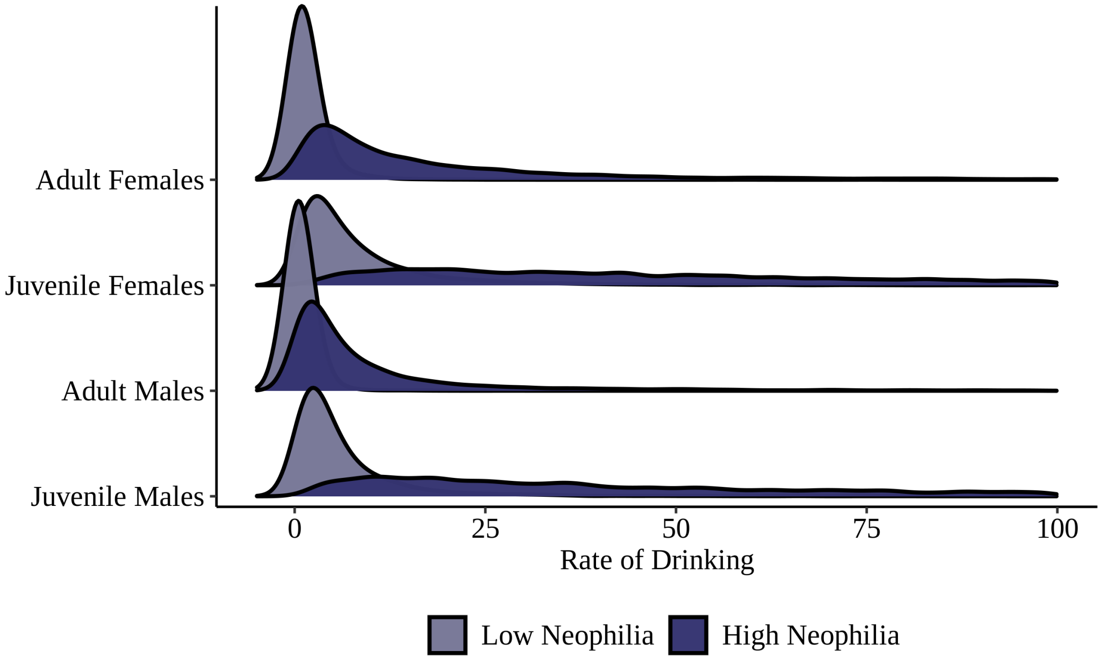
Note. Density plots present the range of probabilities predicted by the model, with the height of the density curve indicating the probability, and the spread of the curve indicating its uncertainty (see Table 5.5c). Probabilities are backtransformed from the log scale into the probability scale.

Drinking. Age/sex class, neophilia score, water availability, and network position all influenced how often animals exploited social information. Animals with higher neophilia scores drank at higher rates per trial (Figure 5.6), and juvenile females drank at slightly higher rates per trial (Table 5.d). Animals with higher measures of spatial proximity strength also drank from the patch at higher rates than those with lower measures (Figure 5.7). There was no evidence that drinking was influenced by rank (Table 5.5d).

Local Ecologies and Looking, Entering, and Drinking

Figure 5.6

Rates of Drinking by Neophilia



Note. Density plots present the range of rates predicted by the model, with the height of the density curve indicating the probability of the predicted rate, and the spread of the curve indicating its uncertainty (see Table 5.5d). Rates are backtransformed from the log scale into the original scale. In this context, rate refers to the average number of exploitations per trial as determined by the model marginal means.

Water availability was negatively correlated with rates of drinking—as days since water increased, animals drank from the water patch at higher rates (Table 5.5 d, Figure 5.8). There was no evidence that water availability influenced looking or entering (Table 5.5b-c).

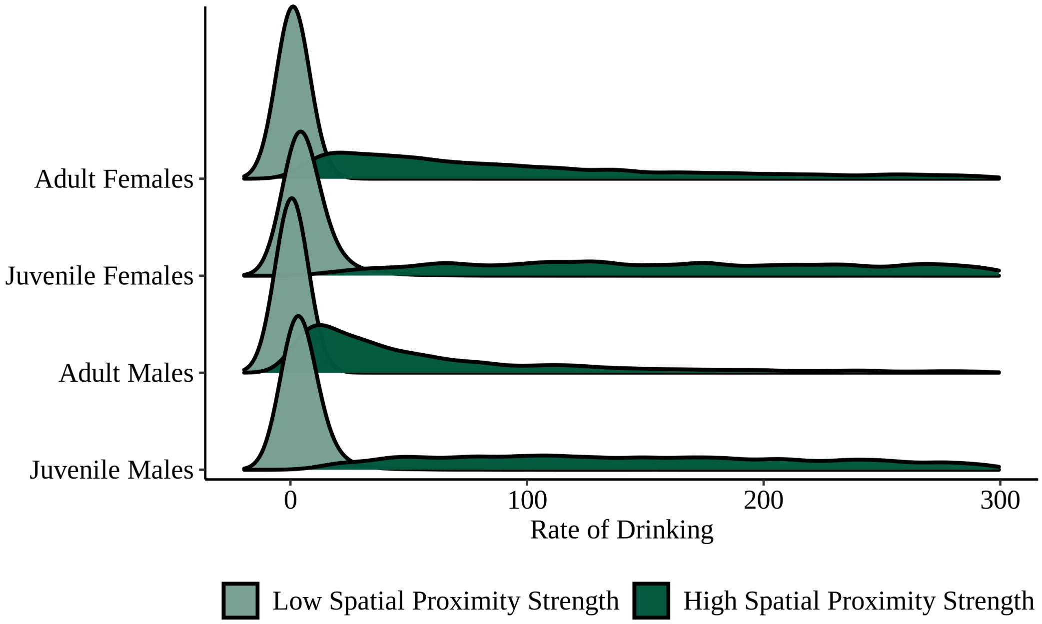
5.4 Discussion

Diffusion Pathways and Individual Attributes of Learners

Contrary to my prediction, there was little to no support that the visual observing or muzzle contact observation networks served as a diffusion pathway novel water patch

Figure 5.7

Rates of Drinking by Spatial Proximity Degree Strength

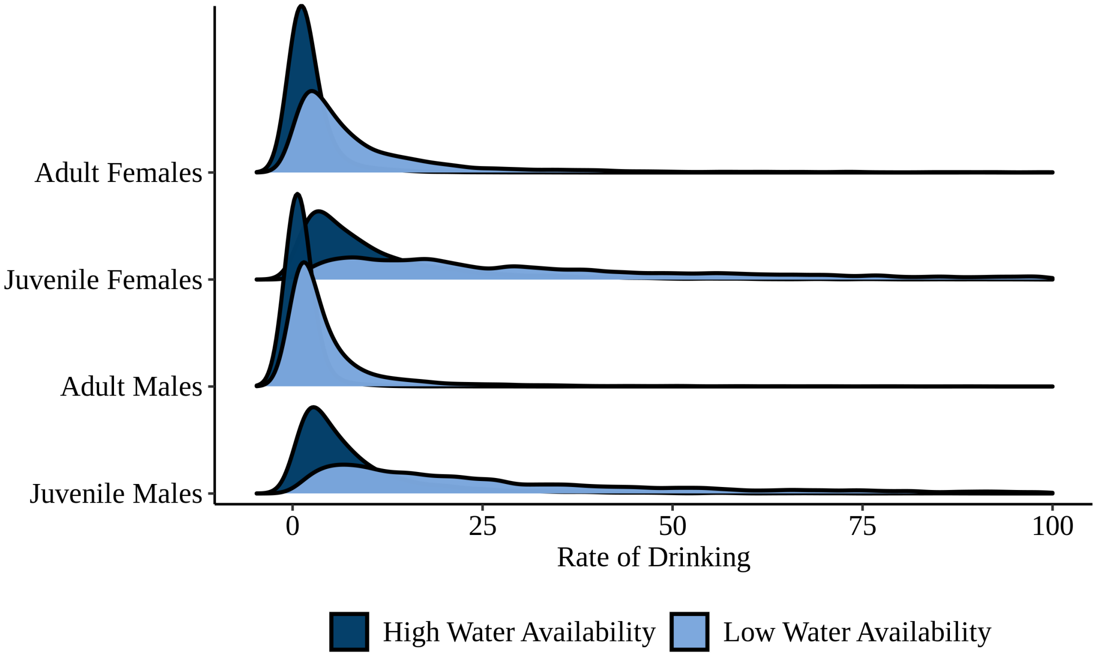


> *Note.* Density plots present the range of rates predicted by the model, with the height of the density curve indicating the probability of the predicted rate, and the spread of the curve indicating its uncertainty (see Table 5.5d). Rates are backtransformed from the log scale into the original scale. In this context, rate refers to the average number of exploitations per trial as determined by the model marginal means.

information. Additionally, social information did not follow periods of association as measured by grooming and spatial proximity networks did not describe information flow. Instead, animals used the co-presence network to learn how to drink from the novel water patch. Taken together, the typical pathways of social transmission for these animals are best described by opportunity rather than by established affiliations—animals did learn from one another, but this learning could not be predicted by their prior relationships nor by a previously established information transmission route. These finding may speak to the fact that, while many animals are capable of social learning, they rarely do so at the

Figure 5.8

Rates of Drinking by Water Availability



Note. Density plots present the range of rates predicted by the model, with the height of the density curve indicating the probability of the predicted rate, and the spread of the curve indicating its uncertainty (see Table 5.5d). Rates are backtransformed from the log scale into the original scale. In this context, rate refers to the average number of exploitations per trial as determined by the model marginal means.

high frequencies seen in humans (Boyd & Richerson, 1996; Whiten et al., 2011). Perhaps animals largely use routes other than their affiliative relationships to gain social information, and are more opportunistic given the resources and social constraints of the moment, similar to the contingency-dependent mechanisms of associative learning (Heyes, 2012).

Females did indeed use social transmission at higher rates than males—females learned to drink from the novel water patch using social information approximately 34 times more than males. However, contrary to my prediction, social learning differed by rank—higher-ranking animals learned to drink from the novel water patch using social information approximately 10.6 times more than lower-ranking animals. It has been suggested that using social information may depend on the social environment (Carter et al., 2016; Lorenz et al., 2011; Racine et al., 2012), a hypothesis supported here by the effects of sex and rank on social transmission. Given that here, the majority of social learning events followed the co-presence network compared to the looking network, higher-ranking animals may have been better able to directly approach drinkers and gain social information that they could then immediately exploit. Furthermore, vervet females formidably influence male dominance hierarchies and network positions (Bonnell et al., 2020; Young et al., 2017)—examples of significant social experience that may have contributed to their ability to use social information more compared to males here. Being philopatric, females may have more experience with ecological conditions than males, affording them more local ecological knowledge (Renevey et al., 2013; van de Waal et al., 2010). Similarly, there might also be a larger pressure on females to exploit social information about water given their needs due to pregnancy, gestation, and lactation (Baldellou & Adan, 1997; Barrett et al., 2006; Gaulin & Sailer, 1985).

However, contrary to my predictions, social learning did not vary by age. Carter et al. (2016) also found no effect of age on social transmission. This was seen as surprising, given that juvenile baboons previously had been found to be particularly adept at social learning (Carter et al., 2014); they proposed that the lack of difficulty in their task (novel food patch discovery) could explain this difference (Aplin et al., 2012). However, Canteloup et al. (2020) also found no effect of age in their likely more difficult task (pushing or pulling the door of a puzzle box to gain food). Thus, juveniles may lack the social experience required to use social information successfully (Hauser, 1988; Reader & Laland, 2001).

Consistent with previous findings that bolder animals rely on personal information to solve novel problems (Smit & van Oers, 2019; van Oers et al., 2005), I found that more neophilic learned to drink from the patch using personal information approximately 1.36 times more than less neophilic animals. Of note here, however, is the fact that, although there was a positive correlation between neophilia and the use of personal information, there was no relationship between neophilia and the use of social transmission. In other words, I did not find, as others have, that neophilia levels correlated with the types of information available—using social information was not dependent on neophilia. This variation may be reflective of the particular social contexts of the learning scenario (Webster & Ward, 2011), as suggested for rank and sex. For example, neophilia in this population is dependent on social facilitation (Chapter 3).

These results lend more support to previous findings that vervets can in part use social learning to solve novel foraging problems (Canteloup et al., 2020; reviewed in Mertz et al., 2019). The NBDA findings here are also in line with three results from a similar experiment—that vervets are capable of social learning during a novel foraging task, that females are more likely than males to use social transmission, and that age does not contribute to social transmission (Canteloup et al., 2020). However, the vervets in my study used social learning to a lesser extent than found in a previous task: 27.7% of the time, compared to 45.1% in Canteloup et al.'s (2020) diffusion experiment.

Individual and Ecological Attributes of Behaviors During Learning

At the level of the individual, rates of looking were correlated with rates of entering, and rates of entering was correlated with rates of drinking. However, there was no such correlation between rates of looking and rates of drinking, e.g., animals that looked at others at high rates were not the same animals that drank at high rates. This finding is consistent with the diffusion findings—social learning did not follow visual observation of animals solving the patch. In contrast, more neophilic animals entered the patch and drank more than less neophilic animals, but relied more on personal information. These finding may seem contradictory given that social transmission most closely followed the co-presence network, which was comprised entirely of animals that entered the patch while another was drinking. However, the measures used to quantify entering the patch, and to construct the co-presence network and, though similar, were not identical; entering the patch was measured by the animal coming within arms-reach of the patch, but the co-presence network was defined by the animal being within arm's-reach of the patch *while another animal was drinking.* Therefore, while more neophilic animals entered the patch more, they didn't necessarily do so while others were present. My finding that higher-ranking animals used social transmission more may better hint at these social contexts and how they are necessary for social transmission—namely the ability to enter the patch when others were also present and drinking. I also found that animals with higher measures of spatial proximity strength drank at higher rates than those with lower measures, and that water availability positively correlated with drinking rates, indicating that drinking was also mediated by social dynamics and the local ecology.

Finally, considering the variation explained by the grouping variables for the model describing rates of looking, entering, and drinking helps to understand how much these behaviors were *not* predicted by attributes, i.e., the predictor variables. Across all three models, variation in behavior rates depended largely on animal and trial ID, and to a lesser extent on the study period. This means that rates of behavior varied by animal beyond the measured attributes of age, sex, rank, neophilia, and network position, supporting the claim that understanding often-ignored sources of individual variation, and measuring the environment in which it occurs (Strum et al., 1997), is critical to understanding variation social learning (Mesoudi et al., 2016).

Do Individual Attributes and Behaviors During Learning Describe Social Transmission?

Taken together, these findings show that individual attributes and rates of specific behaviors cannot independently describe social transmission, and that the context of the learning scenario is also necessary in understanding how animals learn—on their own and from others. For example, social transmission did not follow connections between animals that visually observed, or muzzle contacted, solvers. Instead, learners had to come within close proximity of solvers in the act of solving, which is more likely for animals with certain social opportunities (i.e., being high-ranking) and/or particular learning histories such as those likely coinciding with age and sex. This is not to say that analyzing individual attributes and rates of behavior was not useful in interpreting these results—understanding how local ecologies increase the likelihood of certain behaviors, as was the case with positive correlation drinking and days since access to water, does indeed inform when social learning is more likely to occur. However, considering individual attributes and rates of behavior outside of context can be misleading; for example, although neophilia was correlated with entering the patch and drinking at high rates, it was not correlated with social transmission.

5.4 Limitations

Unfortunately, I was not as behavior analytic as I could have been when organizing these results. In behavior analysis, the reliability of behavioral measurement is constantly monitored—if a measure is not reliable, it will not be used, as there would be no way to know if the independent variables affect behavior. I did not fully use this approach when developing my observational networks, or when deciding what behaviors I should measure during learning. Instead, rather than review my data to understand which behaviors would likely relevant to learning and could capture aspects of social transmission, I decided ahead of time that gaze would be a relevant measure, as previous work that inspired my analyses here all successfully used a measure of gaze to understand social transmission (Carter et al., 2016; Hobaiter et al., 2014), and because a paper that was published while I was running my analyses found that social transmission in vervets can follow visual observation (Canteloup et al., 2020).

During my analysis, it quickly became clear that getting a reliable measure of gaze would be difficult, so I also measured a behavior that was much more salient for observers and also appeared relevant to transmission, task co-presence. However, it is unclear if social transmission followed co-presence more than the visual observation network simply because of a methodological issue—that co-presence was more reliable than visual observation—or some other reason, such as the co-presence network capturing something of behavioral or biological relevance than the looking network did not. For example, higher-ranking animals were less likely to look at others interacting with the patch, but also more likely to use social information to solve it. It could be that looking was too unreliable to seriously consider any findings regarding rates of looking during the experiment. However, it could also be that the co-presence network captured both the opportunity to observe others, but also the motivation or ability to access social information, as higher-ranking animals were likely better able displace or supplant others drinking from the patch. Thus, co-presence may be an indicator of rank, which could in turn explain why rank had no effect on rates of drinking, but did affect its social transmission.

CHAPTER 6: NOVEL GUM BOX TEST

6.1 Introduction

In Chapter 5, I tested whether animals could learn to drink from a novel water patch using social learning. Though the water dish was novel, I did not assume that drinking from it was difficult as, assuming there was water in the dish and barring any social constraints, any animal that had access to the dish could drink. Indeed, the majority of animals that drank from the patch used asocial learning, revealing that the task was not sufficiently difficult to require animals to rely on social information. In this chapter, I exploit a slightly more difficult task to explore the conditions under which vervets use social learning, inspired both by the two-action tasks commonly deployed in the social learning literature, as well as my experience with using operant chambers (i.e., Skinner boxes) to investigate how animals learn complex discriminations. I created a novel foraging device that afforded a gum extraction behavior seen in wild vervet monkeys (see Figure 6.1; Wrangham & Waterman, 1981). Artificial gum boxes are often used as enrichment devices in captivity and allow gum to be accessed by probing holes using a hand/finger, a behavior in the repertoire of gumivorious primates (Carey et al., 2012; Huber & Lewis, 2010). In this experiment, to be successful, animals needed to correctly choose one hole from an array of three possible holes in order to obtain a gum reward, and are therefore more at risk of failure compared to the water patch task, as the water patch only had one option—the dish itself. Therefore, the current experiment allowed me to identify the learning mechanisms responsible acquisition of the novel foraging behavior by providing multiple response alternatives in order to determine if animals paid

Figure 6.1
Monkeys Foraging Natural Acacia Gum

Note. Left: An adult female chews at gum exuding from an acacia tree. Right: An adult female licks gum after extracting it. Photos, C. Vilette.

attention to the behavior of individuals accessing gum. While my novel foraging device was similar in spirit to two-action tasks (Dawson & Foss, 1965; Hoppitt & Laland, 2013) in that it can control for stimulus enhancement (as animals should probe holes at random under asocial learning), it could be considered more ecologically relevant than devices that require animals to push doors or open drawers (e.g., "artificial fruits"; van de Waal et al., 2013; van de Waal et al., 2015; Whiten et al., 1996) because it takes advantage of a behavior that is already present in their repertoire (see Figure 6.1), and can therefore illuminate how a skill in one context can be generalized to another, which is one definition of innovation (Reader & Laland, 2003).

Using a more difficult task also allowed me to explore the costly information hypothesis, which predicts that, as information becomes more costly to acquire through personal means, animals should prefer social information social (Boyd & Richerson, 1985; Boyd & Richerson, 1988). For example, there is strong evidence that antipredator behavior (e.g., alarm calls, avoidance behaviors) is often socially learned, as is found in birds (Curio, 1988) fish (Chivers & Smith, 1995; Kelley et al., 2003; Krause, 1993; Suboski & Templeton, 1989), and monkeys (Mineka & Cook, 1988). Similarly, as difficulty to solve a task increases, so too do the benefits of learning. Task difficulty has previously been quantified as the time required to solve the task (Kendal et al., 2009), the time spent exposed to stimuli (Baron et al., 1996), stimulus complexity (Baracchi et al., 2017) or, for human subjects, as the level of variance in the information provided/ available (McElreath et al., 2005). Increased reliance on social information during difficult tasks has been found in bees (Baracchi et al., 2017; Saleh et al., 2006; Wray et al., 2012), fish (Laland et al., 2011; Webster & Laland, 2008), monkeys (Kendal et al., 2009), and humans (Baron et al., 1996; Morgan et al., 2012).

Thus, in this chapter, I examine the role of task difficulty in social transmission. I again used NBDA to (i) assess the likelihood that learning to extract gum from the box was acquired via social as opposed to asocial learning, (ii) determine whether transmission followed specified observation networks, (iii) identify the percentage of initial learning events that were acquired via asocial or social learning, and (iv) assess the relationship between individual level variables and learning. Given the benefits of social transmission when the use of personal information is particularly costly, and the assumed increased difficulty of the present task, I predicted that, in comparison to the water patch experiment in the previous chapter, animals will rely more on social information to solve the gum box task (i.e., that a higher percentage of learning events will be acquired through social learning). I also predicted that because animals were not experiencing limited water availability at the time of this experiment (see “Study Period 2” in Figure 4.1), and because previous work has found lower rates of social information use by females during a difficult (as compared to the water patch task in the previous chapter) task (Canteloup et al., 2020), that females will engage in social learning at lower rates here compared to rates in the water patch.

I also further considered the validity of my criticism that social learning relies too much on individual attributes and not context (outlined in Chapter 1 and explored in Chapter 5) by examining the extent to which various transmission biases, i.e., model-based social learning strategies, might explain social transmission. I tested whether animals were biased in observing animals of certain dominance rankings, kinship relationships, sexes, and neophilia levels solving the artificial gum box problem. There is contradictory evidence that vervets are (Canteloup et al., 2020), or are not (Botting et al., 2018; Renevey et al., 2013), biased to observe higher-ranking animals during social learning opportunities, and findings vary similarly for kinship (van de Waal et al. (2012) and van de Waal et al. (2014) found a kinship bias in social transmission, whereas Canteloup et al. (2020) did not), and sex (Bono et al. (2018) and Renevey et al. (2013) found that animals preferentially attended to adult females during social transmission, while Canteloup et al. (2020) found no sex bias). As it is difficult to make a directional prediction from these findings, my transmission bias analysis was exploratory.

Finally, I again used a sequential analytical approach to examine how animals learned to eat gum from the artificial gum box, tested if (v) age, sex, rank, neophilia, and resource availability were associated with whether animals visually observed others interacting with the artificial gum box, probed the box (but not the baited hole), and extracted gum from the box, which are behaviors that correspond to Carter et al.'s (2016) categories of acquiring, applying, and exploiting information.

6.2 Methods

6.2.1 Study Period and Subjects

This study was conducted during study period 2, a three-month period lasting between March and May 2018. Group composition varied slightly across the three troops throughout this period, as described in Table 6.1.

Table 6.1

Troop Composition throughout the Study Period-1

Age/Sex	Range	Mean
RST Adult Females	8-8	8
RST Adult Males	7-8	8
RST Juvenile Females	16-16	16
RST Juvenile Males	4-10	7
PT Adult Females	8-9	8
PT Adult Males	5-5	5
PT Juvenile Females	10-10	10
PT Juvenile Males	13-16	15
RBM Adult Females	5-7	6
RBM Adult Males	5-6	6
RBM Juvenile Females	14-14	14
RBM Juvenile Males	10-12	11

6.2.2 Information Diffusion Experiment

For this experiment, the novel foraging device consisted of a plastic rectangular storage box modified to resemble an open, free-operant chamber (Catania, 2007). The black box and blue lid were opaque. The box measured 33 cm x 20 cm by 13 cm and three holes were cut in order to insert three, 35 mL (5 cm in length, 2.5 cm in diameter) sample tubes (Lasec Laboratory Solution Provider, South Africa). The tops of the lids of the sample tubes were cut out, leaving a threaded loop that fit the top of the tubes. These threaded loops were then each taped with colored insulating tape, one red, one yellow, and one blue, creating three color-coded loops that were screwed on top the tubes, providing three response options from which individuals could forage tube contents (Figure 6.2).

Figure 6.2
The Novel Gum Box

Before each experiment, I mixed approximately 30 mL of orange juice with approximately 10 g of gum arabic powder (Frontier Natural Products, Norway, Iowa, USA), creating a gummy, sticky substance. Gum arabic powder is a common food additive made from the gum of acacia trees. I then baited the gum box by placing this mixture into the blue tube. For this experiment, the blue tube was always the baited tube, and the box was always presented with the yellow, red, and blue tubes running from left to right (Figure 6.2). I never changed which tube was baited, or their orientation, because I wanted to ensure that the saliency of the baited tube remained as consistent as possible.

Experimental trials occurred throughout the day and, to increase the possibility that animals saw the box, it was presented when most animals were on the ground, rather than moving arboreally. Experiments were conducted opportunistically when the environment and behavior of the group allowed; that is, when troops were traveling in a single direction, were on the ground, and were not otherwise distracted by events such as intergroup encounters or predator calls. On average, experiments were presented once per troop per week, but more so towards the end of the study period.

Before each experimental trial, a research assistant and I traveled at least 50 m ahead of the group and placed the box on the ground with the tube options oriented towards the approaching animals. We took care to present the gum box out of the direct sight of animals so that the animals would not associate our presence either with the box itself or the gum within. We did this by keeping the box covered with a cloth bag until the time of presentation, uncovering the box when the animals were at least 30 m away, using our bodies and backpacks to block the view of the box itself, and never approaching the presented box while animals were either interacting with it or within 30 m of it.

As the box was light, I placed rocks inside it to increase its stability and to prevent it from moving as the animals were interacting with it (though animals sometimes did tip it over, see Figure 6.3). Sometimes I used a rock or a stick to prop up the box so that the tubes could be more readily accessed by the animals (Figure 6.4).

After the box was presented, we stood at least 10 m away and video recorded the

Figure 6.3
A Juvenile Probes the Novel Gum Box, Which Has Tipped Over, While Another Looks on

Figure 6.4
Animals Interact With the Novel Gum Box

Note. Left: A juvenile probes the blue option. Right: A juvenile probes the red option as another looks on.

experiment using a Canon PowerShot ELPH 100 HS camera. Animals were already habituated to the presence of cameras in many contexts, as well as to the presence of stationary research assistants recording data using the data loggers. As such, I have no reason to believe that animals were cued to box availability by our data recording procedures.

Trials were recorded as "ignore" if no animal approached within 1 m of the box. Trials began when at least one animal came within 1 m of the box and ended once no animals were within 30 m. Trial times varied as a consequence.

Not every trial resulted in participation, as animals sometimes changed their travel direction, or may not have seen the box. Animals also sometimes ignored the box, which was defined as coming within 5 m but not interacting with it. When either of these situations happened, I ended the trial and marked it as unsuccessful/ignored and attempted another later if conditions allowed (Table 6.2).

Table 6.2

Description of the Participants and Trials Across the Study Period

Troop	Participants	Solvers	Successful Trials	Unsuccessful Trials	Ignored Trials	Total Trials
RST	23	8	23	2	3	28
RBM	35	15	23	0	2	25
PT	35	3	16	3	11	30
Total	**93**	**26**	**62**	**5**	**16**	**83**

Note. Parenthetical values indicate the total number of animals for that category in study period 2; counts of unique animals compared to study period 1 are presented before the parenthetical values. For example, RST had 30 total participants in study period 2, but only 5 had not previously participated in study period 1.

All videotapes were scored in the lab by observers using Behavioural Observation Research Interactive Software (BORIS version 7.7.3, Friard & Gamba, 2016). For trials in which animals engaged with the task, we recorded a number of target behaviors that described the interactions of every focal animal (animals that participated in the task) with the task. We recorded all animals who came with 1 m of the box ("trial participation”), gazed at another animal who was within arms-reach of the box (“gaze”; recorded with a modifier of the recipient’s behavior to measure whether the recipient was interacting with the box, “looking”, or extracting gum from it, “visual observation”), came within touching distance of the box (“entering”), and extracted gum from the box and ate it (“eating”). I also recorded all muzzle contacts and aggression that occurred during trials. Approximately 20% of trials were coded by a third observer for inter-rater reliability, which was 82.18% (Cohen’s kappa=0.58, z=14.7, p=0.00; Table 6.3).

Table 6.3

Reliability of Measured Behaviors

Behavior	Agreement (%)	Cohen’s Kappa
Trial Presence	88.30	NA*
Gaze	75.39	0.31 (z = 5.00, p = <0.01)
Probing an Incorrect Tube	84.83	0.49 (z = 6.59, p = <0.01)
Probing the Correct Tube	80.22	0.35 (z = 6.37, p = <0.01)
Overall	82.18	0.58 (z = 14.7, p = 0.00)

Note. Gaze was used for both the looking network and visual observation, with the modifier of whether the gaze recipient was either eating gum from the box, or interacting with it (touching, sniffing) but not eating.

Observation Networks

Given that the muzzle contact observation network received no support in the previous chapter, I limited the observation networks here to the visual observation and co-presence networks. I recorded looking and co-presence observation networks as in Chapter 5. Visual observation was recorded if an animal directed its gaze towards an individual probing the baited tube for ≥ 2 secs as long as the gazing animal was not within-arms reach of the box, as recording gazes when animals were proximity of the box was difficult. There was a total of 115 directed visual observation network dyads (N_{RBM} =

29, $N_{RST} = 85$, $N_{PT} = 1$). Co-presence networks comprised directed dyads where one animal was present in the patch at the time that another was successfully extracting gum from the box (N_{TOTAL}: 501; $N_{RBM} = 212$, $N_{RST} = 288$, $N_{PT} = 1$).

6.2.3 Statistical Analysis

Information Diffusion

Information diffusion was analyzed via NBDA as described in Chapter 5. In particular, I modeled OADA using visual observation and co-presence networks to test whether social learning followed these observational contexts. I modeled three diffusions, as the experiments were conducted across three troops.

While many juveniles learned to extract gum from the box, only one adult solved the task (see Results). As such, model averaged estimates were highly skewed for both age and the estimate of social transmission. I therefore removed age from all models, and included the one adult that solved the task as a seeded demonstrator in order to account for any transmission between it and others. Models did not converge easily, which resulted in large estimates for s. I therefore re-parameterized the continuous variables (i.e., exposure, dominance ranking, and neophilia score) by inverting them additively (i.e., multiplying them by -1) so that high measures had low values, and low measures had high values. This improved model fit.

Transmission Biases

I tested for transmission biases (predictions b, d-f), using the same methods as Canteloup et al. (2020), by extending the NBDA model (Hasenjager et al., 2020a). I limited my transmission pathways tests to the co-presence network because this was the only network for which I found strong evidence of social transmission (see Results below). To test for transmission bias, I partitioned the co-presence network based on the ILV of interest (i.e., sex, rank, neophilia, and kin) and compared models in which there was a transmission bias, in which there was no transmission bias, and in which there was transmission only in each pathway. I included only co-presence dyads of each sex, rank, neophilia, or kin where the parameter of interest was the object of observation. Thus, I tested transmission bias across five pathways—whether animals were biased to observe males, females, high-ranking animals, low ranking animals, neophilic or non-neophilic animals, and/or kin solving the task (For a full explanation of using NBDA to test for observer bias, see Canteloup et al., 2020; Hasenjager et al., 2020a). I then compared the total Akaike weights of each model (i.e., the model with bias, no bias, or transmission only) to determine which was best supported for each transmission bias pathway.

Behaviors During Learning

To understand the rates of behaviors during learning, I constructed three multilevel multivariate Poisson models (i.e., a model that had three response variables, each with identical predictor variables), using a Bayesian framework using the package "brms" (Bürkner, 2017) in R 3.5.2 (R Core Team, 2018). As in the previous chapter's analyses, all models included weakly informative priors (mean = 0, SD=1), and the residual assumptions for each dataset were evaluated using the "DHARMa" package (Hartig, 2017). All datasets met model assumptions.

These models were constructed identically to those in the previous chapter while using the experimental data gathered here, with the substitution of Normalized

Differentiated Vegetation Index (NDVI) for water availability, because this was a task that involved food rather than water, and because water availability remained constant for each troop during this study. Counts of looking at others interacting with the box, probing a non-baited tube, and eating gum extracted from the box served as the response variable in each model as appropriate. Age/sex category, rank, betweenness centrality in the grooming network, betweenness centrality in the proximity network, strength centrality in the grooming network, strength centrality in the proximity network, NDVI, and novel food neophilia rating served as predictor variables. Animal ID, troop membership, and trial ID were entered as group-level variables (i.e., random effects). To account for differences in exposure to the experiment, the duration of each trial was entered as an offset variable. Sample sizes varied with respect to the variables included in each analysis.

6.3 Results

I ran 83 trials. Five were unsuccessful, and 16 were ignored. A total of 93 animals ($N_{RST} = 23$, $N_{RBM} = 35$, $N_{PT} = 35$) participated across the trials, and 26 animals solved the task ($N_{RST} = 8$, $N_{RBM} = 15$, $N_{PT} = 3$. Table 6.1). I found overwhelming support for social transmission as compared to asocial transmission ($\sum wi = 0.97$), indicating that animals used social learning to solve the task.

6.3.1 Information Diffusion

Approximately 24.46% of learning events followed the co-presence network, and there was little support that learning events followed the visual observation network (Table 6.4). I also found no evidence that the networks had interactive effects.

Table 6.4

Diffusion Through the Observation Networks

Parameter	Model-Averaged Estimate (95% CIs)	Backtransformed Effect (95% CIs)	Akaike Weight	ΔAIC
Looking Network	0.002 (lower: 0.00)	0.00 (0.00)*	0.066	4.400
Co-Presence Network	8.827E03 (lower: 105.336)	24.462 (25.058)*	0.593	0.000
ILVs Asocial Transmission				
Sex (Females)	-0.489 (-1.642, 0.766)		0.593	0.000
Inverse Dominance Rank	0.125 (-0.182, 1.13)		0.169	2.513
Inverse Neophilia Score	-0.062 (-.897, 0.040)		0.049	5.006
Inverse Exposure	-0.878 (-1.246, -0.569)	0.415 (0.288, 0.566) *2.408 (1.767, 3.476)†*	0.593	0.000
ILVs Social Transmission				
Sex (Females)	-4.937 (-11.589, 0.421)		0.593	0.000
Inverse Dominance Rank	-18.346 (-31.899, -7.763)	1.077E-08 (1.401E-14, 4.230E-04) *9.285E+07 (2.353E+03, 7.136E+13)†*	0.593	0.000
Inverse Neophilia Score	-15.911 (-28.500, -5.978)	1.23E-07 (4.192E-13, 2.534E-03) *8.131E+06 (3.946E+02, 2.386E+12) †*	0.593	0.000

Note. All continuous variables were inverted to assist with model fit (see main text). Shaded rows indicate variables that received at least 50% support. Age is relative to juveniles; sex is relative to males. Estimates are on the log scale; CI = certainty interval. MAEs and lower CIs for network estimates are conditioned on the models constrained to that network.

*Backtransformed effects for network estimates represent the percentages of events transmitted socially using the best performing model, with the average percentage of events from all models with that network in parentheses.

†Back-transformations relative to the non-inverted variable (see main text). For example, as exposure increased, the rate of social transmission increased by a factor of 2.408.

Rank and Social Transmission. As in the water patch experiment, higher-ranking animals were more likely to use social information to solve the task (Table 6.4).

Neophilia and Social Transmission. Neophilia was very highly correlated with social transmission in this task, rather than with personal information, as found in the water patch experiment (Table 6.4).

Sex and Social Transmission. There was no difference in social information use by males and females (Table 6.4).

Neophilia and Personal Information. I found no evidence that neophilia influenced asocial learning. Similar to the results in the previous chapter, animals that were more exposed to the task were also more likely to use personal information (Table 6.4).

6.3.2 Transmission Biases

I found no evidence of bias in transmission with respect to the sex of the solver (support for no bias = 91.44%), dominance rank (support for no bias = 56.74%), or

Table 6.5

Transmission Pathway Biases

Transmission Pathway Hypothesis	Support (%)
Kinship	
No Bias	86.3
Between Siblings	11.5
Asocial Transmission	2.2
Neophilia	
No Bias	41.0
More to Less Neophilic Only	0.5
Less to More Neophilic Only	43.5
Unequal Rates	13.9
Asocial Transmission	1.0
Rank	
No Bias	56.5
Higher to Lower-ranking Only	33.8
Lower to Higher-ranking Only	0.7
Unequal Rates	7.6
Asocial Transmission	1.4
Sex	
No Bias	91.4
Unequal Rates	6.2
Asocial Transmission	2.3

Note. Total support represents the total Akaike weight for the model constrained for that hypothesis.

kinship (support for no bias = 86.34%; Table 6.5). For neophilia, the largest total Akaike weight favored models representing a bias from animals with lower measures of neophilia to animals of higher levels of neophilia (support for bias = 43.54%), but this was only slightly higher than the models representing no bias, which received 41.04% of the total support (Table 6.5).

6.3.3 Behaviors During Learning

In all, 93 animals participated in the task; 52 looked at others interacting with the box, 24 probed a non-baited tube, and 26 ate gum that they had extracted from the box. The correlated varying effects revealed correlation in animal ID for probing and eating (Table 6.6a).

Table 6.6a

Correlated Varying Effects of Animal ID Across All Models

Models	Correlation	Estimate Error	Lower 95 CI	Upper 95 CI
Acquire & Apply	0.232	0.220	-0.228	0.626
Acquire & Exploit	-0.135	0.221	-0.543	0.308
Apply & Exploit	0.844	0.075	0.655	0.949

Note. CI = credible interval.

There was considerable variation in each model with regard to the grouping variables—looking varied considerably by trial and animal ID, and somewhat by troop (Table 6.6b-d). Probing a non-baited tube and eating varied largely by trial, animal ID, and troop.

Individual Attributes and Looking, Probing, and Eating

Looking. Dominance rank was negatively correlated with looking—higher

Table 6.6b

Posterior Estimates Rates of Looking at Another

Effect	Parameter	Estimate	Est. Error	Lower 95 CI	Upper 95 CI	pd (%)
Population -Level Effects	Intercept (Adult Females)	-1.093	1.109	-3.272	1.042	83.15
	Adult Males	1.001	0.601	-0.200	2.148	94.80
	Juvenile Females	0.383	0.465	-0.543	1.311	80.11
	Juvenile Males	0.583	0.486	-0.403	1.526	88.48
	Novel Food Neophilia	-0.048	0.147	-0.343	0.238	62.76
	Dominance Rank	-0.487	0.166	-0.816	-0.160	99.84
	Troop-level Resource Availability	0.288	0.231	-0.159	0.737	89.69
	Grooming Degree Strength	0.273	0.232	-0.186	0.730	88.20
	Spatial Proximity Degree Strength	-0.004	0.155	-0.300	0.313	52.24
	Grooming Betweenness	-0.283	0.200	-0.683	0.100	92.09
	Spatial Proximity Betweenness	0.013	0.188	-0.371	0.373	54.13
Group-Level Effects	sd(Troop:ID)	0.598	0.146	0.336	0.908	100.00
	sd(Trial ID)	1.203	0.197	0.879	1.643	100.00
	sd(Troop)	7.188	2.739	3.658	13.959	100.00

Note. Age-sex is relative to adult females. Estimates are on the log scale; CI = credible interval, SD = standard deviation, pd = probability of direction. N = 393. LOO-adjusted R^2 = 0.333.

ranking animals were less likely to look at other animals interacting with the box (Table 6.6b; Figure 6.5). There was no evidence that looking varied by age/sex, neophilia, or social network position (Table 6.6b).

Probing. Neophilia was positively correlated with probing a non-baited tube (Table 6.6c; Figure 6.6). There was no evidence that probing varied by age/sex, dominance rank, or social network position (Table 6.6c).

Eating. Unlike the result in the previous chapter, higher-ranking animals solved the task (i.e., ate) at higher rates than lower-ranking animals (Table 6.6c; Figure 6.7). More neophilic animals also solved the box task at higher rates compared to less neophilic animals (Table 6.6d; Figure 6.8). There was no evidence that eating varied by

Table 6.6c

Posterior Estimates Rates of Probing a Non-baited Tube

Effect	Parameter	Estimate	Est. Error	Lower 95 CI	Upper 95 CI	pd (%)
Population-Level Effects	Intercept (Adult Females)	-1.015	1.132	-3.255	1.219	81.49
	Adult Males	-0.619	0.872	-2.363	1.033	75.66
	Juvenile Females	0.619	0.689	-0.753	1.967	81.79
	Juvenile Males	0.828	0.735	-0.647	2.260	86.98
	Novel Food Neophilia	0.722	0.305	0.145	1.345	99.26
	Dominance Rank	0.249	0.277	-0.303	0.803	81.75
	Troop-level Resource Availability	0.051	0.182	-0.312	0.414	61.56
	Grooming Degree Strength	-0.644	0.452	-1.551	0.227	92.86
	Spatial Proximity Degree Strength	0.385	0.319	-0.235	1.018	88.83
	Grooming Betweenness	-0.131	0.430	-1.011	0.695	61.04
	Spatial Proximity Betweenness	-0.720	0.415	-1.574	0.070	96.16
Group-Level Effects	sd(Troop:ID)	1.910	0.383	1.272	2.786	100.00
	sd(Trial ID)	0.816	0.172	0.527	1.193	100.00
	sd(Troop)	9.112	3.294	4.843	17.210	100.00

Note. Age-sex is relative to adult females. Estimates are on the log scale; CI = credible interval, SD = standard deviation. N = 393. LOO-adjusted $R^2 = 0.279$.

age/sex or social network position (Table 6.6d).

Local Ecologies and Looking, Probing, and Eating

There was no evidence that looking, probing, or eating was influenced by troop-level estimates of resource availability (Table 6.6b-d).

6.4 Discussion

As with the water patch task, there was overwhelming evidence that information followed the co-presence and not the visual observation network, and I found no evidence that information that followed the co-presence network was biased in regard to rank, sex, kinship, or neophilia. Contrary to my predictions, animals were not more likely to use social information than they were in the water patch experiment, despite the increased difficulty of the task—approximately 24.46% of learning events were acquired via social

Table 6.6d

Posterior Estimates Rates of Eating Extracted Gum

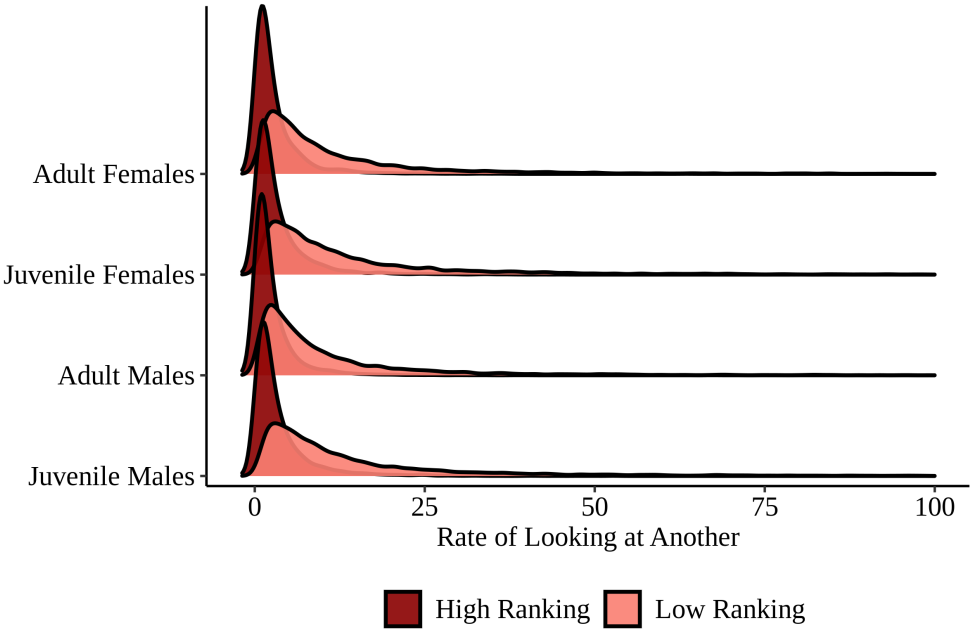
Effect	Parameter	Estimate	Est. Error	Lower 95 CI	Upper 95 CI	pd (%)
Population -Level Effects	Intercept (Adult Females)	-1.132	1.149	-3.372	1.143	84.24
	Adult Males	-0.900	0.899	-2.670	0.830	84.24
	Juvenile Females	1.204	0.785	-0.350	2.716	94.13
	Juvenile Males	0.614	0.806	-0.956	2.176	77.35
	Novel Food Neophilia	1.430	0.502	0.473	2.423	99.74
	Dominance Rank	1.469	0.216	1.059	1.902	100.00
	Troop-level Resource Availability	-0.162	0.265	-0.685	0.357	73.59
	Grooming Degree Strength	-0.699	0.629	-1.922	0.573	87.08
	Spatial Proximity Degree Strength	0.002	0.502	-0.995	0.989	50.10
	Grooming Betweenness	-0.408	0.592	-1.612	0.722	74.95
	Spatial Proximity Betweenness	-0.517	0.524	-1.559	0.530	84.13
Group-Level Effects	sd(Troop:ID)	3.542	0.616	2.522	4.989	100.00
	sd(Trial ID)	1.565	0.235	1.173	2.095	100.00
	sd(Troop)	9.528	3.570	5.048	18.099	100.00

Note. Age-sex is relative to adult females. Estimates are on the log scale; CI = credible interval, SD = standard deviation, pd = probability of direction. N = 393. LOO-adjusted R^2 = 0.401.

transmission, virtually identical to the 25.94% of events via social transmission in the water patch task. However, there are two lines of evidence that the social transmission during this task differed from that in the previous chapter. The first is that more neophilic animals were more likely to probe and eat gum from the novel gum box, much as they were more likely to enter the water patch and drink from it. Nevertheless, while more neophilic animals relied on social information in the water patch task, they were much more likely to use social information here. Previous work has also found that personality correlates with information use. However, this work hypothesized that more neophilic animals would rely more on personal information and exploration (Smit & van Oers, 2019); a hypothesis that, though consistent with the findings is the previous chapter, is not

Figure 6.5

Rates of Looking at Others Eating Gum From the Artificial Gum Box by Rank



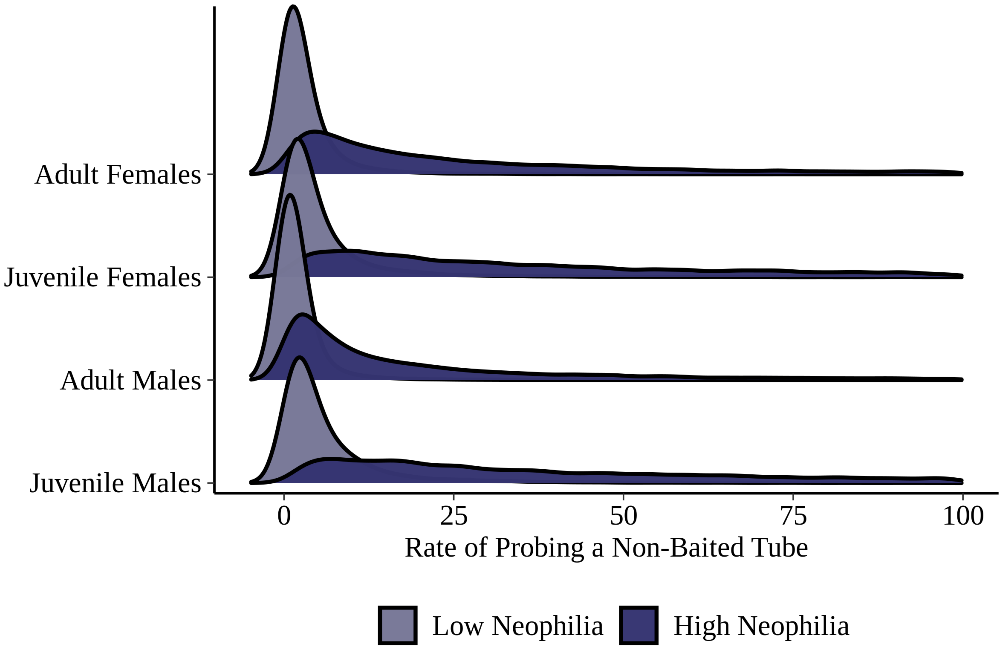
*Note.*Density plots present the range of rates predicted by the model, with the height of the density curve indicating the predicted rate, and the spread of the curve indicating its uncertainty (see Table 6.6b). Rates are backtransformed from the log scale into the original scale. In this context, rate refers to the average number of looks per trial as determined by the model marginal means.

borne out here. Hasenjager et al. (2020b) also found no relationship between boldness and personal information use, but that boldness influenced social transmission, dependent on the personality composition of the group. Additionally, MacGregor et al. (2021) found that consistency in personality measures differed between foraging and non-foraging contexts, demonstrating the importance of context in personality expression.

It is likely that the personality effects on social transmission here were influenced by social context. For example, Hasenjager et al. (2020b) found that the boldness of demonstrators and observers influenced social transmission in guppies, dependent on the

Figure 6.6

Rates of Probing a Non-Baited Tube by Neophilia

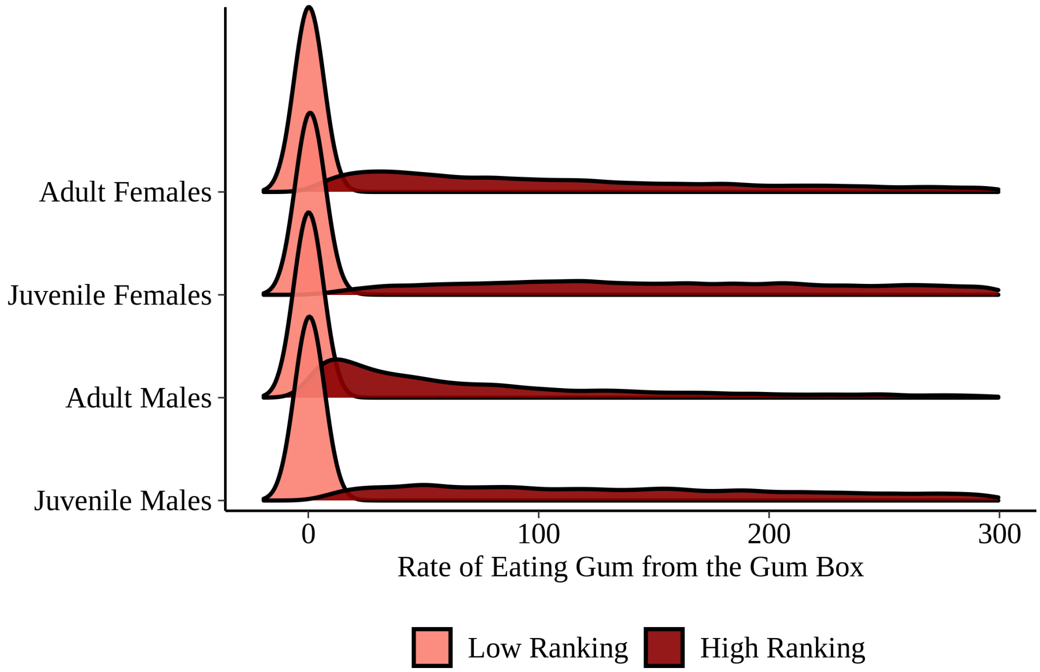


Note. Density plots present the range of rates predicted by the model, with the height of the density curve indicating the predicted rate, and the spread of the curve indicating its uncertainty (see Table 6.6c). Rates are backtransformed from the log scale into the original scale. In this context, rate refers to the average number of probes of a non-baited tube per trial as determined by the model marginal means.

personality composition of the group—the boldness of the observer mattered for social transmission in groups dominated by bold individuals, whereas the boldness of the demonstrator mattered for social transmission in groups dominated by shy individuals. It is unlikely that the personality composition of my groups differed between the experiments, as the experiments overlapped in time and neophilia was repeatable (Chapter 4). However, social context may have played a role, as I previously found that animals with partners within 2 m were more likely to eat the novel food during novel food tests, i.e., there was a social facilitation effect. Social facilitation may also have

Figure 6.7

Rates of Eating Gum From the Artificial Gum Box

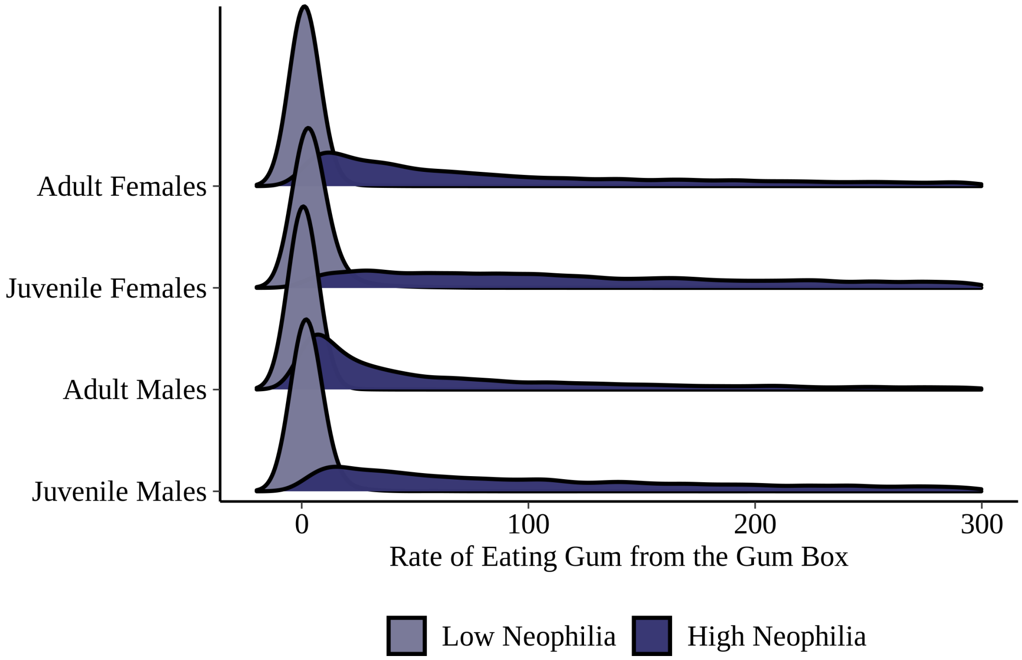


Note. Density plots present the range of rates predicted by the model, with the height of the density curve indicating the predicted rate, and the spread of the curve indicating its uncertainty (see Table 6.6d). Rates are backtransformed from the log scale into the original scale. In this context, rate refers to the average number of times an animal ate gum per trial as determined by the model marginal means.

influenced the ability of more neophilic animals to use social information here. For example, animals not only had to be willing to approach the novel gum box, but also willing to interact with it (i.e., probe the tubes) in order to successfully extract food. Thus, given that the gum box task was more difficult, and that more neophilic animals were more likely to use social information to solve it, it is probable that personality interacted with task difficulty. Furthermore, more neophilic animals presumably had more opportunities to use social learning here compared to the water patch experiment given

Figure 6.8

Rates of Eating Gum From the Artificial Gum Box by Neophilia



Note. Density plots present the range of rates predicted by the model, with the height of the density curve indicating the predicted rate, and the spread of the curve indicating its uncertainty (see Table 6.6d). Rates are backtransformed from the log scale into the original scale. In this context, rate refers to the average number of times an animal ate gum per trial as determined by the model marginal means.

that neophilia is socially facilitated, and that social transmission overwhelmingly followed the co-presence network. That is, more neophilic animals interacted with the gum box more, and were even more likely to do so if others were around, thereby increasing the likelihood that they would be around others when learning how to solve the box and could therefore capitalize on available social information.

The second line of evidence that social transmission was influenced by task difficulty is that only one adult solved the gum box task, despite no evidence that age influenced rates of behaviors during learning. As only one adult solved the task (a young female who had reached sexual maturity about a year prior to the experiment), I could not model the effect of age on social transmission, i.e., whether or not certain ages were more or less likely to use personal or social information to solve the gum box. However, that only one adult female solved the task does offer some insight to the unwillingness of adults to engage with novel gum box, particularly adult males, who were also more likely to ignore novel foods during the novel food tests compared to adult females. As mentioned in the previous chapter, Carter et al. (2016) expected juveniles to use social information more than adults in their task but found no age differences. Carter et al. (2016) suggested that their lack of finding might be due to a lack of task difficulty or sufficient novelty, a finding supported by these results. That is, only juveniles participated in this more difficult and novel task, suggesting that juveniles may be more inclined to innovate, consistent with previous findings that juveniles show a greater propensity for social learning compared to adults (Carter et al., 2014; Thornton & Malapert, 2009), as juveniles are often more curious and exploratory.

Do Individual Attributes and Behaviors During Learning Describe Social Transmission?

I again found that individual attributes and rates of specific behaviors during learning did not independently describe social transmission. The attributes that described which animals engaged in probing a non-baited tube at higher rates (i.e., neophilia) and eating extracted gum at higher rates (neophilia and dominance rank) more closely mapped on to the attributes of animals that used social transmission during this task, as compared to the water patch task. Consequently, these data further illustrate the importance of considering the context of the learning episode in understanding how animals learn from others, insofar as they only make sense in light of the context of the task. For example, if I were to consider attributes alone, it may seem contradictory that neophilia correlated with personal information use in the water patch task, but with social information use in the gum box task. Being more neophilic in general was sufficient to access water patch information—there was no real need to rely on others, and thus neophilia correlated with personal information use during the novel water patch task. However, simply interacting with the gum box did not necessarily mean that animals could solve it, and being more neophilic was therefore not sufficient on its own. Instead, the gum box presented a unique opportunity for more neophilic animals to gain social information because not only were they more likely to interact with the task, their likelihood of doing so increased when more animals were around—if those other animals were also solving the gum box, more neophilic animals could both gain social information and use it to their immediate advantage, benefitting from both behavioral matching (Schuppli et al., 2016) and selective practice (van de Waal et al., 2012). Thus, only after understanding that the gum box task had more degrees of novelty that the water patch task, was more difficult to solve, and the interactive effects between neophilia, social context, and the co-presence network, do these data inform how neophilia likely benefitted social transmission.

6.5 Limitations

Similar to the previous chapter, I developed my measures here without fully considering the makeup of my own dataset. Thus, I again used gaze although I did not think it was very reliable, and I do not know if co-presence was either more reliable than visual observation, or capturing some other relevant factor of social transmission.

CHAPTER 7: GENERAL DISCUSSION

In this thesis, I used a behavior analytic approach in an effort to explain the social learning abilities of wild vervet monkeys. In Chapter 1, I identified three specific areas of social learning that could benefit from using a behavior analytic framework. Here, I summarize the outcomes and then reflect on the limitations of my study, and conclude by discussing future research directions.

7.1 Available Transmission Pathways

The first area of social learning research I considered to be ripe for a behavior analytic approach was the identification of potential transmission pathways between animals. To this end, I investigated whether or not muzzle contact between vervets might provide a direct route of transmission about food. As expected, animals gained social information from muzzle contact, but I found no evidence that this behavior has developed expressly for novel information acquisition. Although muzzle contact potentially could enable the transmission of food-related information, I found that social tolerance was a better predictor of muzzle contact than any particular knowledge of the world that recipients might possess.

While muzzle contact can indeed afford information transfer, social transmission did not follow muzzle contacts during the water patch experiment. Why might this be the case? Perhaps animals may have relied more on muzzle contact had the task used a novel food rather than water. Unfortunately, I did not consider the muzzle contact network for the box task, which did include a novel food, as there was absolutely no evidence that transmission followed muzzle contacts for the water patch task. However, it is unlikely that a muzzle contact observation network would have provided much explanatory power for social transmission during the novel gum box, as muzzle contact frequencies during the experiment were very low ($N_{RBM} = 32$, $N_{RST} = 28$, $N_{PT} = 4$). Thus, the results from the novel water patch experiment further exemplifies the general muzzle contact findings in Chapter 3—that muzzle contact is an available transmission pathway, but is not predominantly used for information transfer.

There was also little evidence that vervets who frequently interacted with one another, as measured by stable grooming and spatial proximity networks, were more likely to learn from one another, at least when it came to learning about the novel water patch. Instead, social transmission best followed the co-presence network, measured by those who were within an arm's reach of the task while another was successfully exploiting it. I included a co-presence network in both tasks because I could clearly observe it, and because I was concerned that empirical limitations on the estimation of gaze direction would constrain the ability of visual observation networks to capture social learning opportunities. Indeed, gaze had the lowest reliability of all of the behaviors measured during both tasks, whereas patch presence (from which the co-presence networks were constructed) was very reliable. Thus, while I have no evidence that social transmission during either the water patch or gum box tasks followed visual observation as I measured it, I do not have enough evidence to conclude that visual observation wasn't sufficient for social transmission. This was so for two main reasons. The first, which I have already mentioned, is that gaze estimation was unreliable, and thus it is possible that my visual observation networks did not actually capture gaze between uninformed and informed animals. The second is that although the co-presence and visual observation networks were coded as mutually exclusive, they may not be. I did not record gaze while animals were co-present in the patches because the close proximity (<0.5-m) of animals to one another made it difficult to detect. Thus, it is possible that the co-presence networks were actually capturing relevant visual observations. If so, my results would be consistent with Canteloup et al. (2020), who found that social transmission did follow visual observation for their population of vervets, as they were able to record gazes when animals were in contact with their task.

It is also possible that the co-presence networks captured something of additional relevance to social learning beyond visual observation, such as a willingness to approach a task when others were around, thereby serving as an index of social tolerance within novel situations. It is obviously necessary that animals need to be near others in order to learn from them, so it is not surprising that social transmission followed co-presence. But the question here is whether or not spatial proximity during the task (or visual observation, for that matter) was sufficient for social learning. High levels of social tolerance (e.g., animals that can be within an arm's reach of one another, or closer), as was observed when animals were co-present, is likely to confer additional advantages beyond observational opportunities compared to social tolerance at longer distances. Selective practice describes situations where social learners can immediately practice their newly acquired skills after observing others engaging in them (Schuppli et al., 2016). The co-presence network not only measured close proximity between demonstrators and learners, but also measured when they were within-touching distance of the task. Thus, co-present animals could both closely observe demonstrators solving the task and then immediately try out the behavior themselves. That is, if animals could put their social knowledge into action immediately, they were likely to experience the same consequences available to demonstrators, thus reinforcing the socially transmitted solution, as well as that that it paid off to closely observe others.

By analyzing both affiliative (i.e., grooming and proximity) and observation (i.e., muzzle contact, visual observation, and co-presence) networks, I was able to use NBDA to consider how social relationships might correlate with social transmission. Ideally, had grooming or proximity relationships predicted transmission, I could then have compared the structure of these networks to the co-presence networks in order to determine precisely which aspects of social structure afforded transmission. My results indicated, however, that social learning was best described as opportunistic: social learning did not follow specific interaction modalities (e.g., grooming, proximity, looking, or muzzle contact) but followed instead from close proximity to the demonstrator, as well as to the task. Animals had to be highly tolerated by others *while near the task* in order to both gain relevant social information and then use it, and such tolerance was not predicted by overall social affiliation.

Additionally, Canteloup et al's (2020) finding that transmission followed visual observation, of which I found no evidence, may also reflect the fact that the troops in Canteloup et al. (2020) were much smaller than those studied here, and may have been more socially constrained in who they could observe. That is, it may have been easier for animals in their smaller groups to monopolize the task and thus only resulting in a biased transmission pathway. That is, if the animals in Canteloup et al. (2020) were more likely to be displaced by higher-ranking animals during their experiment, lower-ranking animals may have learned to wait while the higher-ranking animals accessed the boxes, and took their turns only after the higher-ranking animals were through, much like the small groups in Fruteau, van Damme, and Nöe's (2013) "forbidden circle game." For example, while Canteloup et al. (2020) found that animals were biased to learn from high-ranking animals to open a two-action box, I found no evidence for any biases in transmission pathways, perhaps because my larger groups were less socially constrained by rank (Henzi et al., 2013). Canteloup et al. (2020) found that higher-ranking animals both manipulated their task more and succeeded at their task more than lower-ranking animals, raising the possibility that their animals actually had more opportunities to observe higher-ranking animals solving their task. However, they presented multiple boxes concurrently, which reduced the likelihood that animals could monopolize the task, finding no difference in observing rates of higher-ranking animals compared lower-ranking animals. Thus, animals appeared to observe solvers of all ranks at equal rates, but social transmission was biased towards observing higher-ranking animals, meaning that there was something different in the observations of higher-ranking animals compared to lower-ranking ones. Just *what* this difference was is unclear, but, as I explain below, could be due to learning histories.

I found no such bias for transmission with regard to rank for my gum box task, despite finding that higher-ranking animals solved the box at higher rates than lower-ranking animals. Given the fact that large troop sizes have been shown to influence social dynamics, it is possible that the vervets in my study were not as constrained in their social behavior compared to those in smaller groups, meaning they could easily monopolize the single box I provided and thus constrained in the social pathways through which they could gain food information. For example, while higher-ranking animals may have been better able to supplant others at the box and thereby capitalize on social information, their less-restricted rank-related social behaviors (Henzi et al., 2013) meant that others did not benefit from biasing attention towards them. If rank does not constrain the social behavior of these vervets, animals need not attend selectively to higher-ranking animals in order to gain relevant social information. That is, higher-ranking animals in large groups do not often access resources significantly more than lower-ranking animals, and do not pose as much of a social threat, compared to those in smaller groups.

7.2 Social Dynamics and Social Learning

Coussi-Korbel and Fragaszy (1995) argued that social proximity is the most appropriate metric for characterizing social dynamics. Social proximity is also a measure of social tolerance, and social tolerance can benefit primates in a number of ways, including the ability to access shared feeding and watering sites (Kummer, 1978; Li et al., 2021; Seyfarth & Cheney, 1984), to learn how to exploit novel food sources (van de Waal et al., 2012), and to learn species-typical behaviors (Schuppli et al., 2016). Indeed, tolerance is an important commodity in biological markets—subordinate individuals can trade grooming for tolerance from dominant individuals (Borgeaud & Bshary, 2015; Fairbanks, 1980; Silk, 1982), including around their infants (Muroyama, 1994). Flexibility in social tolerance may also allow primates to vary in their social dynamics despite strong conservatism in their social organization (Barrett et al., 2013; Schradin, 2013; van Schaik, 2013), illustrating the importance of considering social dynamics at the level at which they occur—between individuals (Barrett et al., 1999).

Thus, the second area I identified as benefitting from a more behavior analytic approach to social learning was social dynamics. It is clear that high social tolerance underpinned many of the possible transmission routes seen in this study, from muzzle contact to co-presence. However, being tolerated was not the only means by which animals could succeed. Similar to Li et al. (2021), who found that vervets equally benefitted from being either tolerated or higher-ranking at novel food patches, I found that in addition to social tolerance, dominance ranking influenced social transmission, as higher-ranking animals learned via transmission at higher rates than lower-ranking animals during both tasks. Li et al. (2021) explained that by mostly foraging on highly dispersed resources, being high-ranking is not as beneficial to vervets in accessing foods as it might be for animals that subsist on patchy resources that can be monopolized. They also found that it paid to be tolerated or high-ranking, but only for a resource that could be monopolized. Consequently, drinking rates were not influenced by dominance rankings.

However, I did find that vervets could realize the benefits of being high-ranking when resources are monopolizable, should the opportunity arise—high-ranking animals ate gum from the box at much higher rates than lower-ranking animals. One important difference between my gum box and water patch experiments is that adults only rarely participated in the gum box task. Perhaps juveniles were more flexible in their foraging strategies, and could learn to capitalize on environmental changes that presented a resource that could be monopolized. This could also be why Canteloup et al. (2020) found a rank-based transmission bias—perhaps their animals, being in smaller, rank-restricted groups, and having extensive histories with foraging experiments (e.g., Bono et al., 2018; Botting et al., 2018; van de Waal et al., 2013; van de Waal et al., 2015; van de Waal et al., 2017), had developed rank-based social learning strategies that my animals had not. Furthermore, the animals in Canteloup et al. (2020) relied more heavily on social transmission in their tasks compared to mine, perhaps because gathering personal information was too costly in their smaller social groups, if their animal's social behavior was more restricted by rank (Fruteau et al., 2013; Henzi et al., 2013). If so, the social learning found by Canteloup et al. (2020) could actually be untransmitted social effects (Atton et al., 2012; Hasenjager et al., 2020) rather than social transmission *per se*, as animals would have only solved the task at similar times because they encountered it within the same timeframe. This is why I included a measure of task exposure in both of my diffusion analyses, as task exposure can account for untransmitted social effects (Hasenjager et al., 2020).

Finally, it is also clear that social facilitation was a relevant social dynamic at play during learning. My neophilia findings clearly showed that willingness to engage with novelty increased in the presence of others, and that this effect was positively associated with the number of partners. Furthermore, social transmission during the more difficult gum box task was also likely to have benefitted from social facilitation, as animals had to be near others in order to witness solvers probe the appropriate color, and thus may have been more likely to interact with the task. Thus, understanding social context was key to understanding learning, especially for situations involving novelty (more below). To learn socially, social information had to be available within specific social contexts—when a potential demonstrator was willing to approach a task, interact with it, and allow learners to be socially proximate.

7.3 Individual Differences and Social Learning

The final area I identified as ripe for a behavior analytic approach to social learning was individual differences. My goal here was to develop a measure that could predict how individuals would learn, and I was successful—my neophilia measure predicted performance in both tasks. My approach of using the results from my model of responses to the novel food to estimate the probability that an individual would eat the novel food, rather than using random intercepts allowed me to estimate variation beyond individual attributes, like age and sex (c.f., Dingemanse & Dochtermann, 2013; Nussey et al., 2007). My modeling approach also allowed me to control statistically for factors that I couldn't control when running the experiments, namely social context. That I couldn't test animals only when they were alone paid off, however, because I found that neophilia was dependent on social context, presenting the possibility that similar factors could have been at play during the experiments. Furthermore, given that I found social facilitation, but not response facilitation, during the novel food tests means that the effect of increased neophilia does not rely on the behavior of the social partners, but requires only their spatial proximity. While response facilitation may seem more directly related to social learning, social facilitation may allow animals to be more flexible and respond opportunistically with either asocial or social learning, as appropriate. According to Greenberg (2003), the tendency to approach a novel situation is a necessary, but not sufficient, condition in the development of innovative behavior—animals must not only be willing to approach novel situations, but be able to learn from them, i.e., engage in trial-and-error learning. Indeed, I found that more neophilic animals were more likely to enter the water patch, and probe a non-baited gum box tube compared to less neophilic animals, and exploited both tasks at higher rates. However, neophilia could not alone explain how animals learned, as more neophilic animals relied on asocial learning to solve the water patch, but on social learning to solve the gum box.

The gum box task was rife with novelty that likely afforded engagement for more neophilic animals: the box itself, the orange juice flavored gum it contained, and its requirement for a behavior that is more likely to be performed while arboreal—probing for gum—while on the ground. That more neophilic animals used social transmission to solve the gum box, coupled with the fact that eating novel foods was socially facilitated during the novel food tests, suggests that they may have benefited from a similar social facilitation effect during the gum box task. In other words, it is true that more neophilic animals were more likely to engage with the gum box compared to less neophilic animals. If it was also true that they engaged with the gum box more when others were around, as found during the novel food tests, then there would a clear explanation as to why more neophilic animals used social transmission during the gum box task—they were more likely to approach it, and, as previously explained, could capitalize on the benefits of learning from others in close proximity, possibilities that the gum box afforded more than did the water patch.

Taken together, these findings reveal that vervets could vary how they learned depending on the situation presented to them, and that this variation could partially be explained by consistent interindividual differences in neophilia. However, it is also clear that measuring consistent interindividual differences in one behavior (e.g., neophilia towards novel foods) was not sufficient to predict exactly how animals would respond to learning opportunities. It is also imperative to know the context of the learning scenario—neophilia afforded asocial learning in the water patch task, and social learning in the gum box task. Strum et al. (1997) also argued for expanding the unit of analysis for cognition beyond the individual to one that situates the organism within its environment, arguing that social strategies, like the consort behavior of olive baboons (*Papio anubis*), is best understood alongside environmental contingencies, rather than as strategies that covary with specific attributes. Strum et al. (1997) also emphasized the fact that cognition can be distributed across the environment, meaning that cognition should include not only the behavior of individual animals, but also their interactions with one another and their environments. This was clearly the case for the neophilic animals in my experiments, as their behavior was in accordance with what the social environment provided, relying on social learning when they had access to social information within the appropriate social contexts.

7.4 Limitations and Future Directions

7.4.1 Early Infant Experiences

One crucial limitation to my study is that it often did not include observations of animals less than six months of age (hereafter “infants”) because all of my analyses included the individual-level measures of sex and rank, which were difficult to obtain from infants. Learning what to eat (and what to avoid) is essential to gaining foraging independence during primate ontogeny, and infants do so from others, especially their mothers (Hauser, 1993; Hauser, 1994; King, 1994a; Lycett & Henzi, 1992; van de Waal et al., 2012; van de Waal et al., 2014). For example, older juveniles muzzle contacted kin at lower rates than did younger juveniles, suggesting that muzzle contact may function differently throughout ontogeny (more below)—infants may rely more on muzzle contact as a means of information acquisition compared to older animals (King, 1994b). As such, there is likely much insight to be gained by viewing social learning through the eyes of very young primates.

7.4.2 Muzzle Contact and Social Dynamics

My findings in Chapter 3 suggest that muzzle contact might also serve a social function. Given that I found that muzzle contacts occurred within a foraging context only half of the time, there remains a possibility that muzzle contact functions as an affiliative behavior beyond affording information acquisition. Older juveniles were also less likely to contact kin than were younger juveniles, suggesting that juveniles may use muzzle contact to learn who in the group they can safely approach. As mentioned in the discussion of Chapter 3, muzzle contact might also function as a way for juveniles to integrate themselves into the social group beyond their kin as they age (Jarrett et al., 2018). Thus, questions remain as to how muzzle contact relates to the troop’s overall social dynamics and whether exploring it could help identify possible social affiliative functions.

7.4.3 Simple Vs. Complex Contagion

Another limitation is that all of my social transmission analyses assumed that behavior diffuses through social networks based on its total connections. For example, NBDA estimates the likelihood that social transmission follows a social network by assuming that the likelihood that animals adopt a behavior is based on the total amount of relevant network connections to informed animals (Hasenjager et al., 2020; Hoppitt, 2017). This assumption is analogous to how disease spreads via contacts to infected individuals, and is known as “simple contagion” (Centola & Macy, 2007; Firth, 2019). However, behavior does not always spread like a disease—animals do not always adopt the behavior of others simply because they have witnessed others engaging in it. Behavior spread is likely more complex, dependent on being connected to multiple informed animals that can reinforce the adoption of the behavior, or related to the proportion of contacts to informed animals rather than to the absolute number of connections to them (Firth et al., 2020). Incorporating complex contagion concepts into social learning literature would contribute to the further understanding of social processes in general, as well as to the questions of which behaviors are socially transmitted and how social structure, network positions, interindividual differences influence them (Firth, 2019).

REFERENCES

Albers, P. C. H., & Vries, H. D. (2001). Elo-rating as a tool in the sequential estimation of dominance strengths. *Animal Behaviour*, *61*(2), 489-495. https://dspace.library.uu.nl/bitstream/handle/1874/17488/albers_01_elorating.pdf?sequence=1

Allegue, H., Araya-Ajoy, Y. G., Dingemanse, N. J., Dochtermann, N. A., Garamszegi, L. Z., Nakagawa, S., Réale, D., Schielzeth, H., & Westneat, D. F. (2017). Statistical Quantification of Individual Differences (SQuID): an educational and statistical tool for understanding multilevel phenotypic data in linear mixed models. *Methods in Ecology and Evolution*, *8*(2), 257-267. https://doi.org/10.1111/2041-210x.12659

Altmann, J. (1974). Observational Study of Behavior: Sampling Methods. *Behaviour*, *49*(3), 227-266. https://doi.org/10.1163/156853974x00534

Amici, F., Widdig, A., MacIntosh, A. J. J., Francés, V. B., Castellano-Navarro, A., Caicoya, A. L., Karimullah, K., Maulany, R. I., Ngakan, P. O., & Hamzah, A. S. (2020). Dominance style only partially predicts differences in neophobia and social tolerance over food in four macaque species. *Scientific Reports*, *10*(1), 1-10. https://doi.org/10.1038/s41598-020-79246-6

Antonovics, J., & van Tienderen, P. H. (1991). Ontoecogenophyloconstraints? The chaos of constraint terminology. *Trends in Ecology & Evolution*, *6*(5), 166-168. https://www.sciencedirect.com/science/article/pii/0169534791900597

Aplin, L. M., Farine, D. R., Mann, R. P., & Sheldon, B. C. (2014). Individual-level personality influences social foraging and collective behaviour in wild birds. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1789), 20141016. https://doi.org/10.1098/rspb.2014.1016

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015a). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature Publishing Group*, *518*(7540), 538-541. https://doi.org/10.1038/nature13998

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015). Counting conformity: Evaluating the units of information in frequency-dependent social learning. *Animal Behaviour*, *110*(2015), e5-e8. https://doi.org/10.1016/j.anbehav.2015.09.015

Aplin, L. M., Farine, D. R., Morand-Ferron, J., & Sheldon, B. C. (2012). Social networks predict patch discovery in a wild population of songbirds. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1745), 4199-4205. https://doi.org/10.1098/rspb.2012.1591

Aplin, L. M., Sheldon, B. C., & Morand-Ferron, J. (2013). Milk bottles revisited: Social learning and individual variation in the blue tit, *Cyanistes caeruleus*. *Animal Behaviour*, *85*(6), 1225-1232. https://doi.org/10.1016/j.anbehav.2013.03.009

Atton, N., Hoppitt, W. J. E., Webster, M. M., Galef, B. G., & Laland, K. N. (2012). Information flow through threespine stickleback networks without social transmission. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1745), 4272-4278. https://doi.org/10.1098/rspb.2012.1462

Baer, D. M., Wolf, M. M., & Risley, T. R. (1968). Some current dimensions of applied behavior analysis. *Journal of applied behavior analysis*, *1*, 91-97. https://www.ncbi.nlm.nih.gov/pmc/articles/PMC1310980/pdf/jab

Baer, D. M., Wolf, M. M., & Risley, T. R. (1987). Some still−current dimensions of applied behavior analysis. *Journal of Applied Behavior Analysis*, *20*(4), 313-327. https://onlinelibrary.wiley.com/doi/abs/10.1901/jaba.1987.20-313

Baldellou, M., & Adan, A. N. A. (1997). Time, gender, and seasonality in vervet activity: A chronobiological approach. *Primates*, *38*(1), 31-43.

Baracchi, D., Vasas, V., Jamshed Iqbal, S., & Alem, S. (2017). Foraging bumblebees use social cues more when the task is difficult. *Behavioral Ecology*, *29*(1), 186-192. https://doi.org/10.1093/beheco/arx143

Baron, R. S., Vandello, J. A., & Brunsman, B. (1996). The forgotten variable in conformity research: Impact of task importance on social influence. *Journal of personality and social psychology*, *71*(5), 915-927. https://psycnet.apa.org/record/1996-06593-006

Barrett, B. J., McElreath, R. L., & Perry, S. E. (2017). Pay-off-biased social learning underlies the diffusion of novel extractive foraging traditions in a wild primate. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1856), 20170358. https://doi.org/10.1101/110221

Barrett, L., Halliday, J., & Henzi, S. P. (2006). The ecology of motherhood: the structuring of lactation costs by chacma baboons. *Journal of Animal Ecology*, *75*(4), 875-886. https://doi.org/10.1111/j.1365-2656.2006.01105.x

Barrett, L. (2012). Why behaviorism isn’t satanism. In J. Vonk & T. K. Shackelford (Eds.), *The Oxford Handbook of Comparative Evolutionary Psychology* (pp. 17-38). Oxford University Press.

Barrett, L. (2011). *Beyond the Brain*. Princeton University Press.

Barrett, L., Blumstein, D. T., Clutton-Brock, T. H., & Kappeler, P. M. (2013). Taking note of Tinbergen, or: the promise of a biology of behaviour. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *368*(1618), 20120352. https://doi.org/10.1098/rstb.2012.0352

Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E., & Hill, R. A. (1999). Market forces predict grooming reciprocity in female baboons. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *266*(1420), 665-670. https://royalsocietypublishing.org/doi/abs/10.1098/rspb.1999.0687

Barton, R. A., Purvis, A., & Harvey, P. H. (1995). Evolutionary radiation of visual and olfactory brain systems in primates, bats and insectivores. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *348*(1326), 381-392. https://doi.org/10.1098/rstb.1995.0076

Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: A meta-analysis. *Animal Behaviour*, *77*(4), 771-783. https://doi.org/10.1016/j.anbehav.2008.12.022

Bergman, T. J., & Sheehan, M. J. (2013). Social knowledge and signals in primates. *American Journal of Primatology*, *75*(7), 683-694. https://doi.org/10.1002/ajp.22103

Bernard, C. (2012). *An Introduction to the Study of Experimental Medicine*. Courier Corporation.

Blaszczyk, M. B. (2017). Boldness towards novel objects predicts predator inspection in wild vervet monkeys. *Animal Behaviour*, *123*, 91-100. https://doi.org/10.1016/j.anbehav.2016.10.017

Blaszczyk, M. B. (2019). Primates got personality, too: Toward an integrative primatology of consistent individual differences in behavior. *Evolutionary Anthropology*, *29*(2), 56-67. https://doi.org/10.1002/evan.21808

Bonnell, T. R., Vilette, C., Young, C., Henzi, S. P., & Barrett, L. (2020). Formidable females redux: male social integration into female networks and the value of dynamic multilayer networks. *Current Zoology*, *67*(1), 49-57. https://doi.org/10.1093/cz/zoaa041/33543754/zoaa041.pdf

Bonnell, T. R., & Vilette, C. (2020). Constructing and analysing time−aggregated networks: The role of bootstrapping, permutation and simulation. *Methods in Ecology and Evolution*, *12*(1), 114-126. https://doi.org/10.1111/2041-210x.13351

Bono, A. E. J., Whiten, A., Schaik, C. V., Krützen, M., EichenBerger, F., Schnider, A., & van de Waal, E. (2018). Payoff-and sex-biased social learning interact in a wild primate population. *Current Biology*, *28*(17), 2800-2805. https://doi.org/10.1016/

j.cub.2018.06.015

Boogert, N. J., Nightingale, G. F., Hoppitt, W. J. E., & Laland, K. N. (2014). Perching but not foraging networks predict the spread of novel foraging skills in starlings. *Behavioural Processes*, *109*, 135-144. https://doi.org/10.1016/j.beproc.2014.08.016

Borgeaud, C., & Bshary, R. (2015). Wild vervet monkeys trade tolerance and specific coalitionary support for grooming in experimentally induced conflicts. *Current Biology*, *25*(22), 3011-3016. https://doi.org/10.1016/j.cub.2015.10.016

Botting, J., Whiten, A., Grampp, M., & van de Waal, E. (2018). Field experiments with wild primates reveal no consistent dominance-based bias in social learning. *Animal Behaviour*, *136*, 1-12. https://doi.org/10.1016/j.anbehav.2017.11.025

Bouton, M. E., & Balleine, B. W. (2019). Prediction and control of operant behavior: What you see is not all there is. *Behavior Analysis: Research and Practice*, *19*(2), 202-212. https://doi.org/10.1037/bar0000108

Boyd, R., & Richerson, P. J. (1985). *Culture and the Evolutionary Process*. University of Chicago Press.

Boyd, R., & Richerson, P. J. (1988). An evolutionary model of social learning: The effects of spatial and temporal variation Social Learning. In T. R. Zentall & B. G. Galef (Eds.), *Social learning: Psychological and Biological Perspectives* (pp. 29-48). Psychology Press. https://doi.org/10.4324/9781315801889-7

Boyd, R., & Richerson, P. J. (1996). Why culture is common, but cultural evolution is rare. *Proceedings of the British Academy*, *88*, 77-94.

Brent, L. J. N. (2015). Friends of friends: Are indirect connections in social networks important to animal behaviour. *Animal Behaviour*, *103*(C), 211-222. https://doi.org/10.1016/j.anbehav.2015.01.020

Brown, C., & Laland, K. N. (2003). Social learning in fishes: a review. *Fish and fisheries*, *4*(3), 280-288. https://onlinelibrary.wiley.com/doi/abs/10.1046/j.1467-2979.2003.00122.x

Burkart, J. M., Schubiger, M. N., & van Schaik, C. P. (2017). The evolution of general intelligence. *Behavioral and Brain Sciences*, *40*, 1-65. https://doi.org/10.1017/S0140525X16000959

Bürkner, P.-C. (2017a). Advanced Bayesian multilevel modeling with the R package brms. *arxiv preprint*, *arXiv:1705.11123*(1705.11123). https://arxiv.org/abs/1705.11123

Bürkner, P.-C. (2017b). brms: An R Package for Bayesian Multilevel Models Using Stan. *Journal of Statistical Software*, *80*(1). https://doi.org/10.18637/jss.v080.i01

Butynski, T. M. (1988). Guenon birth seasons and correlates with rainfall and food. In A. Gautier-Hion, F. Bourliere, J.-P. Gautier, & J. Kingdon (Eds.), *A Primate Radiation: Evolutionary Biology of the African Guenons* (pp. 284-322). Cambridge University Press.

Cambefort, J. P. (1981). A comparative study of culturally transmitted patterns of feeding habits in the chacma baboon *Papio ursinus* and the vervet monkey *Cercopithecus aethiops*. *Folia primatologica*, *28*(4), 1249-1254. https://doi.org/10.1016/S0003-3472(80)80113-8

Canteloup, C., Hoppitt, W., & van de Waal, E. (2020). Wild primates copy higher-ranked individuals in a social transmission experiment. *Nature Communications*, *11*(1), 459-469. https://doi.org/10.1038/s41467-019-14209-8

Carey, M. C., West, A. M., Lozano, A., & Samuels, S. (2012). Designing Gum-Based Enrichment for Captive Patas Monkeys (*Erythrocebus patas*). *Science*, *50*. https://doi.org/10.13140/2.1.1387.6002

Carter, A. J. (2013). On validity and controls in animal personality research: a comment on Galhardo et al. (2012). *Biology Letters*, *9*(4), 20121080. https://doi.org/10.1098/rsbl.2012.1080

Carter, A. J., Feeney, W. E., Marshall, H. H., Cowlishaw, G., & Heinsohn, R. (2012a). Animal personality: what are behavioural ecologists measuring. *Biological Reviews*, *88*(2), 465-475. https://doi.org/10.1111/brv.12007

Carter, A. J., Marshall, H. H., Heinsohn, R., & Cowlishaw, G. (2012b). How not to measure boldness: novel object and antipredator responses are not the same in wild baboons. *Animal Behaviour*, *84*(3), 603-609. https://doi.org/10.1016/j.anbehav.2012.06.015

Carter, A. J., Marshall, H. H., Heinsohn, R., & Cowlishaw, G. (2014). Personality predicts the propensity for social learning in a wild primate. *PeerJ*, *2*, e283-22. https://doi.org/10.7717/peerj.283

Carter, A. J., Torrents Ticó, M., & Cowlishaw, G. (2016). Sequential phenotypic constraints on social information use in wild baboons. *eLife*, *5*, e13125. https://doi.org/10.7554/eLife.13125

Catania, A. C. (2007). *Learning*. Sloan Publishing.

Cauchoix, M., Chaine, A. S., & Barragan-Jason, G. (2020). Cognition in Context: Plasticity in Cognitive Performance in Response to Ongoing Environmental Variables. *Frontiers in Ecology and Evolution*, *8*, 1-8. https://doi.org/10.3389/fevo.2020.00106

Centola, D., & Macy, M. (2007). Complex contagions and the weakness of long ties. *American Journal of Sociology*, *113*(3), 702-734. https://doi.org/10.1086/521848

Chauvin, C., & Thierry, B. (2005). Tonkean macaques orient their food search from olfactory cues conveyed by conspecifics. *Ethology*, *111*(3), 301-310. http://onlinelibrary.wiley.com/doi/10.1111/j.1439-0310.2004.01066.x/full

Chivers, D. P., & Smith, R. J. F. (1995). Chemical recognition of risky habitats is culturally transmitted among fathead minnows, *Pimephales promelas* (Osteichthyes, Cyprinidae). *Ethology*, *99*(4), 286-296. https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1439-0310.1995.tb00903.x

Clayton, D. A. (1978). Socially facilitated behavior. *The Quarterly Review of Biology*, *53*(4), 373-392. https://doi.org/10.2307/2826580

Cordoni, G., Norscia, I., Bobbio, M., & Palagi, E. (2018). Differences in play can illuminate differences in affiliation: A comparative study on chimpanzees and gorillas. *PLOS ONE*, *13*(3), e0193096-23. https://doi.org/10.1371/journal.pone.0193096

Cords, M. (2012). The behavior, ecology, and social evolution of cercopithecine monkeys. In J. C. Mitani, J. Call, P. M. Kappeler, R. A. Palombit, & J. B. Silk (Eds.), *The Evolution of Primate Societies* (pp. 91-112). University of Chicago Press.

Coussi-Korbel, S., & Fragaszy, D. M. (1995). On the relation between social dynamics and social learning. *Animal Behaviour*, *50*(6), 1441-1453. https://doi.org/10.1016/0003-3472(95)80001-8

Croft, D. P., James, R., & Krause, J. (2008). *Exploring Animal Social Networks*. Princeton University Press.

Cronin, K. A., Jacobson, S. L., Bonnie, K. E., & Hopper, L. M. (2017). Studying primate cognition in a social setting to improve validity and welfare: A literature review highlighting successful approaches. *PeerJ*, *5*, e3649. https://doi.org/10.7717/peerj.3649

Curio, E. (1988). Cultural transmission of enemy recognition by birds. In T. R. Zentall & B. G. Galef (Eds.), *Social Learning: Psychological and Biological Perspectives* (pp. 75-97). Lawrence Erlbaum Associates, Inc. https://psycnet.apa.org/record/1988-97122-004

Curley, J. P., Shen, K., & Huang, Z. (2015). compete: Analyzing competitive interaction data. *R package v 0.1.*

Dall, S. R. X., Houston, A. I., & McNamara, J. M. (2004). The behavioural ecology of personality: Consistent individual differences from an adaptive perspective. *Ecology Letters*, *7*(8), 734-739. https://doi.org/10.1111/j.1461-0248.2004.00618.x

Dammhahn, M. (2012). Are personality differences in a small iteroparous mammal maintained by a life-history trade-off. *Proceedings of the Royal Society of London. Series B: Biological Science*, *279*(1738), 2645-2651. https://doi.org/10.1098/rspb.2012.0212

Danchin, E., Nöbel, S., Pocheville, A., Dagaeff, A.-C., Demay, L., Alphand, M., Ranty-Roby, S., Van Renssen, L., Monier, M., & Gazagne, E. (2018). Cultural flies: Conformist social learning in fruitflies predicts long-lasting mate-choice traditions. *Science*, *362*(6418), 1025-1030. https://science.sciencemag.org/content/362/6418/1025.abstract

Dawson, B. V., & Foss, B. M. (1965). Observational learning in Budgerigars. *Animal Behaviour*, *13*(4). https://psycnet.apa.org/record/1966-03961-001

Didan, K. (2015). MOD13Q1 MODIS/Terra vegetation indices 16-day L3 global 250m SIN grid V006. NASA EOSDIS Land Processes DAAC. https://lpdaac.usgs.gov/products/mod13q1v006/

Dienes, Z., & Mclatchie, N. (2018). Four reasons to prefer Bayesian analyses over significance testing. *Psychonomic Bulletin & Review*, *25*(1), 207-218. https://doi.org/10.3758/s13423-017-1266-z

Dindo, M., Whiten, A., & Waal, F. B. M. D. (2009). Social facilitation of exploratory foraging behavior in capuchin monkeys (*Cebus apella*). *American Journal of Primatology*, *71*(5), 419-426. https://doi.org/10.1002/ajp.20669

Dingemanse, N. J., Kazem, A. J. N., Réale, D., & Wright, J. (2010). Behavioural reaction norms: animal personality meets individual plasticity. *Trends in Ecology & Evolution*, *25*(2), 81-89. https://doi.org/10.1016/j.tree.2009.07.013

Dingemanse, N. J., & Wolf, M. (2010). Recent models for adaptive personality differences: a review. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *365*(1560), 3947-3958. https://doi.org/10.1098/rstb.2010.0221

Dingemanse, N. J., & Dochtermann, N. A. (2013). Quantifying individual variation in behaviour: mixed-effect modelling approaches. *Journal of Animal Ecology*, *82*(1), 39-54. https://doi.org/10.1111/1365-2656.12013

Drapier, M., Chauvin, C., & Thierry, B. (2002). Tonkean macaques (Macaca tonkeana) find food sources from cues conveyed by group-mates. *Animal Cognition*, *5*(3), 159-165. https://doi.org/10.1007/s10071-002-0145-8

Drea, C. M. (1998). Social context affects how rhesus monkeys explore their environment. *American Journal of Primatology*, *44*(3), 205-214. https://onlinelibrary.wiley.com/doi/abs/10.1002/(SICI)1098-2345(1998)44:3<205::AID-AJP3>3.0.CO;2

Dunlap, A. S., & Stephens, D. W. (2016). Reliability, uncertainty, and costs in the evolution of animal learning. *Current Opinion in Behavioral Sciences*, *12*, 73-79. https://doi.org/10.1016/j.cobeha.2016.09.010

Dyer, J. R. G., Croft, D. P., Morrell, L. J., & Krause, J. (2009). Shoal composition determines foraging success in the guppy. *Behavioral Ecology*, *20*(1), 165-171. https://academic.oup.com/beheco/article/20/1/165/214792

Eley, R. M., Tarara, R. P., Worthman, C. M., & Else, J. G. (1989). Reproduction in the vervet monkey (*Cercopithecus aethiops*): III. The menstrual cycle. *American Journal of Primatology*, *17*(1), 1-10. https://onlinelibrary.wiley.com/doi/abs/10.1002/ajp.1350170102

Enquist, M., Eriksson, K., & Ghirlanda, S. (2007). Critical social learning: A solution to Rogers's Paradox of nonadaptive culture. *American Anthropologist*, *109*(4), 727-734. https://doi.org/10.1525/aa.2007.109.4.727

Enstam, K. L., & Isbell, L. A. (2002). Comparison of responses to alarm calls by patas (*Erythrocebus patas*) and vervet (*Cercopithecus aethiops*) monkeys in relation to habitat structure. *American Journal of Physical Anthropology*, *119*(1), 3-14. https://doi.org/10.1002/ajpa.10104

Fairbanks, L. A. (1980). Relationships among adult females in captive vervet monkeys: testing a model of rank-related attractiveness. *Animal Behaviour*, *28*(3), 853-859. https://www.sciencedirect.com/science/article/pii/S000334728080145X

Fairbanks, L. A. (2001). Individual differences in response to a stranger: social impulsivity as a dimension of temperament in vervet monkeys (*Cercopithecus aethiops sabaeus*). *Journal of Comparative Psychology*, *115*(1), 22-28. https://psycnet.apa.org/record/2001-14761-003

Fairbanks, L. A., & McGuire, M. T. (1984). Determinants of fecundity and reproductive success in captive vervet monkeys. *American Journal of Primatology*, *7*(1), 27-38. https://doi.org/10.1002/ajp.1350070106

Fairbanks, L. A., Newman, T. K., Bailey, J. N., Jorgensen, M. J., Breidenthal, S. E., Ophoff, R. A., Comuzzie, A. G., Martin, L. J., & Rogers, J. (2004). Genetic contributions to social impulsivity and aggressiveness in vervet monkeys. *Biological Psychiatry*, *55*(6), 642-647. https://doi.org/10.1016/j.biopsych.2003.12.005

Farina, W. M., Grüter, C., & Arenas, A. (2012). Olfactory Information Transfer During Recruitment in Honey Bees. In R. Menzel & A. Mercer (Eds.), *Honeybee Neurobiology and Behavior* (pp. 89-101). Springer Netherlands. https://doi.org/10.1007/978-94-007-2099-2_8

Farine, D. R., Aplin, L. M., Sheldon, B. C., & Hoppitt, W. (2015). Interspecific social networks promote information transmission in wild songbirds. *Proceedings of the Royal Society of London. Series B: Biological Science*, *282*(1803), 20142804. https://doi.org/10.1098/rspb.2014.2804

Faust, K. (2010). A puzzle concerning triads in social networks: Graph constraints and the triad census. *Social Networks*, *32*(3), 221-233. https://doi.org/10.1016/j.socnet.2010.03.004

Fawcett, T. W., Hamblin, S., & Giraldeau, L. A. (2012). Exposing the behavioral gambit: the evolution of learning and decision rules. *Behavioral Ecology*, *24*(1), 2-11. https://doi.org/10.1093/beheco/ars085

Fedigan, L., & Fedigan, L. M. (1988). *Cercopithecus aethiop*s: a review of field studies. In A. Gautier-Hion, F. Bourlière, J.-P. Gautier, & J. Kingdon (Eds.), *A Primate Radiation: Evolutionary Biology of the African Guenons* (pp. 389-411). Cambridge University Press.

Firth, J. A. (2019). Considering complexity: Animal social networks and behavioural contagions. *Trends in Ecology & Evolution*, *35*(2), 100-104. https://www.sciencedirect.com/science/article/pii/S0169534719302988

Firth, J. A., Albery, G. F., Beck, K. B., Jarić, I., Spurgin, L. G., Sheldon, B. C., & Hoppitt, W. (2020). Analysing the social spread of behaviour: Integrating complex contagions into network based diffusions. *arXiv preprint arXiv:2012.08925*. https://arxiv.org/pdf/2012.08925

Forkman, B. A. (1991). Social facilitation is shown by gerbils when presented with novel but not with familiar food. *Animal Behaviour*, *42*(5), 860-861. https://psycnet.apa.org/record/1992-15439-001

Foxx, R. M. (2009). Applied behavior analysis for children with autism spectrum disorders. *Child and Adolescent Psychiatric Clinics of North America*, *17*(4), 821-834. https://doi.org/10.1016/j.chc.2008.06.0077

Fragaszy, D., & Visalberghi, E. (2004). Socially biased learning in monkeys. *Animal Learning & Behavior*, *32*(1), 24-35. https://link.springer.com/article/10.3758/BF03196004

Franz, M., & Nunn, C. L. (2009). Network-based diffusion analysis: A new method for detecting social learning. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1663), 1829-1836. https://doi.org/10.1098/rspb.2008.1824

Freeman, N. J., Pasternak, G. M., Rubi, T. L., Barrett, L., & Henzi, S. P. (2012). Evidence for scent marking in vervet monkeys. *Primates*, *53*(3), 311-315. https://doi.org/10.1007/s10329-012-0304-8

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. https://besjournals.onlinelibrary.wiley.com/doi/pdfdirect/10.1111/2041-210X.12584

Fruteau, C., van Damme, E., & Noë, R. (2013). Vervet monkeys solve a multiplayer “forbidden circle game” by queuing to learn restraint. *Current Biology*, *23*(8), 665-670. https://doi.org/10.1016/j.cub.2013.02.039

Gabry, J., Simpson, D., Vehtari, A., Betancourt, M., & Gelman, A. (2019). Visualization in Bayesian workflow. *Journal of the Royal Statistical Society: Series A (Statistics in Society)*, *182*(2), 389-402. https://rss.onlinelibrary.wiley.com/doi/pdf/10.1111/rssa.12378

Galef Jr, B. G. (1993). Functions of social learning about food: a causal analysis of effects of diet novelty on preference transmission. *Animal Behaviour*, *46*(2), 257-265. https://www.sciencedirect.com/science/article/pii/S0003347283711875

Galef Jr, B. G., & Wigmore, S. W. (1983). Transfer of information concerning distant foods: a laboratory investigation of the ‘information-centre’ hypothesis. *Animal Behaviour*, *31*(3), 748-758. https://www.sciencedirect.com/science/article/pii/S0003347283802322

Galef, B. G. (1988). Imitation in animals: History, definition, and interpretation of data from the psychological laboratory Social Learning. In T. R. Zentall & B. G. Galef (Eds.), *Social Learning* (pp. 3-28). Psychology Press. https://doi.org/10.4324/9781315801889-6

Galef, B. G. (1992). The question of animal culture. *Human Nature*, *3*(2), 157-178. https://link.springer.com/content/pdf/10.1007/BF02692251.pdf

Galef, B. G., & Laland, K. N. (2005). Social learning in animals: Empirical studies and theoretical models. *BioScience*, *55*(6), 489. https://doi.org/

10.1641/0006-3568(2005)055[0489:sliaes]2.0.co;2

Galef, B. G., & Giraldeau, L. A. (2001). Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Animal Behaviour*, *61*(1), 3-15. https://doi.org/10.1006/anbe.2000.1557

Galhardo, L., Vitorino, A., & Oliveira, R. F. (2012). Social familiarity modulates personality trait in a cichlid fish. *Biology Letters*, *8*(6), 936-938. https://doi.org/10.1098/rsbl.2012.0500

Gamer, M., Lemon, J., Fellows, I., & Singh, P. (2019). irr: Various Coefficients of Interrater Reliability and Agreement. *R package version 0.84.1*. https://CRAN.R-project.org/package=irr

Garber, P. A. (2000). Evidence for the use of spatial, temporal and social information by some primate foragers. In S. Boinski & P. Garber (Eds.), *On the Move: How and Why Animals Travel in Groups* (pp. 261-298). University of Chicago Press Chicago.

Gaulin, S. J. C., & Sailer, L. D. (1985). Are females the ecological sex. *American Anthropologist*, *87*(1), 111-119. https://doi.org/10.2307/677666

Gelman, A. (2003). A Bayesian formulation of exploratory data analysis and goodness−of−fit testing. *International Statistical Review*, *71*(2), 369-382. https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1751-5823.2003.tb00203.x

Gelman, A., & Hill, J. (2007). *Data Analysis Using Regression and Multilevel/Hierarchical Models*. Cambridge University Press.

Gelman, A., & Shalizi, C. R. (2012). Philosophy and the practice of Bayesian statistics. *British Journal of Mathematical and Statistical Psychology*, *66*(1), 8-38. https://doi.org/10.1111/j.2044-8317.2011.02037.x

Gelman, A., & Shirley, K. (2011). Inference from simulations and monitoring convergence. In S. Brooks, A. Gelman, G. L. Jones, & X.-L. Meng (Eds.), *Handbooks of Markov Chain Monte Carlo* (p. 434). Chapman and Hall/CRC. https://doi.org/10.1201/b10905-7

Grampp, M., Sueur, C., van de Waal, E., & Botting, J. (2019). Social attention biases in juvenile wild vervet monkeys: implications for socialisation and social learning processes. *Primates*, *60*(3), 261-275. https://doi.org/10.1007/s10329-019-00721-4

Greenberg, R. (2003). The role of neophobia and neophilia in the development of innovative behaviour of birds Animal Innovation. In S. M. Reader & K. N. Laland (Eds.), *Animal Innovation* (pp. 175-196). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780198526223.003.0008

Groves, C. P. (2001). Primate Taxonomy. In A. Fuentes (Ed.), *The International Encyclopedia of Biological Anthropology* (p. 350). John Wiley & Sons, Inc.

Guerin, B. (1993). *Social Facilitation*. Cambridge University Press.

Guerin, B. (2010). Social Facilitation. In Weiner, Irving, & W. E. Craighead (Eds.), *The Corsini Encyclopedia of Psychology* (pp. 1-2). John Wiley & Sons, Inc.

Gurmu, S. (1998). Generalized hurdle count data regression models. *Economics Letters*, *58*(3), 263-268. https://doi.org/10.1016/s0165-1765(97)00295-4

Hammerstein, P. (1998). What is evolutionary game theory. In L. A. R. Dugatkin, Hudson Kern (Ed.), *Game Theory and Animal Behavior* (pp. 3-15). Oxford University Press.

Harcourt, J. L., Ang, T. Z., Sweetman, G., Johnstone, R. A., & Manica, A. (2009). Social feedback and the emergence of leaders and followers. *Current Biology*, *19*(3), 248-252. https://doi.org/10.1016/j.cub.2008.12.051

Hartig, F. (2017). DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. *R package version 0.1, 5*.

Hasenjager, M. J., Leadbeater, E., & Hoppitt, W. (2020). Detecting and quantifying social transmission using network−based diffusion analysis. *Journal of Animal Ecology*, *90*(1), 8-26. https://besjournals.onlinelibrary.wiley.com/doi/pdf/10.1111/1365-2656.13307

Hasenjager, M. J., Hoppitt, W., & Dugatkin, L. A. (2020b). Personality composition determines social learning pathways within shoaling fish. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1936), 20201871. https://doi.org/10.1098/rspb.2020.1871

Hasenjager, M. J., Hoppitt, W., & Leadbeater, E. (2020). Network-based diffusion analysis reveals context-specific dominance of dance communication in foraging honeybees. *Nature Communications*, *11*(1), 1-9. https://doi.org/10.1038/s41467-020-14410-0

Hauser, M. D. (1988). Invention and social transmission: New data from wild vervet monkeys. In R. W. Byrne & A. Whiten (Eds.), *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes and Man* (pp. 327-343). Oxford University Press.

Hauser, M. D. (1993). Ontogeny of foraging behavior in wild vervet monkeys (*Cercopithecus aethiops*): Social interactions and survival. *Journal of Comparative Psychology*, *107*(3), 276. https://psycnet.apa.org/record/1994-00598-001

Hauser, M. D. (1994). The transition to foraging independence in free-ranging vervet monkeys. In B. M. Galef Jr., M. Valsecchi, P. (Eds.), *Behavioral Aspects of Feeding* (pp. 165-202). Harwood Academic.

Henzi, S. P., & Barrett, L. (2003). Evolutionary ecology, sexual conflict, and behavioral differentiation among baboon populations. *Evolutionary Anthropology: Issues, News, and Reviews*, *12*(5), 217-230. https://doi.org/10.1002/evan.10121

Henzi, S. P., Forshaw, N., Boner, R., Barrett, L., & Lusseau, D. (2013). Scalar social dynamics in female vervet monkey cohorts. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1618), 20120351. https://doi.org/10.1098/rstb.2012.0351

Henzi, S. P., & Lucas, J. W. (1980). Observations on the Inter-troop movement of adult vervet monkeys (*Cercopithecus aethiops*). *Folia primatologica*, *33*(3), 220-235. https://doi.org/10.1159/000155936

Hespanhol, L., Vallio, C. S., Costa, L. M., & Saragiotto, B. T. (2019). Understanding and interpreting confidence and credible intervals around effect estimates. *Brazilian Journal of Physical Therapy*, *23*(4), 290-301. https://doi.org/10.1016/j.bjpt.2018.12.006

Heyes, C. M. (1994). Social learning in animals: Categories and mechanisms. *Biological Reviews*, *69*(2), 207-231. https://doi.org/10.1111/j.1469-185X.1994.tb01506.x

Heyes, C. M. (2012). What's social about social learning. *Journal of Comparative Psychology*, *126*(2), 193-202. https://doi.org/10.1037/a0025180

Heyes, C. M. (2018). *Cognitive Gadgets*. Harvard University Press.

Heyes, C. M., & Pearce, J. M. (2015). Not-so-social learning strategies. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1802), 20141709. https://doi.org/10.1098/rspb.2014.1709

Heymann, E. W. (2006). The neglected sense–olfaction in primate behavior, ecology, and evolution. *American Journal of Primatology*, *68*(6), 519-524. https://doi.org/10.1002/ajp.20249

Heyser, C. J., & Chemero, A. (2012). Novel object exploration in mice: Not all objects are created equal. *Behavioural Processes*, *89*(3), 232-238. https://doi.org/10.1016/j.beproc.2011.12.004

Hilbe, J. M. (2017). The statistical analysis of count data / El análisis estadístico de los datos de recuento. *Cultura y Educación*, *29*(3), 409-460. https://doi.org/10.1080/11356405.2017.1368162

Hobaiter, C., Poisot, T., Zuberbühler, K., Hoppitt, W., & Gruber, T. (2014). Social network analysis shows direct evidence for social transmission of tool use in wild chimpanzees. *PLoS Biology*, *12*(9), e1001960. https://doi.org/10.1371/journal.pbio.1001960

Hoppitt, W., Boogert, N. J., & Laland, K. N. (2010). Detecting social transmission in networks. *Journal of Theoretical Biology*, *263*(4), 544-555. https://doi.org/10.1016/j.jtbi.2010.01.004

Hoppitt, W. (2017). The conceptual foundations of network-based diffusion analysis: choosing networks and interpreting results. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1735), 20160418. https://doi.org/10.1098/rstb.2016.0418

Hoppitt, W., Kandler, A., Kendal, J. R., & Laland, K. N. (2010b). The effect of task structure on diffusion dynamics: Implications for diffusion curve and network-based analyses. *Learning & Behavior*, *38*(3), 243-251. https://link.springer.com/article/10.3758/LB.38.3.243

Hoppitt, W. J. E., & Laland, K. N. (2013). *Social Learning: An Introduction to Mechanisms, Methods, and Models*. Princeton University Press. https://doi.org/10.1515/9781400846504

Horrocks, J. A. (1986). Life-history characteristics of a wild population of vervets (*Cercopithecus aethiops sabaeus*) in Barbados, West Indies. *International Journal of Primatology*, *7*(1), 31-47. https://doi.org/10.1007/BF02692308

Huber, H. F., & Lewis, K. P. (2011). An assessment of gum−based environmental enrichment for captive gummivorous primates. *Zoo Biology*, *30*(1), 71-78. https://doi.org/10.1002/zoo.20321

Ilany, A., Barocas, A., Koren, L., Kam, M., & Geffen, E. (2013). Structural balance in the social networks of a wild mammal. *Animal Behaviour*, *85*(6), 1397-1405. https://doi.org/10.1016/j.anbehav.2013.03.032

Isbell, L. A., Cheney, D. L., & Seyfarth, R. M. (2004). Why vervet monkeys (*Cercopithecus aethiops*) live in multimale groups. In M. A. Glenn & M. Cords (Eds.), *The Guenons: Diversity and Adaptation in African Monkeys* (pp. 173-187). Springer, Boston, MA. https://doi.org/10.1007/0-306-48417-X_13

Jarrett, J. D., Bonnell, T. R., Young, C., Barrett, L., & Henzi, S. P. (2018). Network integration and limits to social inheritance in vervet monkeys. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1876), 20172668. https://doi.org/10.1098/rspb.2017.2668

Jolles, J. W., Fleetwood-Wilson, A., Nakayama, S., Stumpe, M. C., Johnstone, R. A., & Manica, A. (2015). The role of social attraction and its link with boldness in the collective movements of three-spined sticklebacks. *Animal Behaviour*, *99*, 147-153. https://doi.org/10.1016/j.anbehav.2014.11.004

Kawai, M. (1965). Newly-acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima islet. *Primates*, *6*(1), 1-30. https://doi.org/10.1007/BF01794457

Kelley, J. L., Evans, J. P., Ramnarine, I. W., & Magurran, A. E. (2003). Back to school: can antipredator behaviour in guppies be enhanced through social learning. *Animal Behaviour*, *65*(4), 655-662. https://www.sciencedirect.com/science/article/pii/S0003347203920768

Kendal, R. L., Boogert, N. J., Rendell, L., Laland, K. N., Webster, M. M., & Jones, P. L. (2018). Social learning strategies: bridge-building between fields. *Trends in Cognitive Sciences*, 1-15. https://doi.org/10.1016/j.tics.2018.04.003

Kendal, R. L., Kendal, J. R., Hoppitt, W. J. E., & Laland, K. N. (2009). Identifying social learning in animal populations: a new 'option-bias' method. *PLOS ONE*, *4*(8), e6541-9. https://doi.org/10.1371/journal.pone.0006541

Kennedy, J. S. (1992). *The New Anthropomorphism*. Cambridge University Press.

King, B. J. (1994). Primate infants as skilled information gatherers. *Pre and Perinatal Psychology Journal*, *8*, 287-287.

King, B. J. (1994). *The Information Continuum: Evolution of Social Information Transfer in Monkeys, Apes, and Hominids*. School of American Research Press.

Krause, J. (1993). Transmission of fright reaction between different species of fish. *Behaviour*, *127*(1/2), 37-48. https://www.jstor.org/stable/4535142

Kulahci, I. G., Ghazanfar, A. A., & Rubenstein, D. I. (2018). Knowledgeable lemurs become more central in social networks. *Current Biology*, *28*(8), 1306-1310. e2. https://www.sciencedirect.com/science/article/pii/S0960982218303014

Kummer, H. (1978). On the value of social relationships to nonhuman primates: a heuristic scheme. *Social Science Information*, *17*(4-5), 687-705. https://journals.sagepub.com/doi/pdf/10.1177/053901847801700418

Kurvers, R. H. J. M., Adamczyk, V. M. A. P., van Wieren, S. E., & Prins, H. H. T. (2011). The effect of boldness on decision-making in barnacle geese is group-size-dependent. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1714), 2018-2024. https://royalsocietypublishing.org/doi/pdf/10.1098/rspb.2010.2266

Kurvers, R. H. J. M., Van Oers, K., Nolet, B. A., Jonker, R. M., Van Wieren, S. E., Prins, H. H. T., & Ydenberg, R. C. (2010). Personality predicts the use of social information. *Ecology Letters*, *13*(7), 829-837. https://library.wur.nl/WebQuery/wurpubs/fulltext/177368#page=35

Ladds, Z., Hoppitt, W. J. E., & Boogert, N. J. (2017). Social learning in otters. *Royal Society Open Science*, *4*(8), 170489-170412. https://doi.org/10.1098/rsos.170489

Laidre, M. E. (2009). Informative breath: Olfactory cues sought during social foraging among old world monkeys (*Mandrillus sphinx*, *M. Leucophaeus*, and *Papio anubis*). *Journal of Comparative Psychology*, *123*(1), 34-44. https://doi.org/10.1037/a0013129

Laland, K. N. (2004). Social learning strategies. *Animal Learning & Behavior*, *32*(1), 4-14. https://link.springer.com/article/10.3758/BF03196002

Laland, K. N., & Williams, K. (1998). Social transmission of maladaptive information in the guppy. *Behavioral Ecology*, *9*(5), 493-499. https://doi.org/10.1093/beheco/9.5.493

Laland, K. N., Atton, N., & Webster, M. M. (2011). From fish to fashion: experimental and theoretical insights into the evolution of culture. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1567), 958-968. https://doi.org/10.1098/rstb.2010.0328

Leadbeater, E., & Chittka, L. (2007). Social learning in insects--from miniature brains to consensus building. *Current Biology*, *17*(16), R703-R713. https://doi.org/10.1016/j.cub.2007.06.012

Leadbeater, E., & Florent, C. (2014). Foraging bumblebees do not rate social information above personal experience. *Behavioral Ecology and Sociobiology*, *68*(7), 1145-1150. https://doi.org/10.1007/s00265-014-1725-8

Lee, P. C. (1984). Early infant development and maternal care in free-ranging vervet monkeys. *Primates*, *25*(1), 36-47. https://doi.org/10.1007/BF02382294

Lee, P. C. (1987). Nutrition, fertility and maternal investment in primates. *Journal of Zoology*, *213*(3), 409-422. https://doi.org/10.1111/j.1469-7998.1987.tb03717.x

Lee, V. L. (1988). *Beyond Behaviorism*. Routledge.

Li, M. F., Arseneau-Robar, T. J. M., Smeltzer, E. A., & Teichroeb, J. A. (2021). Be early or be tolerated: vervet monkey, *Chlorocebus pygerythrus*, foraging strategies in a dispersed resource. *Animal Behaviour*, *176*, 1-15. https://www.sciencedirect.com/science/article/pii/S0003347221000889

Lind, J., Ghirlanda, S., & Enquist, M. (2019). Social learning through associative processes: a computational theory. *Royal Society Open Science*, *6*(3), 181777. https://royalsocietypublishing.org/doi/pdf/10.1098/rsos.181777

Lorenz, J., Rauhut, H., Schweitzer, F., & Helbing, D. (2011). How social influence can undermine the wisdom of crowd effect. *Proceedings of the National Academy of Sciences*, *108*(22), 9020-9025. https://doi.org/10.1073/pnas.1008636108

Lycett, J., & Henzi, S. P. (1992). The relevance of sensory modality to the social transmission of information in vervet monkeys (*Cercopithecus aethiops*). *South African Journal of Science*, *88*(3), 177-179.

MacGregor, H. E. A., Cottage, A., & Ioannou, C. C. (2021). Suppression of personality variation in boldness during foraging in three-spined sticklebacks. *Behavioral Ecology and Sociobiology*, *75*(71), 1-10. https://doi.org/10.1007/s00265-021-03007-2

Marr, M. J. (1985). Tis the gift to be simple: A retrospective appreciation of Mach's The Science of Mechanics. *Journal of the Experimental Analysis of Behavior*, *44*(1), 129-138. https://www.ncbi.nlm.nih.gov/pmc/articles/PMC13481688

Marr, M. J. (2003). The what, the how, and the why: The explanation of Ernst Mach. *Behavior and Philosophy*, *31*(2003), 181-192. https://doi.org/10.2307/27759457

Martin, P., Bateson, P. P. G., & Bateson, P. (1986). Recording methods. In P. Martin & P. P. G. Bateson (Eds.), *Measuring Behaviour: An Introductory Guide* (pp. 48-69). Cambridge University Press.

McElreath, R. (2020). *Statistical rethinking: A Bayesian course with examples in R and Stan*. CRC press.

McElreath, R., Lubell, M., Richerson, P. J., Waring, T. M., Baum, W., Edsten, E., Efferson, C., & Paciotti, B. (2005). Applying evolutionary models to the laboratory study of social learning. *Evolution and Human Behavior*, *26*(6), 483-508. https://www.sciencedirect.com/science/article/pii/S1090513805000231

McFarland, R., Barrett, L., Boner, R., Freeman, N. J., & Henzi, S. P. (2014). Behavioral flexibility of vervet monkeys in response to climatic and social variability. *American Journal of Physical Anthropology*, *154*(3), 357-364. https://doi.org/10.1002/ajpa.22518

McFarland, R., Henzi, S. P., Barrett, L., Wanigaratne, A., Coetzee, E., Fuller, A., Hetem, R. S., Mitchell, D., & Maloney, S. K. (2015). Thermal consequences of increased pelt loft infer an additional utilitarian function for grooming. *American Journal of Primatology*, *78*(4), 456-461. https://doi.org/10.1002/ajp.22519

McGuire, M. T., Raleigh, M. J., & Pollack, D. B. (1994). Personality features in vervet monkeys: the effects of sex, age, social status, and group composition. *American Journal of Primatology*, *33*(1), 1-13. https://onlinelibrary.wiley.com/doi/abs/10.1002/ajp.1350330102

McHugh, M. L. (2012). Interrater reliability: the kappa statistic. *Biochemia Medica*, *22*(3), 276-282. https://doi.org/10.1016/j.jocd.2012.03.005

McLachlan, J. R., Ratnayake, C. P., & Magrath, R. D. (2019). Personal information about danger trumps social information from avian alarm calls. *Proceedings of the Royal Society B*, *286*(1899), 20182945. https://doi.org/10.1098/rspb.2018.2945

Mertz, J., Surreault, A., van de Waal, E., & Botting, J. (2019). Primates are living links to our past: the contribution of comparative studies with wild vervet monkeys to the field of social cognition. *Cortex*, *118*, 65-81. https://doi.org/10.1016/j.cortex.2019.03.007

Mesoudi, A., Chang, L., Dall, S. R. X., & Thornton, A. (2016). The evolution of individual and cultural variation in social learning. *Trends in Ecology & Evolution*, *31*(3), 215-225. https://doi.org/10.1016/j.tree.2015.12.012

Michelena, P., Jeanson, R., Deneubourg, J.-L., & Sibbald, A. M. (2010). Personality and collective decision-making in foraging herbivores. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1684), 1093-1099. https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2842771

Miltenberger, R. G. W., T. M. (2013). Observation and measurement in behavior analysis. In G. J. Madden (Ed.), *APA Handbook of Behavior Analysis: Methods and Principles* (pp. 127-150). American Psychological Association.

Mineka, S., & Cook, M. (1988). Social learning and the acquisition of snake fear in monkeys Social Learning. In B. G. Galef & T. R. Zentall (Eds.), *Social Learning: Psychological and Biological Perspectives* (pp. 51-73). Lawrence Erlbaum Associates, Inc.

Morgan, T. J., Rendell, L. E., Ehn, M., Hoppitt, W., & Laland, K. N. (2012). The evolutionary basis of human social learning. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1729), 653-662. https://doi.org/10.1098/rspb.2011.1172

Morand‐Ferron, J., Cole, E. F., & Quinn, J. L. (2016). Studying the evolutionary ecology of cognition in the wild: a review of practical and conceptual challenges. *Biological Reviews*, *91*(2), 367-389. https://doi.org/10.1111/brv.12174

Morris, E. K. (1988). Contextualism: The world view of behavior analysis. *Journal of Experimental Child Psychology*, *46*(3), 289-323. https://www.sciencedirect.com/

science/article/pii/002209658890063X

Morris, E. K. (1992). The aim, progress, and evolution of behavior analysis. *The Behavior Analyst*, *15*(1), 3-29. https://link.springer.com/article/10.1007/BF03392582

Morris, E. K. (1993a). Behavior analysis and mechanism: One is not the other. *The Behavior Analyst*, *16*(1), 25-43. https://link.springer.com/article/10.1007/BF03392606

Morris, E. K. (1993b). Mechanism and contextualism in behavior analysis: Just some observations. *The Behavior Analyst*, *16*(2), 255-268. https://link.springer.com/article/10.1007/BF03392634

Moxley, R. A. (2001). Sources for Skinner's pragmatic selectionism in 1945. *The Behavior Analyst*, *24*(2), 201-212. pmc/articles/PMC2731505/?report=abstract

Munson, A., Michelangeli, M., & Sih, A. (2021). Stable social groups foster conformity and among-group differences. *Animal Behaviour*, *174*, 197-206. https://doi.org/10.1016/j.anbehav.2021.02.011

Muroyama, Y. (1994). Exchange of grooming for allomothering in female patas monkeys. *Behaviour*, *128*(1-2), 103-119. https://doi.org/10.2307/4535166

Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biological Reviews*, *85*(4), 935-956. https://doi.org/10.1111/j.1469-185X.2010.00141.x

Nakagawa, S., & Schielzeth, H. (2012). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2), 133-142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

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

Niemelä, P. T., & Dingemanse, N. J. (2014). Artificial environments and the study of 'adaptive' personalities. *Trends in Ecology & Evolution*, *29*(5), 245-247. https://doi.org/10.1016/j.tree.2014.02.007

Nightingale, G., Boogert, N., Laland, K., & Hoppitt, W. (2015). Quantifying diffusion in social networks: a Bayesian approach. In J. Krause, R. James, D. W. Franks, & D. P. Croft (Eds.), *Animal Social Networks* (pp. 38-52). Oxford University Press Oxford, UK.

Nord, C. M., Bonnell, T. R., Dostie, M. J., Henzi, S. P., & Barrett, L. (2021). Tolerance of muzzle contact underpins the acquisition of foraging information in vervet monkeys (*Chlorocebus pygerythrus*). *Journal of Comparative Psychology*. https://psycnet.apa.org/record/2021-19654-001

Nussey, D. H., Wilson, A. J., & Brommer, J. E. (2007). The evolutionary ecology of individual phenotypic plasticity in wild populations. *Journal of Evolutionary Biology*, *20*(3), 831-844. https://doi.org/10.1111/j.1420-9101.2007.01300.x

O'Mara, M. T., Dechmann, D. K. N., & Page, R. A. (2014). Frugivorous bats evaluate the quality of social information when choosing novel foods. *Behavioral Ecology*, *25*(5), 1233-1239. https://doi.org/10.1093/beheco/aru120

Palagi, E., Nicotra, V., & Cordoni, G. (2015). Rapid mimicry and emotional contagion in domestic dogs. *Royal Society Open Science*, *2*(12), 150505-150509. https://doi.org/10.1098/rsos.150505

Pasternak, G. M., Brown, L. R., Kienzle, S., Fuller, A., Barrett, L., & Henzi, S. P. (2013). Population ecology of vervet monkeys in a high latitude, semi-arid riparian woodland. *Koedoe*, *55*(1), 1-10. https://doi.org/10.4102/koedoe.v55i1.1078

Peters-Scheffer, N., Didden, R., Korzilius, H., & Sturmey, P. (2011). A meta-analytic study on the effectiveness of comprehensive ABA-based early intervention programs for children with Autism Spectrum Disorders. *Research in Autism Spectrum Disorders*, *5*(1), 60-69. https://doi.org/10.1016/j.rasd.2010.03.011

Pike, T. W., & Laland, K. N. (2010). Conformist learning in nine-spined sticklebacks' foraging decisions. *Biology Letters*, *6*(4), 466-468. https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2936200

Pongrácz, P., Miklósi, Á., Kubinyi, E., Topál, J., & Csányi, V. (2003). Interaction between individual experience and social learning in dogs. *Animal Behaviour*, *65*(3), 595-603.

Provecho, Y., & Josens, R. (2009). Olfactory memory established during trophallaxis affects food search behaviour in ants. *Journal of Experimental Biology*, *212*(20), 3221-3227. https://doi.org/10.1242/jeb.033506

R Core Team (2018). *R: A language and environment for statistical computing*. https://www.R-project.org

Racine, F., Giraldeau, L.-A., Patenaude-Monette, M., & Giroux, J.-F. (2012). Evidence of social information on food location in a ring-billed gull colony, but the birds do not use it. *Animal Behaviour*, *84*(1), 175-182. https://doi.org/10.1016/j.anbehav.2012.04.028

Reader, S. M., Bruce, M. J., & Rebers, S. (2008). Social learning of novel route preferences in adult humans. *Biology Letters*, *4*(1), 37-40. https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2412949

Reader, S. M., & Laland, K. N. (2001). Primate innovation: sex, age and social rank differences. *International Journal of Primatology*, *22*(5), 787-805. http://www.springerlink.com/index/ln47117526184421.pdf

Reader, S. M., & Laland, K. N. (2003). *Animal Innovation*. Oxford University Press.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, *82*(2), 291-318. https://doi.org/10.1111/j.1469-185X.2007.00010.x

Rendell, L., Fogarty, L., Hoppitt, W. J. E., Morgan, T. J. H., Webster, M. M., & Laland, K. N. (2011). Cognitive culture: theoretical and empirical insights into social learning strategies. *Trends in Cognitive Sciences*, *15*(2), 68-76. https://doi.org/10.1016/j.tics.2010.12.002

Rendell, L., Fogarty, L., & Laland, K. N. (2010). Rogers' paradox recast and resolved: Population structure and the evolution of social learning strategies. *Evolution*, *64*(2), 534-548. https://doi.org/10.1111/j.1558-5646.2009.00817.x

Renevey, N., Bshary, R., & van de Waal, E. (2013). Philopatric vervet monkey females are the focus of social attention rather independently of rank. *Behaviour*, *150*(6), 599-615. https://doi.org/10.1163/1568539X-00003072

Rogers, A. R. (1988). Does biology constrain culture. *American Anthropologist*, *90*(4), 819-831. https://doi.org/10.1525/aa.1988.90.4.02a00030

Saleh, N., Ohashi, K., Thomson, J. D., & Chittka, L. (2006). Facultative use of the repellent scent mark in foraging bumblebees: complex versus simple flowers. *Animal Behaviour*, *71*(4), 847-854. https://doi.org/10.1016/j.anbehav.2005.06.014

Saliveros, A. M., Blyth, E. C. E., C. Hume, G. V. McAusland, F., Hoppitt, W., & Boogert, N. J. (2020). Learning strategies and long-term memory in Asian short-clawed otters (*Aonyx cinereus*). *Royal Society Open Science*, *7*(11), 201215. https://doi.org/10.1098/rsos.201215

Schradin, C. (2013). Intraspecific variation in social organization by genetic variation, developmental plasticity, social flexibility or entirely extrinsic factors. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *368*(1618), 20120346. https://doi.org/10.1098/rstb.2012.0346

Schuppli, C., Meulman, E. J. M., Forss, S. I. F., Aprilinayati, F., van Noordwijk, M. A., &

van Schaik, C. P. (2016). Observational social learning and socially induced practice of routine skills in immature wild orang-utans. *Animal Behaviour*, *119*, 87-98. https://doi.org/10.1016/j.anbehav.2016.06.014

Scruggs, T. E., & Mastropieri, M. A. (1998). Summarizing single-subject research. *Behavior Modification*, *22*(3), 221-242. https://doi.org/10.1177/01454455980223001

Seyfarth, R. M. (1980). The distribution of grooming and related behaviours among adult female vervet monkeys. *Animal Behaviour*, *28*(3), 798-813. https://doi.org/10.1016/s0003-3472(80)80140-0

Seyfarth, R. M., & Cheney, D. L. (1984). Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature*, *308*(5959), 541-543. https://www.nature.com/articles/308541a0

Shettleworth, S. J. (2010). Clever animals and killjoy explanations in comparative psychology. *Trends in Cognitive Sciences*, *14*(11), 477-481. https://www.sciencedirect.com/science/article/pii/S1364661310001488

Sidman, M. (1988). *Tactics of Scientific Research*. Authors Cooperative, Inc.

Silk, J. B. (1982). Altruism among female *Macaca radiata*: explanations and analysis of patterns of grooming and coalition formation. *Behaviour*, *79*(2-4), 162-188. https://doi.org/10.2307/4534159

Skinner, B. F. (1938). *The Behavior of Organisms*. D. Appleton-Century Company, Incorporated.

Skinner, B. F. (1977). Why I am not a cognitive psychologist. *Behaviorism*, *5*(2), 1-10. http://www.jstor.org/stable/27758892

Skinner, B. F. (1984). Methods and theories in the experimental analysis of behavior. *Behavioral and Brain Sciences*, *7*(4), 511-523. https://doi.org/10.1017/S0140525X00026996

Skinner, B. F. (1981). Selection by consequences. *Science*, *213*(4507), 501-504. https://science.sciencemag.org/content/213/4507/501.short

Skinner, B. F. (1931). The concept of the reflex in the description of behavior. *The Journal of General Psychology*, *5*(4), 427-458. https://www.tandfonline.com/doi/abs/10.1080/00221309.1931.9918416

Smit, J. A. H., & van Oers, K. (2019). Personality types vary in their personal and social information use. *Animal Behaviour*, *151*, 185-193. https://doi.org/10.1016/

j.anbehav.2019.02.002

Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2018). An introduction to repeatability estimation with rptR. *https://cran.r-project.org/web/packages/rptR/vignettes/rptR.html*.

Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *8*(11), 1639-1644. https://doi.org/10.1111/2041-210x.12797

Struhsaker, T. T. (1967). Ecology of vervet monkeys (*Cercopithecus aethiops*) in the Masai-Amboseli game reserve, Kenya. *Ecology*, *48*(6), 891. https://doi.org/10.2307/1934531

Strum, S. C., Forster, D., & Hutchins, E. (1997). Why Machiavellian intelligence may not be Machiavellian. In A. Whiten & R. W. Byrne (Eds.), *Machiavellian intelligence II: Extensions and evaluations* (pp. 50-85). Cambridge University Press.

Suboski, M. D., & Templeton, J. J. (1989). Life skills training for hatchery fish: social learning and survival. *Fisheries Research*, *7*(4), 343-352. https://www.sciencedirect.com/science/article/pii/0165783689900660

Swaney, W., Kendal, J., Capon, H., Brown, C., & Laland, K. N. (2001). Familiarity facilitates social learning of foraging behaviour in the guppy. *Animal Behaviour*, *62*(3), 591-598. https://doi.org/10.1006/anbe.2001.1788

Thompson, T. (1984). The examining magistrate for nature: A retrospective review of Claude Bernard's An Introduction to the Study of Experimental Medicine. *Journal of the Experimental Analysis of Behavior*, *41*(2), 211. https://www.ncbi.nlm.nih.gov/pmc/articles/PMC1348034

Timberlake, W. (1993). Behavior systems and reinforcement: An integrative approach. *Journal of the Experimental Analysis of Behavior*, *60*(1), 105-128. https://onlinelibrary.wiley.com/doi/abs/10.1901/jeab.1993.60-105

Tomasello, M. (1996). Do apes ape. In C. M. Heyes & B. G. Galef (Eds.) *Social Learning in Animals: The Roots of Culture* (pp. 319-346). Academic Press.

Tournier, E., Tournier, V., van de Waal, E., Barrett, A. S., Brown, L., & Bshary, R. (2014). Differences in diet between six neighbouring groups of vervet monkeys. *Ethology*, *120*(5), 471-482. https://doi.org/10.1111/eth.12218

Trompf, L., & Brown, C. (2014). Personality affects learning and trade-offs between private and social information in guppies, *Poecilia reticulata*. *Animal Behaviour*, *88*, 99-106.

Truskanov, N., & Lotem, A. (2017). Trial-and-error copying of demonstrated actions reveals how fledglings learn to 'imitate' their mothers. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1849). https://doi.org/10.1098/rspb.2016.2744

Truskanov, N., Shy, R., & Lotem, A. (2018). Context-specific learning and its implications for social learning. *Behavioral Ecology*, *29*(5), 1046-1055. https://doi.org/10.1093/beheco/ary078

Tung, J., Barreiro, L. B., Burns, M. B., Grenier, J.-C., Lynch, J., Grieneisen, L. E., Altmann, J., Alberts, S. C., Blekhman, R., & Archie, E. A. (2015). Social networks predict gut microbiome composition in wild baboons. *eLife*, *4*, e05224. https://doi.org/10.7554/elife.05224.001

Turner, T. R., Anapol, F., & Jolly, C. J. (1997). Growth, development, and sexual dimorphism in vervet monkeys (*Cercopithecus aethiops*) at four sites in Kenya. *American Journal of Physical Anthropology*, *103*(1), 19-35. https://doi.org/10.1002/(SICI)1096-8644(199705)103:1<19::AID-AJPA3>3.0.CO;2-8

Turner, T. R., Schmitt, C. A., & Cramer, J. D. (2019). Behavioral Ecology of Savanna Monkeys. In T. R. Turner, C. A. Schmitt, & J. D. Cramer (Eds.), *Savanna Monkeys: The Genus Chlorocebus* (pp. 109-126). Cambridge University Press.

Turner, T. R., Schmitt, C. A., & Cramer, J. D. (2019). Introduction. In T. R. Turner, C. A. Schmitt, & J. D. Cramer (Eds.), *Savanna Monkeys: The Genus Chlorocebus* (pp. 3-15). Cambridge University Press.

Turner, T. R., Schmitt, C. A., & Cramer, J. D. (2019). Life History of Savanna Monkeys. In *Savanna Monkeys: The Genus Chlorocebus* (pp. 163-198). Cambridge University Press.

Vágási, C. I., Fülöp, A., Osváth, G., Pap, P. L., Pénzes, J., Benkő, Z., Lendvai, Á. Z., & Barta, Z. (2021). Social groups with diverse personalities mitigate physiological stress in a songbird. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1943), 20203092. https://doi.org/10.1098/rspb.2020.3092

Valsecchi, P., & Galef Jr, B. G. (1989). Social influences on the food preferences of house mice (*Mus musculus*). *International Journal of Comparative Psychology*, *2*(4), 245-256.

Varsanyi, S. (2021). *Maternal investment and offspring viability in vervet monkeys* [Unpublished master's thesis]. University of Lethbridge.

van de Waal, E., Borgeaud, C., & Whiten, A. (2013). Potent social learning and conformity shape a wild primate's foraging decisions. *Science*, *340*(6131), 483-485. https://doi.org/10.1126/science.1233675 van de Waal, E., Bshary, R., & Whiten, A. (2014). Wild vervet monkey infants acquire the food-processing variants of their mothers. *Animal Behaviour*, *90*(2014), 41-45. https://doi.org/10.1016/j.anbehav.2014.01.015

van de Waal, E., Claidière, N., & Whiten, A. (2013b). Social learning and spread of alternative means of opening an artificial fruit in four groups of vervet monkeys. *Animal Behaviour*, *85*(1), 71-76. https://doi.org/10.1016/j.anbehav.2012.10.008

van de Waal, E., Claidière, N., & Whiten, A. (2015). Wild vervet monkeys copy alternative methods for opening an artificial fruit. *Animal Cognition*, *18*(3), 617-627. https://doi.org/10.1007/s10071-014-0830-4

van de Waal, E., Krützen, M., Hula, J., Goudet, J., & Bshary, R. (2012). Similarity in food cleaning techniques within matrilines in wild vervet monkeys. *PLOS ONE*, *7*(4), e35694-8. https://doi.org/10.1371/journal.pone.0035694

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. https://doi.org/10.1098/rspb.2009.2260

van de Waal, E., van Schaik, C. P., & Whiten, A. (2017). Resilience of experimentally seeded dietary traditions in wild vervets: Evidence from group fissions. *American Journal of Primatology*, *79*(10), e22687. https://doi.org/10.1002/ajp.22687

van de Waal, E., & Whiten, A. (2012). Spontaneous emergence, imitation and spread of alternative foraging techniques among groups of vervet monkeys. *PLOS ONE*, *7*(10), e47008-7. https://doi.org/10.1371/journal.pone.0047008

van Leeuwen, E. J. C., Kendal, R. L., Tennie, C., & Haun, D. B. M. (2015). Conformity and its look-a-likes. *Animal Behaviour*, *110*, e1-e4. https://doi.org/10.1016/j.anbehav.2015.07.030

van Noordwijk, M. A., & van Schaik, C. P. (2005). Development of ecological competence in Sumatran orangutans. American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists, 127(1), 79-94. https://doi.org/10.1002/ajpa.10426

van Oers, K., Klunder, M., & Drent, P. J. (2005). Context dependence of personalities: risk-taking behavior in a social and a nonsocial situation. *Behavioral Ecology*, *16*(4), 716-723. https://doi.org/10.1093/beheco/ari045

van Schaik, C. P., Fragaszy, D., & Perry, S. (2003). Local traditions in orangutans and chimpanzees: Social learning and social tolerance. In D. Fragaszy & S. Perry (Eds.), *The Biology of Traditions: Models and Evidence* (pp. 297-328). Cambridge

University Press. https://doi.org/10.1017/CBO9780511584022.012

van Schaik, C. P. (2013). The costs and benefits of flexibility as an expression of behavioural plasticity: a primate perspective. *Philosophical Transactions of the Royal Society B*, *368*(1618), 20120339. https://doi.org/10.1098/rstb.2012.0339

Vehtari, A., Gelman, A., & Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and computing*, *27*(5), 1413-1432. https://arxiv.org/pdf/1507.04544.pdf).

Vilette, C., Bonnell, T., Henzi, P., & Barrett, L. (2020). Comparing dominance hierarchy methods using a data-splitting approach with real-world data. *Behavioral Ecology*, *31*(6), 1379-1390. https://doi.org/10.1093/beheco/araa095/5934850?casa_token=wz6WduWTg5QAAAAA:1TDOIH4W6S1aMG8WnXS-EeQWW2-Bk945N1z54eiPnflfg_QUZjzQZNsFO4Pd76lIlXa4qmIgfgyQ

Visalberghi, E., & Fragaszy, D. M. (1990). Do monkeys ape. In Parker, S.T & K. R. Gibson (Eds.), *Language and Intelligence in Monkeys and Apes: Comparative Developmental Perspectives* (pp. 27-273). Cambridge University Press. https://doi.org/10.1017/CBO9780511665486.011

Visalberghi, E., & Fragaszy, D. M. (1996). Social learning in monkeys. In C. M. Heyes & B. G. Galef Jr. (Eds.), *Social Learning in Animals. The Roots of Culture* (pp. 65-84). Academic Press.

Visalberghi, E., & Addessi, E. (2000). Seeing group members eating a familiar food enhances the acceptance of novel foods in capuchin monkeys. *Animal Behaviour*, *60*(1), 69-76. https://doi.org/10.1006/anbe.2000.1425

Visalberghi, E., & Fragaszy, D. (1995). The behaviour of capuchin monkeys, *Cebus apella*, with novel food: the role of social context. *Animal Behaviour*, *49*(4), 1089-1095.

Ward, A. J. W., Thomas, P., Hart, P. J. B., & Krause, J. (2004). Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology*, *55*(6), 561-568. https://link.springer.com/article/10.1007/s00265-003-0751-8

Webber, Q. M. R., Schneider, D. C., & Vander Wal, E. (2020). Is less more? A commentary on the practice of 'metric hacking' in animal social network analysis. *Animal Behaviour*, *168*, 109-120. https://doi.org/10.1016/j.anbehav.2020.08.011

Webster, M. M., Atton, N., Hoppitt, W. J. E., & Laland, K. N. (2013). Environmental complexity influences association network structure and network-based diffusion of foraging information in fish shoals. *The American Naturalist*, *181*(2), 235-244.

Webster, M. M., & Laland, K. N. (2008). Social learning strategies and predation risk: minnows copy only when using private information would be costly. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1653), 2869-2876. https://doi.org/10.1098/rspb.2008.0817

Webster, M. M., & Ward, A. J. W. (2011). Personality and social context. *Biological Reviews*, *86*(4), 759-773. https://doi.org/10.1111/j.1469-185X.2010.00169.x

Webster, M. M., Ward, A. J. W., & Hart, P. J. B. (2007). Boldness is influenced by social context in threespine sticklebacks (*Gasterosteus aculeatus*). *Behaviour*, 351-371. https://www.jstor.org/stable/4536449

Westneat, D. F., Hatch, M. I., Wetzel, D. P., & Ensminger, A. L. (2011). Individual Variation in Parental Care Reaction Norms: Integration of Personality and Plasticity. *The American Naturalist*, *178*(5), 652-667. https://doi.org/10.1086/662173

Wey, T. W., Jordán, F., & Blumstein, D. T. (2019). Transitivity and structural balance in marmot social networks. *Behavioral Ecology and Sociobiology*, *73*(6), 2108-2113. https://doi.org/10.1007/s00265-019-2699-3

Whalen, A., & Hoppitt, W. J. E. (2016). Bayesian model selection with network based diffusion analysis. *Frontiers in Psychology*, *7*, 409. https://doi.org/10.3389/fpsyg.2016.00409

Whiten, A., Custance, D. M., Gomez, J.-C., Teixidor, P., & Bard, K. A. (1996). Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *110*(1), 3-14. https://doi.org/10.1037/0735-7036.110.1.3

Whiten, A., Hinde, R. A., Laland, K. N., & Stringer, C. B. (2011). Culture evolves. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *366*(1567), 938-948. https://doi.org/10.1098/rstb.2010.0372

Willems, E. P., Barton, R. A., & Hill, R. A. (2009). Remotely sensed productivity, regional home range selection, and local range use by an omnivorous primate. *Behavioral Ecology*, *20*(5), 985-992. https://doi.org/10.1093/beheco/arp087

Wilson, A. J. (2018). How should we interpret estimates of individual repeatability? *Evolution Letters*, *219*, 631-635. https://doi.org/10.1002/evl3.40

Wolak, M. E., Fairbairn, D. J., & Paulsen, Y. R. (2011). Guidelines for estimating repeatability. *Methods in Ecology and Evolution*, *3*(1), 129-137. https://doi.org/10.1111/j.2041-210X.2011.00125.x

Wolf, M., van Doorn, G. S., Leimar, O., & Weissing, F. J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature*, *447*(7144), 581-584. https://doi.org/10.1038/nature05835

Wrangham, R. W., Jones, J. H., Laden, G., Pilbeam, D., & Conklin-Brittain, N. (1999). The Raw and the Stolen. Cooking and the Ecology of Human Origins. *Current Anthropology*, *40*(5), 567-594. http://eutils.ncbi.nlm.nih.gov/entrez/eutils/elink.fcgi?dbfrom=pubmed&id=10539941&retmode=ref&cmd=prlinks

Wrangham, R. W., & Waterman, P. G. (1981). Feeding behaviour of vervet monkeys on *Acacia tortilis* and *Acacia xanthophloea*: with special reference to reproductive strategies and tannin production. *The Journal of Animal Ecology*, *50*(3), 715-731. https://doi.org/10.2307/4132

Wray, M. K., Klein, B. A., & Seeley, T. D. (2012). Honey bees use social information in waggle dances more fully when foraging errors are more costly. *Behavioral Ecology*, *23*(1), 125-131. https://doi.org/10.1093/beheco/arr165

Young, C., Bonnell, T. R., Brown, L. R., Dostie, M. J., Ganswindt, A., Kienzle, S., McFarland, R., Henzi, S. P., & Barrett, L. (2019a). Climate induced stress and mortality in vervet monkeys. *Royal Society Open Science*, *6*(11), 191078. https://doi.org/10.1098/rsos.191078

Young, C., McFarland, R., Barrett, L., & Henzi, S. P. (2017). Formidable females and the power trajectories of socially integrated male vervet monkeys. *Animal Behaviour*, *125*(2017), 61-67. https://doi.org/10.1016/j.anbehav.2017.01.0066

Young, C., McFarland, R., Ganswindt, A., Young, M. M. I., Barrett, L., & Henzi, S. P. (2019b). Male residency and dispersal triggers in a seasonal breeder with influential females. *Animal Behaviour*, *154*, 29-37. https://doi.org/10.1016/j.anbehav.2019.06.010

Zajonc, R. B. (1965). Social facilitation. *Science*, *149*(3681), 269-274.

Zentall, T. R. (1996). An analysis of imitative learning in animals. In *Social Learning in Animals: The Roots of Culture* (pp. 221-243). Academic Press.

Zentall, T. R., Smith, A. P., & Beckmann, J. (2019). Differences in rats and pigeons suboptimal choice may depend on where those stimuli are in their behavior system. *Behavioural Processes*, *159*(2019), 37-41. https://doi.org/10.1016/j.beproc.2018.11.012

Zentall, T. R. (1988). Experimentally manipulated imitative behavior in rats and pigeons. In T. R. Zentall & B. G. Galef Jr. (Eds.), *Social Learning: Psychological and Biological* (pp. 203-218). Psychology Press.

Zschoke, A., & Thomsen, R. (2014). Sniffing Behaviours in Guenons. *Folia primatologica*, *85*(4), 244-251. https://doi.org/10.1159/000363409

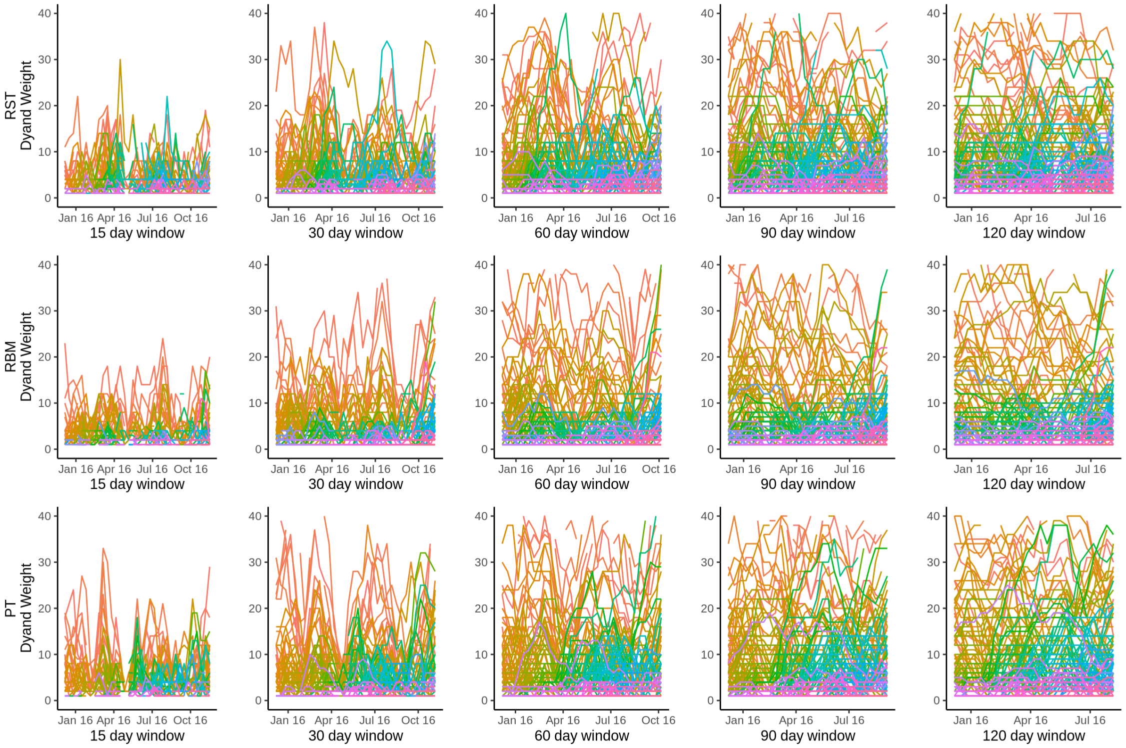
APPENDICES

Appendix A

A.1 Dyad Weights of Grooming and Spatial Proximity Networks

The figure below illustrates the dynamics of the (a) grooming and (b) spatial proximity networks through time. Dyad weights (also known as "ties") were calculated for 15-,30-, 60-, 90-, and 120-day sampling windows (columns) across each troop (rows) for each observed dyad (lines).

(a)



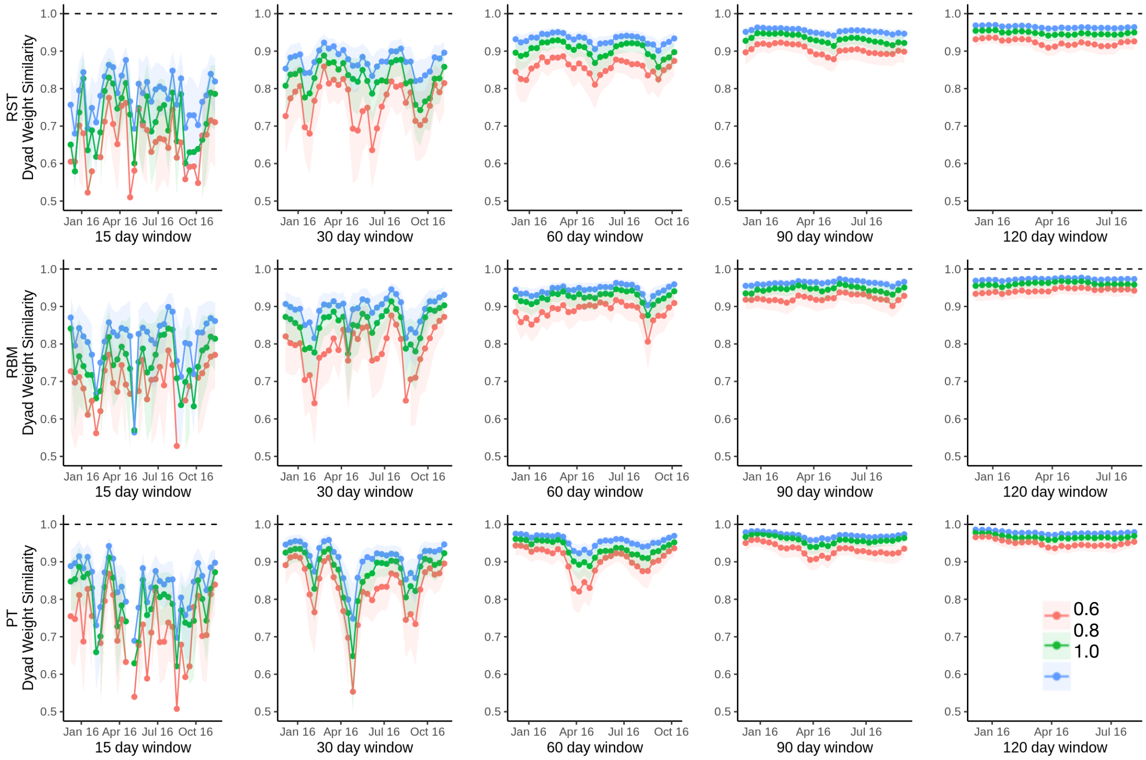
(b)


RST
Dyand Weight
RBM
Dyand Weight
PT
Dyand Weight
0
100
200
300
400
600
500
1000
1500
Jan 16
Apr 16
Jul 16
Oct 16
15 day window
30 day window
60 day window
90 day window
120 day window

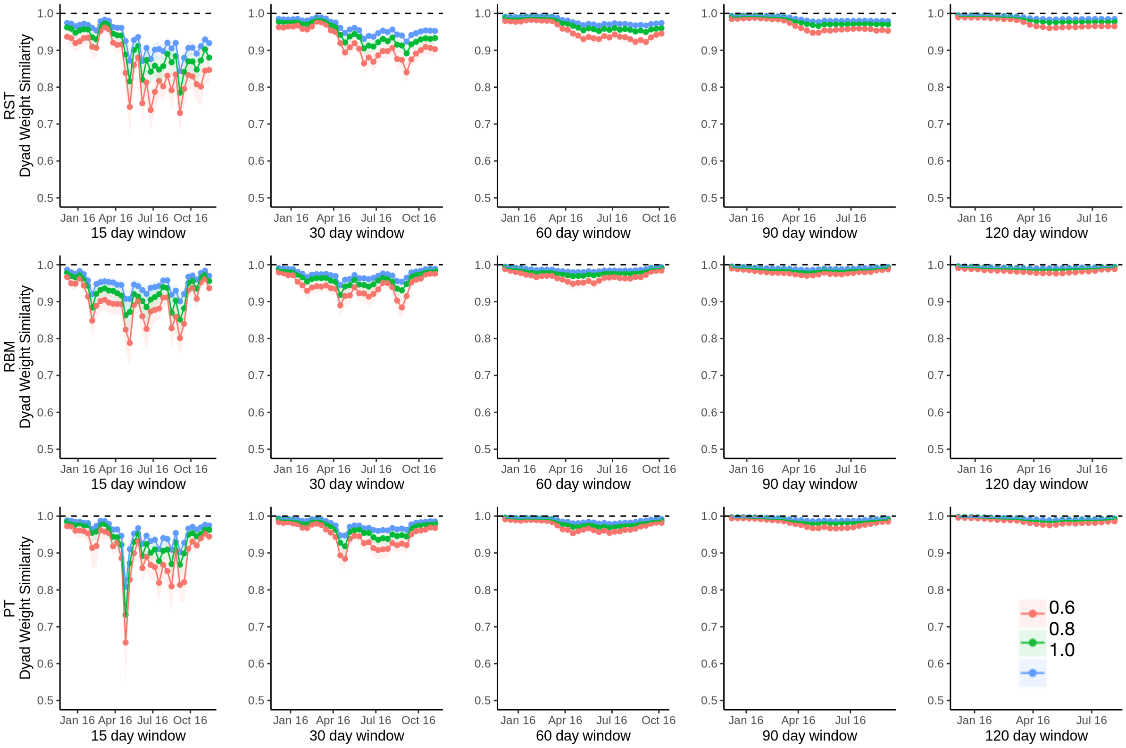
A.2 Determining Stability and Robustness of Network Sampling Windows

The figure below illustrates results of estimating the lower bound of window size choice using bootstrapping and subsampling for the (a) grooming and (b) spatial proximity networks across 15-, 30-, 60-, 90-, and 120-day sampling windows (columns) for each troop (rows). Lines represent mean dyad weight similarity, and the shaded region the 95% quantile, from 1000 bootstrap comparisons between dyad weights in the observed and bootstrapped networks. Network robustness was estimated by measuring the sensitivity to missing dyads using a random subsample of 60% (red points and lines) and 80% (green points and lines) the original dataset, and compared to the full sample (blue points and lines).

(a)



(b)



RST
Dyad Weight Similarity
RBM
Dyad Weight Similarity
PT
Dyad Weight Similarity
1.0
0.9
0.8
0.7
0.6
0.5
Jan 16
Apr 16
Jul 16
Oct 16
15 day window
30 day window
60 day window
90 day window
120 day window
0.6
0.8
1.0

Appendix B

B.1 Muzzle Contacts During Foraging and Social Contexts

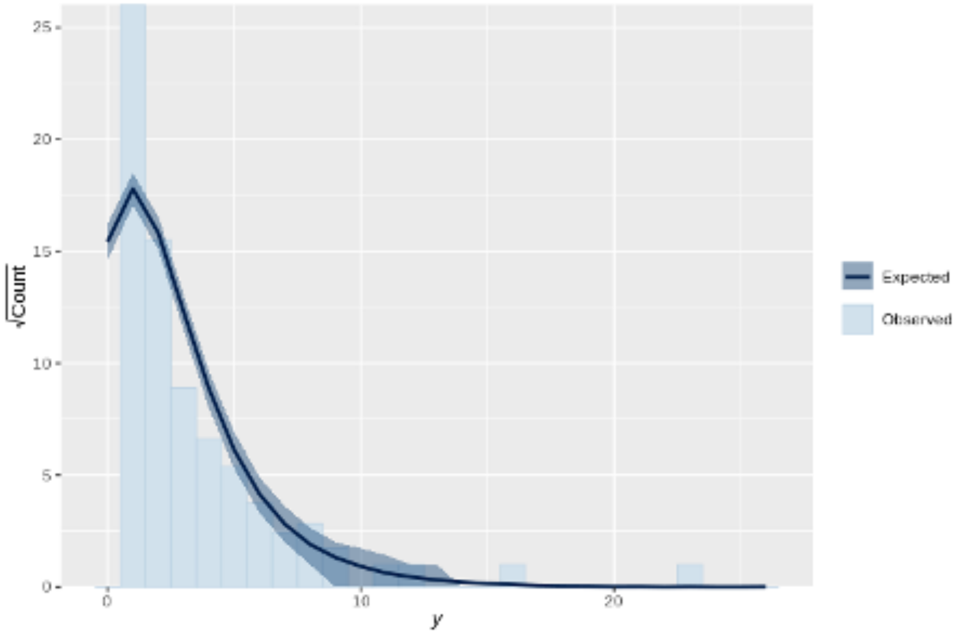
This video shows two examples of muzzle contact. Each example is first presented with annotation, and then presented again unedited. In the first example, an initiator (adult male) approaches a receiver (adult female) who is foraging on a succulent (*Sansevieria aethiopica*). The initiator then begins to forage within close proximity of the receiver after contact. In the second example, the initiator (juvenile male) muzzle contacts a juvenile female. The initiator then attempts to play with the receiver, and after the receiver does not reciprocate, the initiator remains within close proximity of the initiator.

B.2 How Often Do Juveniles Contact Kin? (Prediction E)

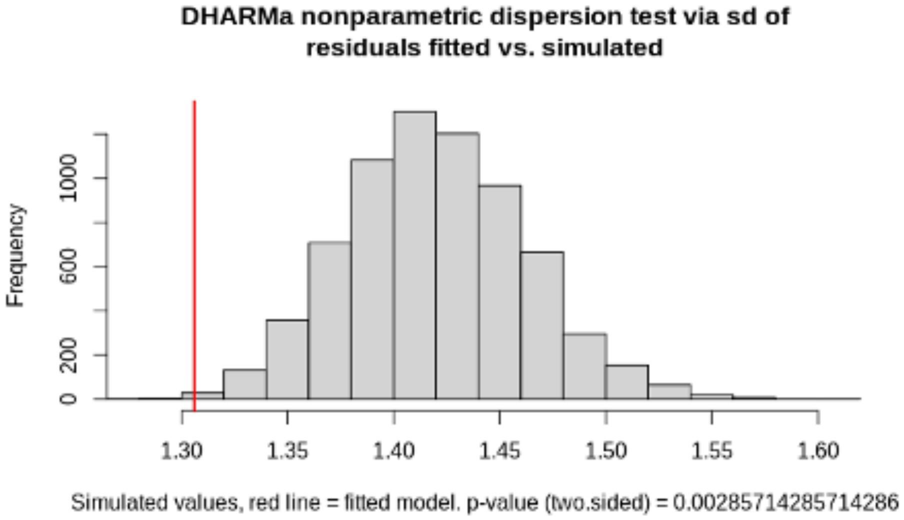
For this model, our response variable was a count of dyads association indices (i.e., dyad weights), indicating the use of a Poisson distribution. However, posterior predictive checks (using the *pp_check* function of the “brms” package: B.3; Bürkner, 2017; using the “testdispersion” function of the “DHARMa” package: B.4; Hartig, 2017) indicated that the dataset for this model was underdispersed. The output of this Poisson model is provided in the main text (Table 3.3), and presented as posterior density plots in B.3.

Observing underdispersion in our model indicated that the Poisson model was misspecified; that is, our data had less variance than expected by a Poisson distribution the dataset mean did not equal the dataset variance; Hilbe, 2017). As Hilbe (2017) notes, one possible means of correcting for underdispersed count data is to use a hurdle model. A hurdle model allows for the assumption of fewer (or greater) zeros than assumed by a count distribution, which, in our case, is a Poisson distribution. “Hurdle” models are so

B.3 Comparing the Observed Outcome Variable (Dyad Weights) to Datasets Simulated From the Posterior Predictive Distribution of the Association Indices Model Using a Poisson Distribution



B.4 Underdispersion in the Association Indices Dataset When Modeling Using a Poisson Distribution as Revealed Using the Dharma Nonparametric Dispersion Test

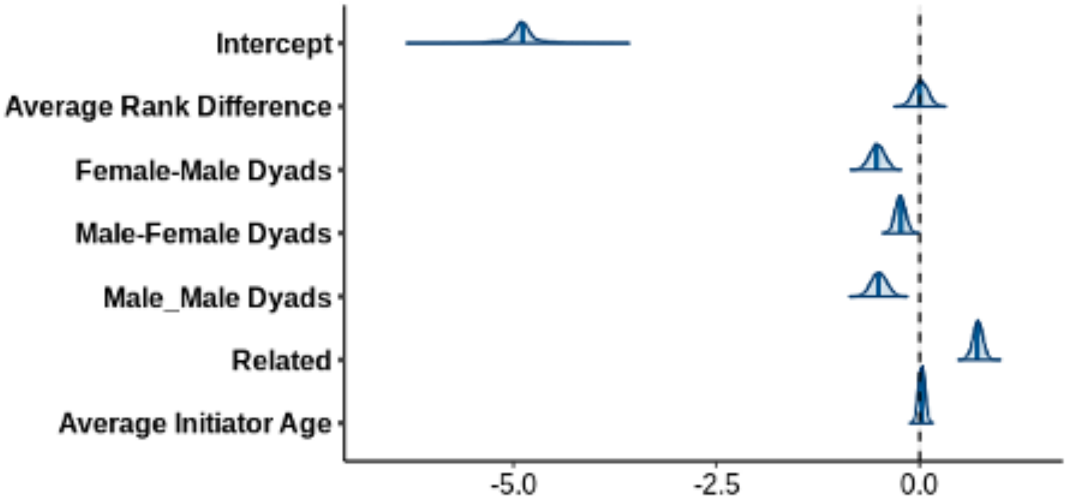


named because positive counts in the data are assumed to only result after first crossing some zero barrier, the "hurdle." Hurdle models partition the data into two parts: The first part assumes data are generated via a binary process creating positive versus zero counts, and the second part assumes data are generated from a process that generates only positive counts (Gurmu, 1998). Although the dataset for our model did not include zeros, the hurdle portion of a hurdle model can include values higher than zero (Hilbe, 2017), meaning that the hurdle is only overcome after exceeding the value set as the hurdle. As our dataset was underdispersed for dyads weights equaling one (B.3), we transformed the dataset by subtracting all weights by a value of one (i.e., weights of one count were transformed to weights of zero count, weights of two counts were transformed to weights of one count, etc.).

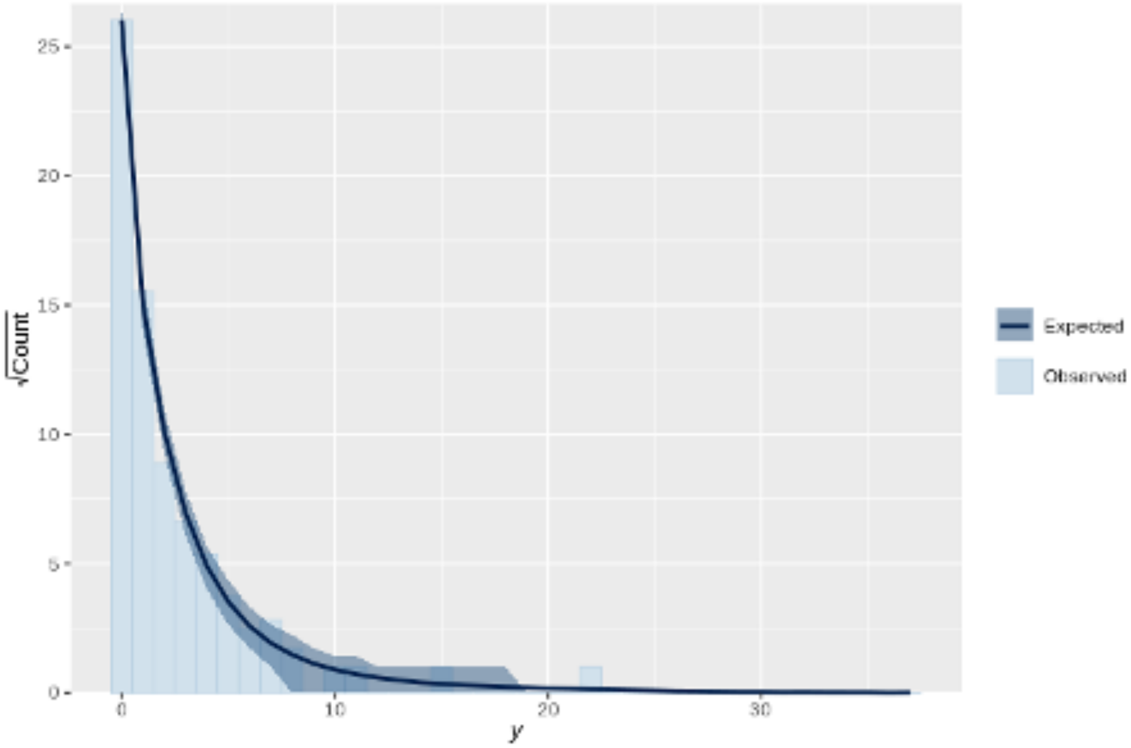
Hurdle models allow for different predictions for the hurdle and count portions of the model. We had no predictions as to what may generate differences in processes for the hurdle and count portion of our data and therefore specified the same fixed effects and random effects for each portion of the model, identical to the construction of the Poisson version of the model presented in the main text. Thus, dyad identity served as our response variable, and we included dyad sex, dyad dominance difference, average initiator age during the study period, and whether or not the dyad was related (yes/no) as fixed effects. We included muzzle contact initiator ID, muzzle contact receiver ID, initiator troop membership, and receiver troop membership as crossed random effects, as well as an offset variable accounting for the number of days each dyad was present during the sample period. Summary output for the hurdle model is given below (B.10, B.8).

Posterior predictive checks indicated that the hurdle model met model assumptions (B.6 and B.12). Additionally, the summary output revealed that all effects were relatively similar to the Poisson model presented in the main text (Table 3.3): we found low association indices between most muzzle contact dyads, kin-based muzzle contacts occurred at the highest rates compared to nonkin-based muzzle contact, there was no effect of average initiator age, and R^2 values reveal a moderate effect of individual differences on overall model performance (B.6).

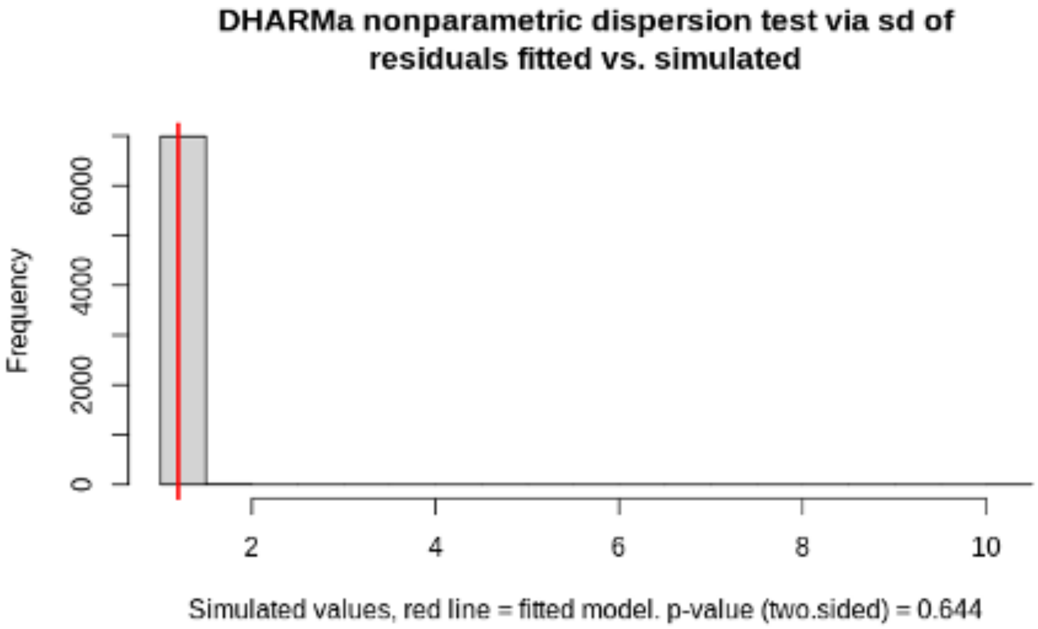
B.5 Posterior Density Plot of the Association Indices Model Using a Poisson Distribution



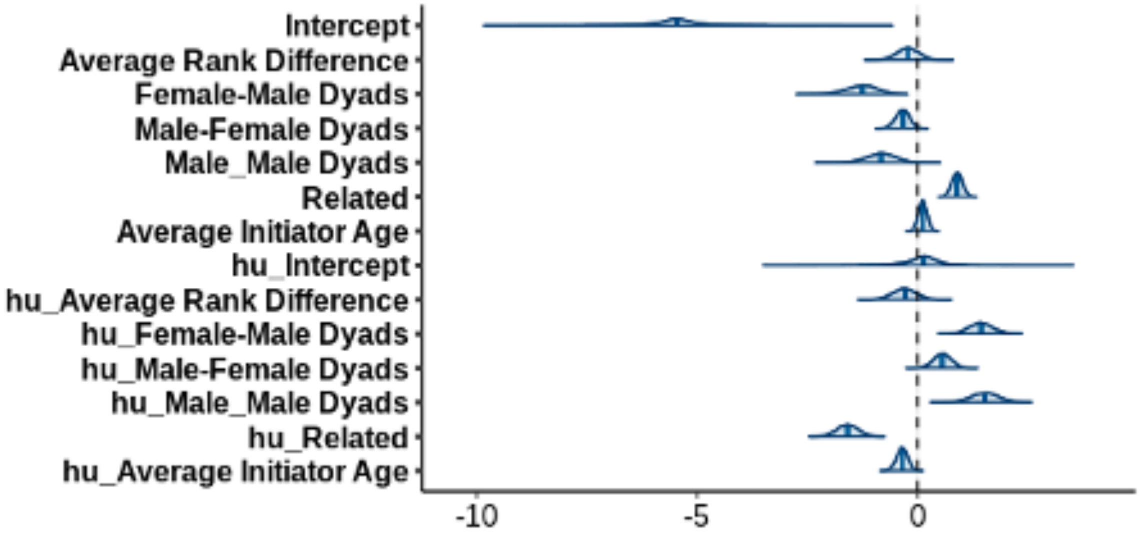
B.6 Comparing the Observed Outcome Variable (Dyad Weights) to Datasets Simulated From the Posterior Predictive Distribution of the Association Indices Model Using a Hurdle Poisson Distribution



B.7 No Underdispersion in the Association Indices Dataset When Modeling Using a Hurdle Poisson Distribution as Revealed Using the Dharma Nonparametric Dispersion Test



B.8 Posterior Density Plot of the Association Indices Model Using a Hurdle Poisson Distribution



B.9 Is There a Kin Basis to Muzzle Contact?

How Often Do Juveniles Contact Kin?

While we contend that contacting kin less than 10% of the time does not constitute large biological relevance, and thus do not conclude that animals are targeting kin more than nonkin for muzzle contact, some readers may prefer to test this null against expected rates of contacting kin given their availability to initiators. In B.11, we present observed rates of contact directed towards kin by each juvenile in the analysis alongside expected rates calculated by using the average proportion of kin within 2 m (calculated from the scan samples) as well as the proportion of kin to nonkin in their troop. B.12 presents these data as violin plots.

How Often Do Initiators Contact Foragers?

Footnote 1 in the Discussion explains that we could use an alternative null to test our targeting foragers hypothesis against. Rather than comparing rates of contacting foragers to a null that expects this to happen 50% of the time (given that initiators could target foragers or nonforagers equally), we could compare contact rates to a null that would expect initiators to contact foragers on par with the proportion of animals that are foraging at any given time.

To determine this proportion, we first calculated the average proportion of animals that were foraging during instantaneous scan samples (Altmann, 1974) collected every 30 min from all individuals that could be located within a 10 min time window (Young et al., 2017) across our study period, yielding 18,039 scan samples. Then, because these proportions included both scan samples when no animals were foraging (zeros) and all animals were foraging (ones), we constructed a zero-one-inflated-beta model to determine the average proportion of animals foraging during any given scan sample. For this model, the proportion of animals foraging during the scan was the response variable, and scan identity nested within troop identity served as a random effect (because we were not testing any predictions, this model did not contain any fixed effects). Model main effects are presented in B.13.

We found that on average, 27.0% of animals are foraging at any given time (B.13; we calculated percentages using model marginal means and backtransformed this value into the original scale). We could amend our interpretations to say that using this null, we did find that initiators are targeting foragers since they do so 46.7% of the time. However, we decided against doing so, since this 27.0% value does not take into consideration variables known in our population to affect foraging rates (such as sex and seasonality; McFarland et al., 2014; Young et al., 2019).

B.10 Posterior Estimates of Association Indices Using a Hurdle Poisson

Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept (Female-Female Dyads)	-5.460	0.890	-7.527	-3.427
	Average Rank Difference	-0.217	0.241	-0.689	0.245
	Relatedness	0.901	0.117	0.674	1.130
	Female-Male Dyads	-1.266	0.340	-1.969	-0.634
	Male-Female Dyads	-0.340	0.155	-0.654	-0.043
	Male-Male Dyads	-0.827	0.319	-1.472	-0.220
	Average Initiator Age	0.121	0.097	-0.070	0.314
	hu_Intercept (Female-Female Dyads)	0.070	0.555	-1.324	1.092
	hu_Average Rank Difference	-0.297	0.273	-0.847	0.237
	hu_Relatedness	-1.590	0.246	-2.076	-1.108
	hu_Female-Male Dyads	1.444	0.269	0.926	1.984
	hu_Male-Female Dyads	0.565	0.208	0.144	0.970
	hu_Male-Male Dyads	1.534	0.308	0.930	2.153
	hu_Average Initiator Age	-0.349	0.128	-0.613	-0.103
Group-Level Effects	sd(Initiator)	0.108	0.078	0.004	0.289
	sd(Initiator troop)	0.547	0.851	0.010	2.928
	sd(Receiver)	0.129	0.087	0.006	0.326
	sd(Receiver troop)	0.722	1.348	0.009	5.300
	sd(hu_Initiator)	0.522	0.126	0.278	0.778
	sd(hu_Initiator troop)	0.537	0.896	0.009	2.901
	sd(hu_Receiver)	0.573	0.125	0.328	0.826
	sd(hu_Receiver troop)	0.553	0.880	0.013	2.875

Note. Sex is relative female-female dyads. All initiators are juveniles. Estimates are on the logit scale for the hurdle portion of the model (hu), and on the log scale for the count portion of the model; CI = credible interval, SD = standard deviation. N = 1,105. R^2 marginal = .140; R^2 conditional = .315.

B.11 Proportion of Kin Available to Initiators

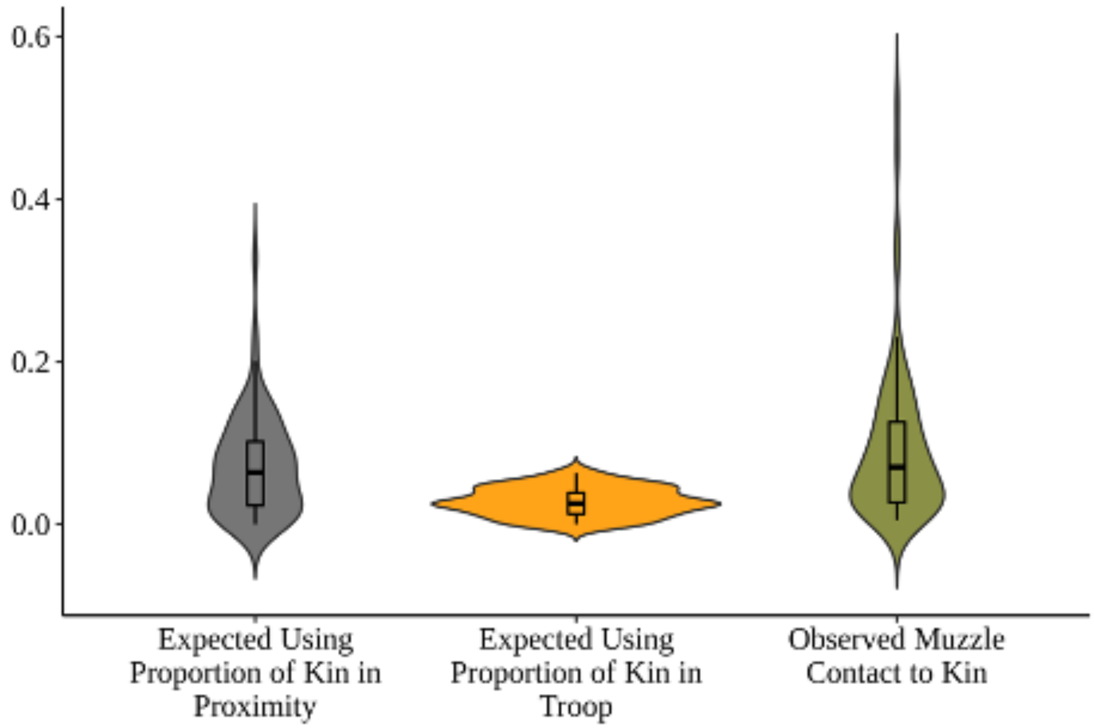
ID	Observed Proportion Muzzle Contacts to Kin	Expected Using Proportion of Kin in Proximity	Expected Using Proportion of Kin in Troop
socr	0.027	0.141	0.063
hect	0.190	0.013	0.026
fent	0.110	0.044	0.013
saff	0.101	0.327	0.013
glue	0.049	0.031	0.012
katn	0.027	0.057	0.012
elto	0.132	0.105	0.048
ligh	0.178	0.034	0.036
wolo	0.012	0.117	0.013
dart	0.022	0.128	0.024
peet	0.016	0.142	0.048
deso	0.033	0.124	0.024
lia	0.034	0.039	0.038
thor	0.038	0.072	0.026
tucs	0.070	0.006	0.026
tita	0.519	0.017	0.026
grub	0.077	0.056	0.012
pumb	0.139	0.112	0.026
nife	0.038	0.013	0.026
timm	0.093	0.000	0.051
damo	0.043	0.052	0.038
polk	0.154	0.083	0.026
cind	0.011	0.017	0.013
fina	0.036	0.000	0.000
pino	0.024	0.078	0.050
lore	0.022	0.009	0.025
puck	0.149	0.022	0.051
omni	0.025	0.098	0.025
cact	0.070	0.034	0.013

dire	0.115	0.099	0.000
pupi	0.021	0.030	0.012
spoc	0.134	0.087	0.063
amy	0.033	0.033	0.036
rock	0.078	0.000	0.000
torn	0.035	0.078	0.048
gord	0.008	0.020	0.000
band	0.054	0.078	0.038
tarz	0.016	0.000	0.000
loki	0.074	0.033	0.036
cola	0.119	0.086	0.050
oreo	0.010	0.085	0.025
glac	0.044	0.057	0.000
leon	0.110	0.000	0.024
emil	0.081	0.085	0.048
disn	0.024	0.061	0.038
howz	0.043	0.000	0.026
shel	0.072	0.082	0.038
home	0.173	0.007	0.025
funk	0.024	0.028	0.013
vect	0.072	0.000	0.000
piec	0.076	0.064	0.026
sarg	0.352	0.163	0.063
gizm	0.174	0.156	0.025
daen	0.151	0.129	0.000
swee	0.067	0.065	0.013
trip	0.016	0.093	0.048
prof	0.023	0.026	0.012
kumq	0.083	0.023	0.012
eve	0.137	0.082	0.048
caba	0.015	0.126	0.050
bilb	0.023	0.061	0.038
stru	0.033	0.065	0.038

luxe	0.214	0.034	0.038
gats	0.118	0.124	0.025
unfu	0.087	0.012	0.000
arag	0.086	0.027	0.036
podg	0.230	0.154	0.048
nobo	0.005	0.000	0.000
pean	0.061	0.071	0.050
dice	0.177	0.102	0.024
octo	0.117	0.118	0.025
kiss	0.026	0.000	0.000
guge	0.177	0.148	0.025
wood	0.034	0.099	0.013
port	0.070	0.234	0.048
swaz	0.454	0.200	0.063
cura	0.325	0.138	0.050
sava	0.144	NA	0.025
crea	0.098	NA	0.025
Mean	0.093	0.071	0.028

Note. “Sava” and “Crea” were infants during the study period and thus not focal subjects during scan sampling as we do not collect behavioral data on infants. Although these infants do appear as proximity partners for animals that are the focus of scan samples, we chose to calculate kin proximities using only scans for which the animal of interest was the focal animal during the scan sample to ensure equal sampling across animals.

B.12 Expected and Observed Proportions of Initiators That Muzzle Contacted Foragers



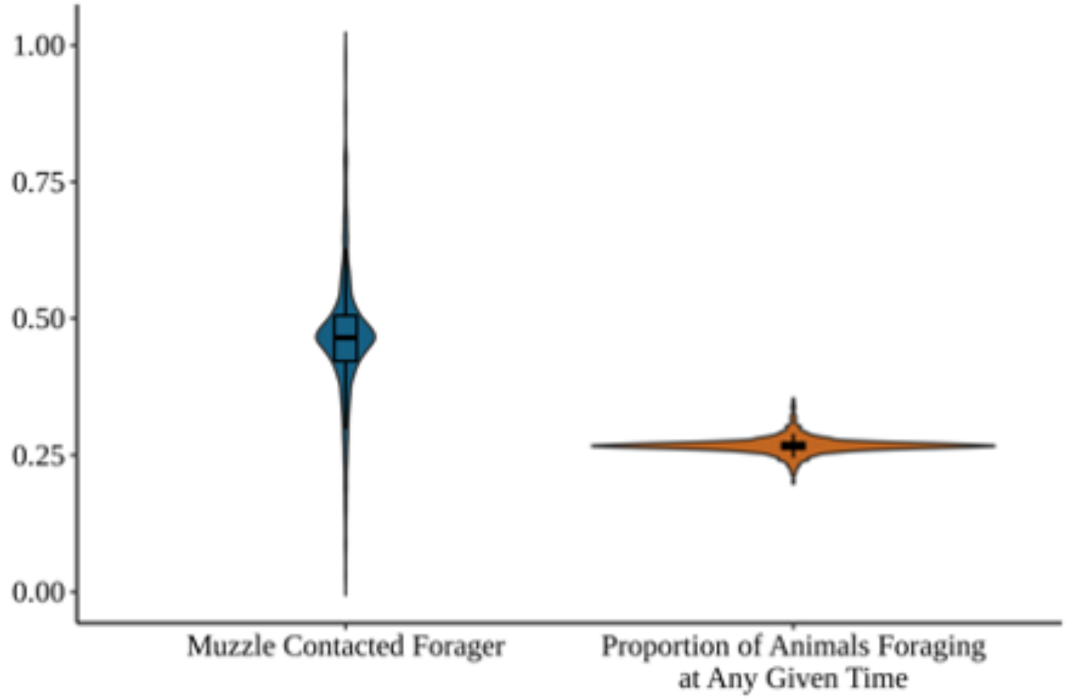
Note. Proportions are backtransformed from the logit scale into the original scale (Expected Using Proportion of Kin in Proximity and Troop, B.11; Observed Muzzle Contact to Kin, B.11).

B.13 Posterior Estimates of Proportions of Animals Foraging at Any Given Time

Effect	Parameter	Estimate	Estimate Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept	-0.632	0.094	-0.842	-0.420
Group-Level Effects	Troop	0.142	0.164	0.024	0.618
	Scan	0.234	0.018	0.200	0.268

Note. N = 18,039. R^2 marginal = .000; R^2 conditional = .023.

B.14 Proportion of Initiators That Muzzle Contacted Foragers and the Proportions of Animals Foraging at Any Given Time



Note. Proportions are backtransformed from the logit scale into the original scale (Muzzle Contacted Forager, Table 3.7; Proportion of Animals Foraging at Any Given Time, B.13).

Appendix C

C.1 Description of the Novel Food Trials for Each Animal

Date	ID	Age/ Sex	Rank	Troop	Trial	Stim.	Total Trials	Dur.	Expose (y/n)	Interrupt (y/n)
11/21/16	Arwe	AF	-0.07	RST	2018	pink potato	2	44.8	n	n
11/26/16	Vect	JM	-0.14	RST	2324	blue potato	1	37.0	n	n
11/26/16	Loki	JM	-0.16	RST	2327	blue potato	4	31.2	n	y
11/30/16	Pino	JM	-0.01	RBM	2335	blue potato	2	41.9	n	n
11/30/16	Panc	AM	0.82	RBM	2336	blue potato	2	152.2	n	y
12/2/16	Stru	JM	-0.20	PT	2362	blue potato	4	37.3	n	n
12/8/16	Brie	AF	0.25	PT	2425	pink apple	3	163.0	n	n
12/8/16	Rock	JM	0.05	PT	2426	pink apple	2	43.1	n	n
12/9/16	Peet	JF	0.47	RST	2432	baby corn	4	232.0	n	y
1/6/17	Xavi	AM	0.29	PT	2627	blue potato	1	29.1	n	n
1/6/17	Clou	AM	0.19	PT	2635	blue potato	1	121.5	n	n
1/7/17	Guge	JF	-0.36	RBM	2648	blue potato	3	29.1	n	n
1/7/17	Caba	JF	-0.17	RBM	2652	blue potato	4	40.0	n	y
1/7/17	Sarg	JF	-0.00	RBM	2652	blue potato	4	40.0	n	y
1/7/17	Dori	AF	-0.26	RBM	2652	blue potato	1	40.0	n	y
1/19/17	Mori	AM	1.00	PT	1544	blue potato	4	114.9	n	n
1/23/17	Unfu	JM	-0.27	RST	553.1554	red grape	1	201.5	n	n
1/23/17	Podg	JF	0.32	RST	1557	red grape	1	402.6	n	n
1/23/17	Zool	AM	0.52	RST	1567	red grape	4	31.8	y	n
1/25/17	Meg	AF	0.17	RST	1558	red grape	2	14.8	n	n
1/25/17	Deso	JF	-0.17	RST	1562	red grape	6	303.0	n	n
1/25/17	Ligh	JM	-0.07	RST	1564	red grape	2	184.2	n	n
1/25/17	Kumq	JF	-0.42	RST	1565	red grape	4	55.7	n	n
1/25/17	Zool	AM	0.52	RST	1566	red grape	4	89.5	n	n
1/25/17	Grub	JM	-0.24	RST	1568	red grape	2	35.5	n	n
1/25/17	Katn	JF	-0.40	RST	1571	red grape	4	116.0	n	n
1/26/17	Pumb	JM	-0.21	PT	1578	red grape	2	121.2	n	y
1/26/17	Polk	JF	-0.35	PT	1580	red grape	3	14.0	n	n
1/26/17	Herm	AF	-0.19	PT	1583	red grape	4	80.1	n	n

Date	ID	Age/ Sex	Rank	Troop	Trial	Stim.	Total Trials	Dur.	Expose (y/n)	Interrupt (y/n)
1/26/17	Mori	AM	1.00	PT	1583	red grape	4	80.1	n	n
1/26/17	Piec	JM	-0.23	PT	1584	red grape	3	144.8	n	n
1/26/17	Polk	JF	-0.35	PT	1584	red grape	3	144.8	n	n
1/26/17	Shel	JM	0.08	PT	2941	red grape	3	175.7	n	n
1/27/17	Sash	AF	1.00	RBM	1592	blue potato	4	85.5	n	n
1/27/17	Octo	JM	-0.23	RBM	1598	red grape	3	64.4	n	n
1/27/17	Oreo	JF	-0.23	RBM	1600	red grape	2	54.5	n	n
1/27/17	Lore	JF	-0.12	RBM	1602	red grape	3	66.3	n	n
1/27/17	Gizm	JF	0.04	RBM	1603	blue potato	3	135.6	n	n
1/27/17	Funk	JM	-0.03	RBM	1605	red grape	3	69.2	n	n
1/30/17	Saff	AF	0.57	RBM	1616	red grape	3	192.5	n	y
1/30/17	Cind	JF	-0.08	RBM	1616	red grape	5	192.5	n	y
1/30/17	Saffin f16	JM	NA	RBM	1616	red grape	1	192.5	n	y
1/30/17	Wolo	JF	-0.24	RBM	1618	red grape	4	143.1	n	n
1/31/17	Obi	AM	0.32	RST	1624	yellow marrow	2	60.4	n	n
1/31/17	Ligh	JM	-0.07	RST	1627	yellow marrow	2	16.6	y	n
1/31/17	Dice	JF	-0.38	RST	1635	yellow marrow	3	122.6	n	n
1/31/17	Laur	AF	-0.13	RST	1635	yellow marrow	3	122.6	n	n
2/1/17	Turt	AF	-0.14	PT	1647	blue potato	2	18.1	n	n
2/1/17	Lisa	AF	0.05	PT	1660	yellow marrow	4	48.9	n	n
2/1/17	Thor	JF	0.17	PT	1662	yellow marrow	1	229.4	n	n
2/1/17	Nife	JF	-0.38	PT	1662	yellow marrow	3	229.4	n	n
2/2/17	Cind	JF	-0.08	RBM	1664	yellow marrow	5	43.3	y	n
2/2/17	Oreo	JF	-0.23	RBM	1665	yellow marrow	2	91.3	n	n
2/6/17	Razo	AM	0.15	RBM	1684	yellow marrow	1	64.1	n	n
2/6/17	Wolo	JF	-0.24	RBM	1690	yellow marrow	4	51.4	n	n
2/6/17	Spoc	JM	0.09	RBM	1691	yellow marrow	2	112.5	n	n
2/7/17	Puzz	AF	-0.08	PT	1701	yellow marrow	1	47.2	n	n
2/7/17	Tyle	AM	0.33	PT	1705	yellow marrow	2	11.1	n	n
2/7/17	Tarz	JM	-0.10	PT	1708	yellow marrow	2	62.5	n	n
2/7/17	Octo	JM	-0.23	RBM	1720	yellow marrow	3	78.1	n	y

Date	ID	Age/ Sex	Rank	Troop	Trial	Stim.	Total Trials	Dur.	Expose (y/n)	Interrupt (y/n)
2/10/17	Fina	JF	-0.29	RBM	1717	yellow marrow	2	48.3	n	n
2/10/17	Coco	AF	0.41	RBM	1719	yellow marrow	3	59.5	n	n
2/10/17	Sarg	JF	-0.00	RBM	1723	yellow marrow	4	57.4	n	n
2/10/17	Caba	JF	-0.17	RBM	1723	yellow marrow	4	57.4	n	n
2/10/17	Daen	JF	-0.44	RBM	1725	yellow marrow	1	196.9	n	n
2/13/17	Need	AF	0.06	PT	1728	yellow marrow	2	15.4	n	n
2/13/17	Daff	AF	-0.11	PT	1738	yellow marrow	3	23.9	n	n
2/13/17	Glac	JM	-0.21	PT	1739	yellow marrow	1	48.7	n	n
2/14/17	Cact	JM	-0.06	RBM	1744	blue potato	1	56.4	n	n
2/14/17	Pean	JF	-0.34	RBM	1750	blue potato	4	151.4	n	n
2/14/17	Cola	JF	-0.11	RBM	1754	blue potato	3	243.4	n	n
2/15/17	Torn	JM	-0.19	RST	1762	blue potato	2	54.6	n	y
2/15/17	Wall	AM	0.68	RST	1765	blue potato	2	176.2	n	n
2/15/17	Trip	JM	-0.23	RST	1765	blue potato	4	176.2	n	n
2/15/17	Eve	JF	-0.21	RST	1766	blue potato	2	17.6	n	n
2/15/17	Prof	JM	-0.12	RST	1771	blue potato	2	45.8	n	n
2/15/17	Leon	JM	0.04	RST	1779	blue potato	3	40.9	n	y
2/15/17	Glue	JF	-0.20	RST	1784	blue potato	4	15.7	n	n
2/16/17	Fent	JM	0.21	RBM	1789	blue potato	1	41.6	n	n
2/16/17	Puck	JM	-0.24	PT	1791	blue potato	1	66.8	n	n
2/17/17	Arag	JF	-0.26	RST	1798	blue potato	2	128.2	n	n
2/17/17	Peet	AF	0.61	RST	1804	blue potato	4	133.8	n	n
2/17/17	Dart	JF	0.03	RST	1804	blue potato	1	133.8	n	y
2/20/17	Elto	JF	-0.44	RST	1808	blue potato	3	59.6	n	n
2/20/17	Kiss	JM	-0.04	RST	1811	blue potato	2	168.5	n	n
2/20/17	Alla	AM	0.60	RST	1811	blue potato	3	168.5	n	n

Date	ID	Age/ Sex	Rank	Troop	Trial	Stim.	Total Trials	Dur.	Expose (y/n)	Interrupt (y/n)
2/20/17	Ella	AF	-0.14	RST	1812	blue potato	2	57.0	n	n
2/20/17	Deso	JF	-0.17	RST	1819	blue potato	6	101.8	n	y
2/20/17	Amy	JF	-0.30	RST	1819	blue potato	2	101.8	y	n
2/20/17	Yoda	AM	0.25	RST	1820	blue potato	2	7.3	n	n
2/20/17	Socr	JF	0.18	RBM	1827	blue potato	3	50.3	y	y
2/21/17	Home	JM	-0.17	RBM	1822	blue potato	2	56.1	n	n
2/21/17	Wood	JM	-0.23	RBM	1823	blue potato	1	58.5	n	n
2/21/17	Pean	JF	-0.34	RBM	1824	blue potato	4	126.8	y	n
2/21/17	Swee	JM	0.00	RBM	1824	blue potato	3	126.8	n	n
2/21/17	Swaz	JF	NA	RBM	826.182	blue potato	4	52.8	n	y
2/21/17	Sash	AF	1.00	RBM	1827	blue potato	4	50.3	y	y
2/22/17	Pupi	JF	-0.24	RST	1832	blue potato	3	105.9	n	n
2/23/17	Hect	JM	-0.21	PT	1834	blue potato	2	111.2	n	n
3/18/17	Dodg	AM	0.12	PT	1875	yellow marrow	2	239.4	n	n
3/19/17	Disn	JF	-0.22	PT	1862	yellow marrow	2	253.0	n	n
3/19/17	Stru	JM	-0.14	PT	1862	yellow marrow	4	253.0	y	n
3/19/17	Shum	AF	-0.49	PT	1863	yellow marrow	2	16.5	n	n
3/19/17	Tucs	JM	-0.34	PT	1864	yellow marrow	3	68.0	n	n
3/19/17	Howz	JF	-0.33	PT	1865	yellow marrow	5	71.6	y	y
3/19/17	Timm	JM	-0.07	PT	1874	yellow marrow	3	126.1	n	n
3/19/17	Dire	JF	-0.57	RBM	1882	yellow marrow	2	104.4	n	n
3/19/17	Holl	AF	-0.06	RBM	3625	yellow marrow	3	12.8	n	n
3/19/17	Shel	JM	0.08	PT	3628	yellow marrow	3	141.5	n	y
5/4/17	Bilb	JM	-0.02	PT	1910	pink potato	3	82.3	n	n
5/4/17	Gord	JF	-0.21	PT	1914	pink potato	2	67.2	n	n
5/4/17	Herm	AF	-0.24	PT	1917	pink potato	4	46.4	n	n

Date	ID	Age/ Sex	Rank	Troop	Trial	Stim.	Total Trials	Dur.	Expose (y/n)	Interrupt (y/n)
5/4/17	Schm	AM	0.48	PT	1917	pink potato	1	46.4	n	n
5/5/17	Swaz	JF	0.01	RBM	1921	blue eggplant	4	111.0	n	y
5/5/17	Guge	JF	-0.22	RBM	1921	pink potato	3	111.0	y	y
5/5/17	Sarg	JF	0.07	RBM	1921	pink potato	4	111.0	y	y
5/5/17	Gizm	JF	-0.10	RBM	1921	blue eggplant	3	111.0	n	n
5/5/17	Socr	JF	0.26	RBM	1922	pink potato	3	34.0	n	n
5/5/17	Saff	AF	0.43	RBM	1923	pink potato	3	116.6	n	n
5/5/17	Sarg	JF	0.07	RBM	1923	pink potato	4	116.6	y	y
5/5/17	Flyn	AM	0.89	RBM	1924	pink potato	1	41.7	n	n
5/5/17	Lucy	AF	0.33	RBM	1929	pink potato	3	18.8	n	y
5/5/17	Pean	JF	-0.21	RBM	1930	pink potato	4	48.4	n	n
5/5/17	Cind	JF	0.04	RBM	1930	pink potato	5	48.4	y	n
5/8/17	Piec	JM	-0.25	PT	1932	pink potato	3	66.2	n	n
5/8/17	Daff	AF	0.05	PT	1932	pink potato	3	66.2	n	n
5/8/17	Timm	JM	-0.07	PT	1934	pink potato	3	95.2	n	n
5/8/17	Lisa	AF	0.02	PT	1940	blue potato	4	39.0	n	y
5/8/17	Luxe	JM	-0.14	PT	1940	pink potato	2	39.0	n	y
5/8/17	Tarz	JM	-0.02	PT	1941	pink potato	2	68.7	n	n
5/8/17	Pumb	JM	-0.20	PT	4381	pink potato	2	193.7	n	n
5/9/17	Laya	AF	-0.17	RST	1945	pink potato	1	21.2	n	n
5/9/17	Leon	JM	-0.03	RST	1945	pink potato	3	21.2	n	n
5/9/17	Peet	AF	0.73	RST	1946	pink potato	4	114.9	y	n
5/9/17	Torn	JM	-0.26	RST	1946	pink potato	2	114.9	y	y
5/9/17	Pupi	JF	-0.24	RST	1949	pink potato	3	126.4	y	y
5/9/17	Kumq	JF	-0.66	RST	1949	pink potato	4	126.4	n	n
5/9/17	Katn	JF	-0.30	RST	1949	blue eggplant	4	126.4	y	n

Date	ID	Age/ Sex	Rank	Troop	Trial	Stim.	Total Trials	Dur.	Expose (y/n)	Interrupt (y/n)
5/9/17	Alla	AM	0.66	RST	1949	blue eggplant	3	126.4	n	n
5/9/17	Deso	JF	-0.19	RST	1962	pink potato	6	125.3	n	n
5/9/17	Arag	JF	-0.28	RST	1964	blue potato	2	77.5	y	n
5/9/17	Grub	JM	-0.18	RST	1964	pink potato	2	77.5	n	n
5/9/17	Glue	JF	-0.09	RST	1972	pink potato	4	38.9	n	n
5/9/17	Elto	JF	-0.36	RST	1974	pink potato	3	60.2	n	n
5/9/17	Alla	AM	0.66	RST	1975	pink potato	3	173.3	n	n
5/10/17	Cind	JF	0.04	RBM	4406	blue eggplant	5	72.2	y	n
5/10/17	Wolo	JF	-0.51	RBM	4410	pink potato	4	79.5	n	n
5/10/17	Fina	JF	-0.35	RBM	4413	pink potato	2	54.6	y	n
5/10/17	Phoe	AF	-0.03	RBM	4416	blue eggplant	3	89.7	n	n
5/10/17	Panc	AM	0.87	RBM	4416	pink potato	2	89.7	y	y
5/10/17	Dire	JF	-0.34	RBM	4424	pink potato	2	248.4	n	y
5/10/17	Home	JM	-0.30	RBM	4429	pink potato	2	23.9	y	n
5/10/17	Lore	JF	-0.19	RBM	4431	pink potato	3	271.0	n	n
5/10/17	Sash	AF	1.00	RBM	4431	pink potato	4	271.0	n	n
5/11/17	Emil	JF	-0.26	RST	1978	pink potato	1	141.6	n	n
5/11/17	Zool	AM	0.35	RST	1978	pink potato	4	141.6	n	n
5/11/17	Ella	AF	-0.07	RST	1981	pink potato	2	60.9	n	n
5/11/17	Katn	JF	-0.30	RST	1983	pink potato	4	164.0	y	y
5/11/17	Peet	AF	0.73	RST	1983	pink potato	4	164.0	y	y
5/11/17	Cycl	AF	-0.05	RST	1983	pink potato	1	164.0	n	n
5/11/17	Obi	AM	0.14	RST	1986	pink potato	2	46.5	n	n
5/11/17	Lucy	AF	0.33	RBM	4416	pink potato	3	89.7	y	n
6/1/17	Damo	JM	-0.27	PT	2136	blue potato	4	91.3	n	y
6/2/17	Phoe	AF	-0.03	RBM	1688	yellow marrow	3	52.3	n	n
4/2/18	Zool	AM	0.54	RST	1998	pumpkin	4	106.8	n	n

Date	ID	Age/ Sex	Rank	Troop	Trial	Stim.	Total Trials	Dur.	Expose (y/n)	Interrupt (y/n)
4/2/18	Dice	JF	-0.44	RST	2002	pumpkin	3	161.1	n	n
4/2/18	Glue	JF	-0.35	RST	2002	pumpkin	4	161.1	y	y
4/2/18	Arwe	AF	-0.09	RST	2002	pumpkin	2	161.1	y	y
4/2/18	Leon	JM	NA	RST	2004	pumpkin	3	120.7	n	n
4/2/18	Meg	AF	-0.13	RST	2006	pumpkin	2	51.5	n	n
4/2/18	Loki	JM	0.04	RST	2008	yellow marrow	4	30.3	n	n
4/2/18	Tear	AF	-0.17	RST	2009	pumpkin	1	165.0	n	n
4/2/18	Pupi	JF	-0.23	RST	2011	pumpkin	3	125.6	n	n
4/2/18	Kiss	JM	0.06	RST	1999	pumpkin	2	265.5	n	y
4/3/18	Sava	JM	-0.11	RBM	2016	pumpkin	2	67.5	n	n
4/3/18	Octo	JM	-0.26	RBM	2024	pumpkin	3	154.0	n	n
4/3/18	Cola	JF	-0.03	RBM	2026	pumpkin	3	154.8	n	n
4/3/18	Spoc	JM	0.13	RBM	2026	pumpkin	2	154.8	n	n
4/3/18	Phoe	AF	0.04	RBM	2031	pumpkin	3	123.3	n	n
4/3/18	Holl	AF	-0.21	RBM	2033	pumpkin	3	116.8	n	n
4/3/18	Cura	JM	-0.37	RBM	2036	pumpkin	2	246.5	n	n
4/4/18	Bold	JM	-0.10	PT	2039	pumpkin	3	123.3	n	n
4/4/18	Brie	AF	0.11	PT	2039	pumpkin	3	123.3	n	n
4/5/18	Yoda	AM	0.16	RST	2048	pumpkin	2	132.3	n	n
4/5/18	Trip	JM	-0.09	RST	2053	pumpkin	4	63.8	y	n
4/5/18	Eve	JF	-0.11	RST	2059	pumpkin	2	56.5	n	n
4/5/18	Trip	JM	-0.09	RST	2064	blue potato	4	283.9	y	n
4/5/18	Kumq	JF	-0.56	RST	2065	blue potato	4	57.3	n	n
4/6/18	Need	AF	0.08	PT	2068	pumpkin	2	123.8	y	n
4/6/18	Tucs	JM	-0.30	PT	2085	pumpkin	3	345.1	y	y
4/6/18	Bold	JM	-0.10	PT	2085	pumpkin	3	345.1	y	y
4/6/18	Luxe	JM	-0.27	PT	2085	pumpkin	2	345.1	n	n
4/6/18	Bilb	JM	-0.26	PT	2085	pumpkin	3	345.1	n	n
4/6/18	Hect	JM	-0.19	PT	2088	pumpkin	2	67.4	n	n
4/6/18	Mori	AM	1.00	PT	2090	pumpkin	4	101.3	n	n
4/6/18	Stru	JM	-0.40	PT	2091	pumpkin	4	193.2	n	n
4/6/18	Howz	JF	-0.41	PT	2092	pumpkin	5	85.8	n	n
4/6/18	Howz	JF	-0.41	PT	2094	pumpkin	5	123.2	y	n
4/6/18	Damo	JM	-0.23	PT	2095	pumpkin	4	22.6	y	y
4/6/18	Piec	JM	-0.38	PT	2095	pumpkin	3	22.6	n	y
4/6/18	Lisa	AF	0.06	PT	2096	pumpkin	4	115.0	n	n
4/6/18	Herm	AF	-0.07	PT	2097	pumpkin	4	217.0	n	n
4/6/18	Nife	JF	-0.31	PT	2097	pumpkin	3	217.0	y	n
4/6/18	Gord	JF	-0.23	PT	2098	pumpkin	2	31.1	n	n
4/9/18	Coco	AF	0.27	RBM	2109	pumpkin	3	64.5	y	y
4/9/18	Cura	JM	-0.37	RBM	2109	green bean	2	64.5	n	y

Date	ID	Age/ Sex	Rank	Troop	Trial	Stim.	Total Trials	Dur.	Expose (y/n)	Interrupt (y/n)
4/9/18	Guge	JF	-0.56	RBM	2109	green bean	3	64.5	y	y
4/9/18	Swaz	JF	-0.02	RBM	2110	pumpkin	4	70.9	n	n
4/9/18	Funk	JM	-0.08	RBM	2110	green bean	3	70.9	y	n
4/9/18	Socr	JF	0.60	RBM	2110	green bean	3	70.9	y	n
4/9/18	Coco	AF	0.27	RBM	2118	green bean	3	104.7	y	y
4/9/18	Sava	JM	-0.11	RBM	2118	green bean	2	104.7	y	y
4/11/18	Deso	JF	-0.49	RST	2136	green bean	6	82.5	n	n
4/11/18	Kumq	JF	-0.56	RST	2138	green bean	4	86.5	n	n
4/16/18	Loki	JM	0.04	RST	2182	baby corn	4	104.7	n	n
4/16/18	Prof	JM	-0.06	RST	2183	baby corn	2	220.9	n	n
4/16/18	Katn	JF	-0.18	RST	2184	baby corn	4	159.9	n	y
4/16/18	Deso	JF	-0.49	RST	2184	baby corn	6	159.9	y	n
4/16/18	Elto	JF	-0.38	RST	2185	baby corn	3	153.7	y	n
4/16/18	Swee	JM	-0.09	RBM	2193	baby corn	3	594.7	y	y
4/16/18	Saff	AF	0.94	RBM	2193	baby corn	3	594.7	y	n
4/16/18	Caba	JF	-0.36	RBM	2193	baby corn	4	594.7	n	y
4/16/18	Omni	JM	-0.16	RBM	2193	baby corn	1	594.7	y	y
4/16/18	Cind	AF	0.08	RBM	2193	baby corn	5	594.7	n	y
4/16/18	Holl	AF	-0.21	RBM	2195	green bean	3	35.0	n	n
4/16/18	Gizm	JF	-0.24	RBM	2196	baby corn	3	217.1	n	n
4/16/18	Crea	JF	-0.32	RBM	2196	baby corn	1	217.1	y	y
4/16/18	Pean	JF	-0.49	RBM	2196	baby corn	4	217.1	n	n
4/23/18	Dice	JF	-0.44	RST	2279	red green bean	3	89.6	n	y
4/23/18	Deso	JF	-0.49	RST	2280	green bean	6	91.5	y	n
4/23/18	Loki	JM	0.04	RST	2280	red green bean	4	91.5	n	n
4/23/18	Wall	AM	0.64	RST	2280	red green bean	2	91.5	n	n
4/23/18	Amy	JF	-0.23	RST	2285	red green bean	2	24.2	n	n

Date	ID	Age/ Sex	Rank	Troop	Trial	Stim.	Total Trials	Dur.	Expose (y/n)	Interrupt (y/n)
4/23/18	Laur	AF	-0.12	RST	2286	green bean	3	86.5	n	n
4/24/18	Shum	AF	-0.26	PT	2300	baby corn	2	66.5	n	n
4/24/18	Damo	JM	-0.23	PT	2301	baby corn	4	43.9	n	n
4/24/18	Tyle	AM	0.31	PT	2303	baby corn	2	23.9	n	n
4/24/18	Bilb	JM	-0.26	PT	2304	baby corn	3	31.2	n	n
4/24/18	Herm	AF	-0.07	PT	2306	blue potato	4	23.2	n	n
4/24/18	Howz	JF	-0.41	PT	2307	baby corn	5	41.5	n	y
4/24/18	Shumi nf17	NA	NA	PT	2307	baby corn	2	41.5	y	y
4/24/18	Disn	JF	-0.16	PT	2307	baby corn	2	41.5	y	y
4/24/18	Dodg	AM	0.17	PT	2308	baby corn	2	86.1	n	n
4/24/18	Turt	AF	-0.12	PT	2309	baby corn	2	72.1	n	n
4/24/18	Nobo	JF	0.21	PT	2311	baby corn	1	162.8	n	n
4/24/18	Wolo	JF	-0.47	RBM	2313	baby corn	4	242.6	n	n
4/24/18	Caba	JF	-0.36	RBM	2313	baby corn	4	242.6	y	y
4/24/18	Funk	JM	-0.08	RBM	2315	baby corn	3	28.1	n	n
4/24/18	Lucy	AF	0.22	RBM	2317	baby corn	3	34.2	n	n
4/24/18	Pino	JM	-0.35	RBM	2318	baby corn	2	10.7	n	n
4/24/18	Nife	JF	-0.31	PT	2322	baby corn	3	28.2	n	n
4/24/18	Rock	AM	-0.02	PT	2323	baby corn	2	122.5	n	n
4/25/18	Pris	AF	1.00	RST	2331	baby corn	1	129.3	n	n
4/25/18	Tyva	AF	0.92	PT	2370	baby corn	2	113.5	n	n
4/30/18	Gats	JM	-0.39	RBM	2357	baby corn	1	60.4	n	y
4/30/18	Swaz	JF	-0.02	RBM	2360	baby corn	4	78.6	n	y
4/30/18	Trip	JM	-0.09	RST	2361	baby corn	4	114.8	n	n
4/30/18	Glue	JF	-0.35	RST	2377	baby corn	4	16.3	y	n
4/30/18	Laur	AF	-0.12	RST	2378	baby corn	3	8.1	n	n

Date	ID	Age/ Sex	Rank	Troop	Trial	Stim.	Total Trials	Dur.	Expose (y/n)	Interrupt (y/n)
5/2/18	Mori	AM	1.00	PT	2438	baby corn	4	16.5	y	n
5/2/18	Lia	JF	0.05	PT	2439	baby corn	1	28.7	n	n
5/2/18	Damo	JM	-0.23	PT	2440	baby corn	4	30.9	y	n
5/2/18	Lisa	AF	0.06	PT	2440	baby corn	4	30.9	n	y
5/2/18	Howz	JF	-0.41	PT	2443	green bean	5	154.5	y	y
5/2/18	Shumi nf17	NA	NA	PT	2443	baby corn	2	154.5	y	y
5/2/18	Daff	AF	0.02	PT	2443	baby corn	3	154.5	n	n
5/2/18	Bold	JM	-0.10	PT	2444	baby corn	3	269.7	y	n
5/2/18	Stru	JM	-0.40	PT	2444	baby corn	4	269.7	y	y
5/2/18	Tucs	JM	-0.30	PT	2444	baby corn	3	269.7	y	y
5/2/18	Polk	JF	-0.30	PT	2444	baby corn	3	269.7	y	y
5/2/18	Timm	JM	0.14	PT	2444	baby corn	3	269.7	y	y
5/7/18	Sash	AF	1.00	RBM	2468	blue eggplant	4	98.5	n	n
5/7/18	Swee	JM	-0.09	RBM	2469	blue eggplant	3	286.0	n	n
5/7/18	Cola	JF	-0.03	RBM	2469	blue eggplant	3	286.0	n	n
5/7/18	Lore	JF	-0.03	RBM	2469	blue eggplant	3	286.0	n	n
5/7/18	Balu	AM	0.27	RBM	2469	blue eggplant	1	286.0	n	n
5/8/18	Shel	JM	-0.10	PT	2494	blue eggplant	3	11.1	n	n
5/8/18	Tyva	AF	0.92	PT	2500	blue eggplant	2	16.4	n	n
5/8/18	Tita	JF	0.45	PT	2501	blue eggplant	1	74.9	n	n
5/8/18	Brie	AF	0.11	PT	2502	pumpkin	3	87.9	n	n

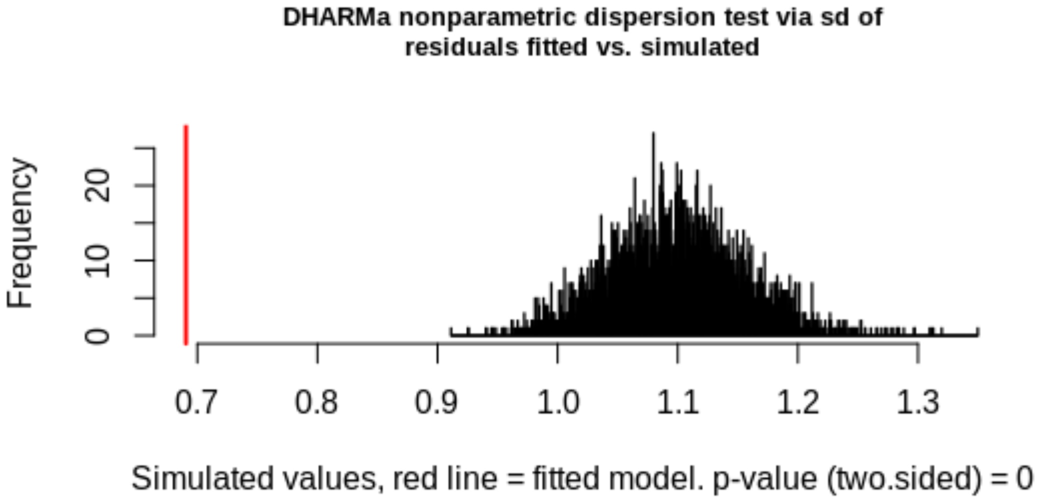
C.2 Posterior Estimates of Animals Eating the Novel Food Using 1 M Partner Presence Threshold

Effect	Parameter	Estimate	Est. Error	Lower 95 CI	Upper 95 CI
Population-Level Effects	Intercept (Adult Female, Food: Baby Corn)	-2.962	1.783	-6.579	0.562
	Exposed (y/n)	0.116	0.518	-0.901	1.146
	Interrupted (y/n)	0.316	0.512	-0.680	1.325
	Food: Eggplant, blue	-1.008	0.763	-2.535	0.477
	Food: Green Bean	0.203	0.722	-1.191	1.588
	Food: Green Apple	-0.116	0.942	-1.939	1.719
	Food: Potato, pink	-0.625	0.634	-1.841	0.591
	Food: Pumpkin	-0.894	0.673	-2.211	0.421
	Food: Red Grape	1.342	0.716	-0.052	2.753
	Food: Green Bean, red	-0.046	0.893	-1.828	1.671
	Food: Marrow, yellow	-0.008	0.655	-1.269	1.304
	Food: Potato, blue	0.396	0.595	-0.767	1.587
	Partner Presence (y/n)	1.818	0.496	0.898	2.806
	Adult Males	-0.840	0.865	-2.513	0.886
	Juvenile Females	0.934	0.644	-0.333	2.200
	Juvenile Males	0.822	0.640	-0.417	2.068
	Total Trials	0.122	0.291	-0.412	0.725
	Dominance Rank	-0.847	0.407	-1.731	-0.137
	Troop-Level Resource Availability	0.272	0.514	-0.752	1.306
Group-Level Effects	sd(Collector)	1.105	1.070	0.032	3.930
	sd(Study Period)	1.409	1.340	0.058	5.060
	sd(ID)	2.118	0.632	1.074	3.528
	sd(Troop)	1.524	1.186	0.156	4.517
	sd(Trial ID)	0.613	0.477	0.023	1.827

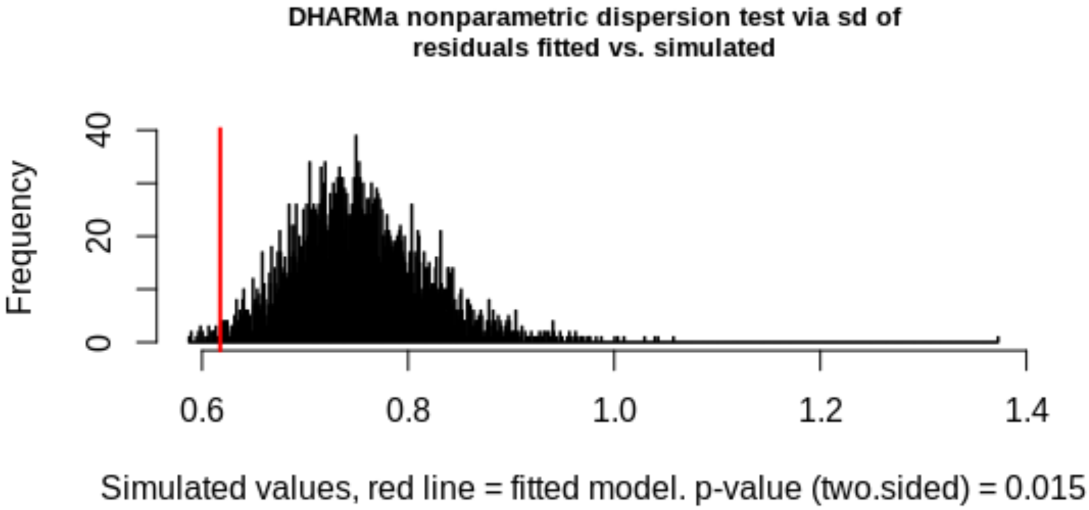
Note. Age-sex is relative to adult females, food type is relative to baby corn. Estimates are on the login scale; CI = credible interval, sd = standard deviation. N = 276. LOO-adjusted R^2=0.271.

Appendix D

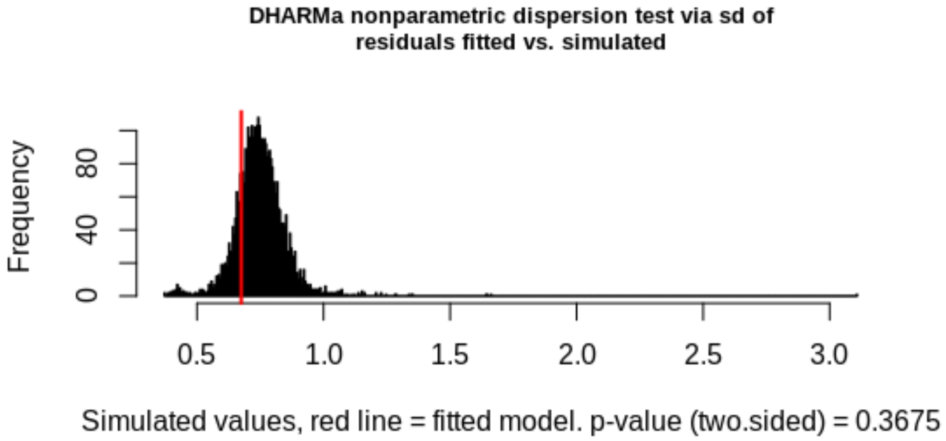
D.1 Underdispersion in the Poisson Model for Entering the Patch



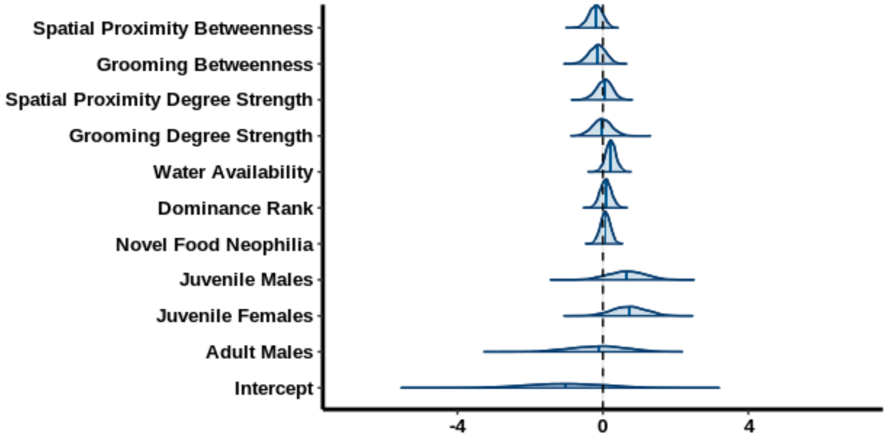
D.2 Underdispersion in the Hurdle Poisson Model for Entering the Patch



D.3 Dispersion in the Hurdle Negative Binomial Model for Entering the Patch



D.4 Posterior Density Plot of the Hurdle Negative Binomial Model for Entering the Patch



D.5 Posterior Density Plot of the Poisson Model for Entering the Patch