

DO GREAT APES CHOOSE TO CHOOSE?:
AN INVESTIGATION OF PREFERENCE FOR COMPUTER-PROVIDED CHOICE
IN ORANGUTANS (*PONGO ABELII*)

SARAH E. RITVO

A DISSERTATION SUBMITTED TO
THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

GRADUATE PROGRAM IN PSYCHOLOGY

YORK UNIVERSITY
TORONTO, ONTARIO

December 2020

© Sarah E. Ritvo, 2020

ABSTRACT

This dissertation examined orangutans' preference for computer touchscreen-provided choice and their capacity to recognize the content of 2-D pictures. Investigation of these factors is important for advancing our understanding of orangutan cognition and the development of Animal-Computer Interaction systems that provide captive great apes environmental enrichment through provision of choice. Using a concurrent chain procedure presented on a touchscreen computer, the first experiment examined three orangutans' intrinsic valuation of choice by assessing preference for free- or forced- choice when neither choice options nor outcomes vary. Initial results indicated a preference for free-choice across all participants. However, in two control conditions, preferences varied, suggesting a weaker tendency to exercise choice than species previously tested. Motivated by subjects' difficulty learning associations between application icons and food rewards, a series of three experiments investigated five orangutans' capacity to spontaneously recognize the content of novel pictorial stimuli by assessing if they demonstrated the same hierarchical preferences for food and pictures of food. Results indicated that orangutans only recognized picture content in certain formats and that they were more proficient in print than in digital mediums. Having confirmed that orangutans could recognize digital food images in a single format, this format was employed in the final pair of experiments to examine whether increasing the fidelity of the experimental choice paradigm elicited stronger free-choice preferences. This research question was investigated in a stepwise manner: Experiment 1 provided varied choices options that led to a single outcome and Experiment 2 varied both the choice options and outcomes. Results indicated a preference for free-choice in orangutans, but one that can be overwhelmed by competing factors and depend on the advantage

afforded by it. Moreover, findings indicated that for orangutans, the strength and quality of preference for free-choice can be affected by the fidelity of the choice paradigm and vary between individuals. In light of these results, I suggest that preference for choice may be more accurately conceptualized along a spectrum rather than a dichotomy of 'preference for choice' or lack thereof.

DEDICATION

I dedicate this dissertation to all of the great apes who chose day in and day out to support me throughout this journey, and without whom, none of this would be possible:

Humans:

To my mom, Janet Ritvo, my first teacher. You are the wisest and most thoughtful person I know. You inspired in me a love of learning, nature, art, and BIG projects from an early age, and taught me that conventionalism isn't all it's cracked up to be. I continue to learn from you every day.

To my dad, Paul Ritvo, my wild, lighthearted, and unflinching advocate. Your incredible drive both inside and outside of academia been an inspiration to me. Many times I would have given up, or never tried at all, if you hadn't been so convinced of my success. You made me believe in the impossible and taught me that it's not silly to dream big.

To my husband, James Kitts, my partner and confidant. You have been with me from the very beginning to the end of this long road. I know it hasn't been easy, but you never let on. Thank you for your boundless support and patience, and for always believing in me even when I didn't believe in myself.

To my daughter, Isabel Kitts, my wild, ambitious, and feisty one and a half year old. Much to my surprise, upon your birth you became the motivation to push for the summit of a lifelong dream. I hope that you never lose the wonder and enthusiasm with which you explore the world and always find the courage to pursue your own dreams. May you find a path worthy of your passion, dedication, and talent. If you don't, may you forge one.

Orangutans:

To Puppe, Ramai, Sekali, Budi, Kembali, and Jingga, in the hopes that this work may in some way contribute to your lives and the lives of your species living in captivity. You have taught me so much beyond the limits of this dissertation. You have both challenged me and inspired me beyond measure. I will never forget you.

ACKNOWLEDGEMENTS

This dissertation owes so much to so many.

Thanks to Laura Adams, Jennifer Colbourne, Jeannine Holmes, and Amanda Nickerson, for your camaraderie, moral support, and inspiring shared love for comparative cognition.

Thanks to the zookeepers at the IndoMalayan Pavillion at the Toronto Zoo. The data collection for this dissertation would not have been possible without you. Your enthusiasm for my research, diligence in timing orangutan schedules around testing sessions, tolerance for my unwieldy apparatus in your workspace, and most of all, your friendship have been indispensable. I will miss those long humid days in the orangutan holding.

Thanks to my dissertation committee members, Dr. Robert Allison and Dr. David Flora, and the referees who reviewed the papers submitted for publication within this dissertation. Your constructive criticisms and insightful contributions have greatly improved this work.

Thanks to my mother and father, Janet and Paul Ritvo, for your infinite and unconditional love and support, and for the thousands of hours of babysitting that made the last year of work on this dissertation possible. Mom, I still don't know how you survived walking a colicky four-month-old around the zoo for hours at a time while I collected data, let alone the long days spent on the playground with a toddler. Dad, thanks for all the countless games of 'Haroo!', for being Izzy's 'camel', and for supporting mom's retirement career as a nanny.

Thanks to my husband, James Kitts, for your unwavering belief in me and this dream, for the emotional and physical effort it took to walk this path with me while simultaneously working so hard to build your law practice, for the countless pep talks (even in the wee hours), and for solo parenting when I needed those extra weekend workdays.

Thanks to my graduate supervisor, Dr. Suzanne MacDonald who has provided me with the guidance of a mentor, the respect of a colleague, and the freedom to pursue avenues of enquiry that genuinely interested me. I will miss our meetings at McDonalds, swapping our latest animal stories while sipping on a Diet Coke and Coke Zero, respectively. Your passion and enthusiasm for comparative cognition were contagious, and your encouragement and reassurance were motivating. But most of all, thank you for providing me with the opportunity to fulfill a childhood dream. For that, I can't thank you enough.

Finally, to the five orangutans who graciously participated in this research, I will be forever grateful for your patience, your intelligence, your comedic relief, and for your remarkable and touching displays of friendship. Thank you for everything you taught me, both scientific and otherwise, and for keeping me blissfully grounded in the knowledge that we are all just big apes trying to make the best choices we can with the options we have.

TABLE OF CONTENTS

Abstract	ii
Dedication	iv
Acknowledgements	v
List of Tables	viii
List of Figures	ix
Chapter One: Introduction	1
The Value of Choice	1
Intrinsic Preference for Choice	2
The Evolutionary Advantages of Choice	2
The Benefits of Choice	3
Animals' Preference for Choice	4
Choice as Environmental Enrichment	5
Choice in Captive Great Ape Facilities	6
Animal-Computer Interaction (ACI)	8
ACI as a Mechanism for Choice	10
Choice Facilitating ACI Systems for Great Apes	12
Species of Investigation	14
The Task at Hand	16
References	19
Chapter Two: Do orangutans prefer free-choice when choice options and outcomes do not vary?	37
Experiment: Unvaried Choices, Unvaried Outcomes	38
Chapter Three: Can orangutans recognize picture content?	76
Experiment 1: Digital Mediums	85
Experiment 2: Print Mediums	89
Experiment 3: Digital and Print Mediums	91
Chapter Four: Are orangutans' preferences for free-choice stronger when choice options or outcomes vary?	117
Experiment 1: Varied Choices, Unvaried Outcomes	121
Experiment 2: Varied Choices, Varied Outcomes	127

Chapter Five: Discussion and Conclusions.....	157
Preference for Touchscreen-Provided Choice	157
Picture Recognition	163
Implications for Choice-Providing Orangutan ACI	165
The Task Ahead.....	167
References.....	173

LIST OF TABLES

Chapter 2

Table 1.1 Order of Delivery of Training and Testing Stages.....	65
Table 1.2 Free- vs. Forced- Choice Preference Results in Each Condition Per Subject.....	66

Chapter 3

Table 2.1 Format and Mode of Conditions in Experiment 1.....	105
Table 2.2 Consistency Among Rank Order Selections of Food and Digital Food Images.....	106
Table 2.3 Format and Mode of Conditions in Experiment 2.....	107
Table 2.4 Consistency Among Rank Order Selections of Food and Print Food Images	108
Table 2.5 Format and Mode of Conditions in Experiment 3.....	109
Table 2.6 Consistency Among Rank Order Selections of Food and Digital or Print Food Images	110
Table 2.7 Percent-Agreement Between Selections of Food and Digital or Printed Food Images ..	111

Chapter 4

Table 3.1 Experiment 2: Tofu Selections x Free-Choice Selections Correlations Per Subject.....	143
Table 3.2 Free- vs. Forced- Choice Preferences Per Subject.....	144

LIST OF FIGURES

Chapter 2

Figure 1.1 Example of a Testing Trial in the Free-Choice Right Condition	67
Figure 1.2 Example of Color Training Procedure.....	68
Figure 1.3 Example of Terminal Link Keys Color Training Procedure.	69
Figure 1.4 Frequency of Free- and Forced- Choice Selections in the Free-Choice Left Condition.	70
Figure 1.5 Frequency of Free- and Forced- Choice Selections in the Free-Choice Right Condition.	72
Figure 1.6 Frequency of Free- and Forced- Choice Selections in the Free-Choice Top Condition.	75

Chapter 3

Figure 2.1 Photographs of Food Slices from Hierarchy 1 and Hierarchy 2 Respectively	112
Figure 2.2 Photographs of Whole Foods from Hierarchy 1 and Hierarchy 2 Respectively	113
Figure 2.3 Experiment 1 Stimuli for Carrot-Celery Food Pairing in Conditions 1-A to 1-E	114
Figure 2.4 Experiment 2 Stimuli for Banana-Carrot Food Pairing in Conditions 2-A to 2-E	115
Figure 2.5 Experiment 3 Stimuli for Beet-Zucchini Food Pairing in Conditions 3-A to 3-G	116

Chapter 4

Figure 3.1 Example of a Testing Trial in the Free-Choice Right Condition of Experiment 1	145
Figure 3.2 Free- and Forced- Choice Selections in the Free-Choice Left Condition of Experiment 1 ...	146
Figure 3.3 Free- and Forced- Choice Selections in the Free-Choice Right Condition of Experiment 1 .	149
Figure 3.4 Free- and Forced- Choice Selections in the Free-Choice Top Condition of Experiment 1....	150
Figure 3.5 Example of a Testing Trial in the Free-Choice Right Condition of Experiment 2	151
Figure 3.6 Free- and Forced- Choice Selections in the Free-Choice Left Condition of Experiment 2 ...	153
Figure 3.7 Free- and Forced- Choice Selections in the Free-Choice Right Condition of Experiment 2 .	155
Figure 3.8 Free- and Forced- Choice Selections in the Free-Choice Top Condition of Experiment 2....	156

CHAPTER 1: GENERAL INTRODUCTION

*“You have brains in your head.
You have feet in your shoes.
You can steer yourself
any direction you choose”*

Dr. Seuss – Oh The Places You’ll Go

The Value of Choice

Freedom of choice is one of the most fundamental, prevalent, and protected tenets in the Western world. Choice is ubiquitous in human life and essential to development of our individual sense of freedom, meaning, and purpose (Helzer & Jayawickreme, 2015). From when we wake, what we eat, or how we recreate, to which career we pursue, or whom we love - all voluntary behaviours involve choices (Leotti et al., 2010). Some characterize life itself as a struggle against uncertainty in which we make choices in pursuit of a “unique individualized order” (Perlmutter & Monty, 1977, p. 759). We passionately defend choice as a human right: to choose political representatives, to choose religions, to choose to bear arms, to choose to end pregnancies, to choose whom to marry, and to choose which brand of coffee to buy. These choices are so highly valued, that many have died to acquire or protect them, and many more have affirmed commitments to do so. In fact, the only agreed upon limiting factor of our freedom of choice is the requirement that we do not violate the liberties of others. Indeed, one of the most basic and severe forms of punishment for crime is limiting opportunities for choice through incarceration in prisons. Ironically, it is also speculated that crime itself may result from lack of opportunities to choose or exert control. A criminal can be driven to lawbreaking as a means of enhancing their own freedom to choose or expanding their available choices (Perlmutter & Monty, 1977).

Intrinsic Preference for Choice

Some argue that personal control, exercised through choice, is not only a basic human right, but an innate, biologically-based need (Phares, 1976; White, 1959). Extant research indicates that humans prefer having a choice over no choice, and more choices over fewer choices (Bown et al., 2003; Leotti et al., 2010; Suzuki, 1997). This is even true of infants. At only 5 months old, human infants express sadness and anger over loss of control of pleasant visual or auditory stimuli (Sullivan & Lewis, 2003). This reaction is strongest in non-contingency conditions, in which pleasant stimuli continue to be presented but onset is no longer dependent on the infants' actions (i.e., is not chosen). According to standard economic theory, preference for choice is attributable to an increased probability of obtaining preferred outcomes (Fujiwara et al., 2013). However, there are indications that our predilection for choice may be more fundamental than that. Humans choose to choose even when doing so requires additional energy and offers no tangible advantage, suggesting that choice, and the freedom it affords, is also valued in and of itself (Bobadilla-Suarez et al., 2017; Bown et al., 2003; Leotti et al., 2010; Suzuki, 1997). Neural data support this premise. Opportunities to choose activate striatal regions of the human brain as a function of the amount of choice provided (Fujiwara et al., 2013; Tricomi et al., 2004). The same brain regions are involved in goal-directed behavior and processing rewards that are earned rather than provided. Variation in the degree to which individuals value choice is associated with varying amounts of striatal activation, suggesting that this neural activity is a function of the degree to which choice is intrinsically valued (Fujiwara et al., 2013).

The Evolutionary Advantages of Choice

There is compelling evidence that the need for control is evolutionarily adaptive. Engaging with the environment as causal agents rather than passive observers is advantageous to both survival and reproduction. By making choices for oneself one can maximize rewards and minimize punishments (Leotti et al., 2010). Choice-making also provides information about future events, thereby affording a more predictable environment and minimizing the stress of uncertainty (Goodstein et al., 1984). Preference for choice may also increase biological fitness by allowing organisms to manage and respond to an ever-changing environment and pursue alternatives to the status quo (e.g., better food, territory, or mates). (Fujiwara et al., 2013; Perlmutter & Monty, 1977). Furthermore, opportunities to exercise control through choice-making reinforces self-efficacy, a belief in one's capacity to produce desired outcomes (Bandura, 2010; Henry & Sniezek, 1993; Leotti et al., 2010; Tafarodi et al., 1999). This core belief is directly associated with human motivation and performance (Bandura, 2010). In circumstances in which unreliable response-outcome contingencies weaken self-efficacy beliefs, motivation to confront and overcome challenges to survival are weakened (Leotti et al., 2010; Overmier & Seligman, 1967). This maladaptive state of passivity described as "learned helplessness" is associated with deleterious mental and physical consequences (Seligman, 1972; Seligman, 1992). Choice motivates us to survive and affords us access to opportunities to do so.

The Benefits of Choice

There is substantial evidence that exercising choice fosters a propensity not only to survive but also to thrive. Provision of choice has been associated with multiple benefits, from affective (Stotland & Blumenthal, 1964) to cognitive (Winocur et al., 1987) and motivational (Greenberger et al., 1989; Patall et al., 2008; Zuckerman et al., 1978), to physiological (DeGood, 1975; Lundberg & Frankenhaeuser, 1978; Rodin, 1983, 1986). Environmental control or the

illusion of control is associated with increased motivation (Deci & Ryan, 2013; Langer & Rodin, 1976), improved task performance (Perlmutter & Monty, 1977), and reduced systolic blood pressure (DeGood, 1975). Perceived control also appears to be protective against stressors, inhibiting autonomic arousal (Geer et al., 1970; Hokanson et al., 1971; Staub et al., 1971), lowering anxiety levels (Glass & Singer, 1972), reducing stress hormones (Bandura et al., 1985), and limiting immune system suppression (Leotti & Delgado, 2011; Maier et al., 2014).

Conversely, reduced personal and environmental control in choice-limited environments can be detrimental and has been associated with stress (Averill, 1973; Miller, 1979; Thompson, 1981), withdrawal (Abramson et al., 1978; Langer & Rodin, 1976), decreased performance (Bazerman, 1982; Glass & Singer, 1972), hopelessness, and depression (Seligman, 1992). Controlling our environment through choice appears to be critical for our health and competence.

Animals' Preference for Choice

Despite limited investigation of equivalent preferences and effects in nonhuman animals (hereafter, animals), there is preliminary evidence that species from a variety of genera value choice and benefit from environmental control or suffer from lack of it. In experimental studies, rats (Singh, 1970; Voss & Homzie, 1970), pigeons (Catania, 1975; Catania & Sagvolden, 1980), and some monkey species (Perdue et al., 2014; Suzuki, 1999) have demonstrated a preference for choice even when the selection of a free-choice alternative has no positive effect on outcome.

Observational data following choice-provision interventions in captive animal environments suggest that choice-making may also have affective (Faircloth, 1974; Ross, 2006), motivational (Beran et al., 2007; Washburn et al., 1991), and physiological (Owen et al., 2005) effects on animals. Providing animals choice has been observed to reduce stress hormones and behavioural indicators of agitation (Owen et al., 2005), decrease stereotypies (Ross, 2006), and increase

social play (Ross, 2006). These findings suggest that provision of choice and environmental control could serve as a promising means of enrichment for captive animals.

Choice as Environmental Enrichment

Environmental enrichment is undoubtedly the most common method for addressing captive animal welfare problems (Swaigood, 2007). It has proven imperative not only for zoos and aquariums (Shepherdson et al., 2012; Young, 2003), but it has also become an important prerequisite for ex situ conservation activities (e.g., captive breeding) (Carlstead & Shepherdson, 1994; Swaigood, 2007). Enrichment is preferred over other methods of addressing captive animal welfare (e.g., genetic selection, pharmacological treatment, reinforcement of alternative behaviours, and punishment) because it has proven the most successful in targeting root causes of behavioral problems (e.g., stereotypies and inactivity) with little to no side effects (Mason et al., 2007). In practice, enrichment has improved activity outcomes and biological functioning and reduced fearful, aggressive, and abnormal behaviors such as self-harm, pacing, and regurgitation (Bayne et al., 1992; Beattie et al., 2000; Brent et al., 1989; Jones & Waddington, 1992; Carlstead & Shepherdson, 2000; Chamove et al., 1982; Kessel & Brent, 1998; O'Connell & Beattie, 1999; Swaigood et al., 2001; Swaigood & Shepherdson, 2005; Tarou et al., 2004; Young et al., 1999; Zebunke et al., 2013).

Motivated by these findings, several theories of enrichment have been proposed. One of the most popular is the behavioral contingency theory of motivation which proposes that captive animals benefit from opportunities to choose among several behavioral options that directly affect their environment (de Azevedo et al., 2007). This benefit is believed to be especially true of behaviors related to resource acquisition. In this way, the behavioral contingency theory bears considerable resemblance to the ethological needs model of motivation. The ethological needs

model proposed by Hughes and Duncan (1988) suggests that animals have evolved the need to perform certain behaviors that in a natural environment are necessary for acquiring resources. Accordingly, animals are reinforced by both the desired *consequences* of their behavior (e.g., acquiring food) and by the *appetitive* behaviors that are used to achieve desired consequences (e.g., foraging) (Swaigood, 2007). Consequently, captive environments that do not provide opportunities to perform these ethological behaviors result in poor welfare outcomes. For example, providing foraging and hunting opportunities rather than feeding captive animals prepared foods has been demonstrated to improve welfare outcomes (Shepherdson et al., 1993; Swaisgood et al., 2001). An important difference between the ethological needs model and the behavioral contingency theory is *behavior-environment contingency*. The behavioral contingency theory includes the caveat that in addition to providing animals opportunities to perform appetitive behaviors, an animal's behavior should also control some aspect of the environment (e.g., food, light, and temperature) (Swaigood, 2007). In other words, for optimal welfare outcomes, captive animals should be provided choices that affect their environment.

Choice in Captive Great Ape Facilities

Growing research interest in enrichment theory has resulted in the establishment of a variety of enrichment modalities in captive animal environments. Consistent with the behavioral contingency model of motivation, provision of choice and control has emerged as one of the most central, especially with respect to non-human great apes (hereafter great apes) (Scheel, 2018). All great apes (gorillas, chimpanzees, orangutans, and bonobos) are endangered or critically endangered. Captive members of these species play an important role in conservation management plans and efficacious enrichment is critical for maintaining healthy captive populations (Kim-McCormack et al., 2016). Moreover, great apes' large size, activeness, and

intelligence make them particularly vulnerable to the adverse effects of lack of choice.

Accordingly, the International Primatological Society (IPS) *International Guidelines for the Acquisition, Care, and Breeding of Nonhuman Primates* lists “opportunities to exert choice and control over the environment” (2016, p. 45) as a top behavioural priority, warning that, “lack of control experienced by captive animals may be highly detrimental to their welfare” (p. 46).

Likewise, The Association of Zoos and Aquariums’ (AZA) *Orangutan Care Manual* advises that “providing managed animals with increased control over their environment is essential for maximizing welfare” (AZA Ape Taxon Advisory Group, 2017). They recommend allowing animal control over several environmental factors including movement, location, access to outdoors, social partners, light, temperature, food, water spritzers, music, and viewing by the public (AZA Ape Taxon Advisory Group, 2017). Moreover, as an essential aspect of effective environmental enrichment and as a means of providing welfare-promoting animal environmental control, the IPS prescribe “a complex, responsive environment” (*IPS International Guidelines for the Acquisition Care and Breeding of Nonhuman Primates*, 2016, p. 46).

However, by their very nature captive primate facilities are limited in their ability to provide individual animals environmental control equivalent to the natural world. Nearly every aspect of captive primate environments are strictly scheduled and regulated by human caregivers (e.g., diet quantity and type, meal timing, lighting, temperature, humidity, sound, location and physical spacing, social contact, sleep timing, etc.). Zoos and rehabilitation facilities that house a large number of animals of varying taxa from diverse ecological niches face particular challenges in this regard (Swaisgood, 2007). Given limited space, fixed exhibit installations (e.g., jungle gyms, ladders, swings, ropes, and food puzzles) are often a primary enrichment intervention. Although fixed apparatuses do much to foster cognitive and physical wellbeing,

they are limited in their capacities to offer great apes choice and environmental control. That is, they are static systems, selected and implemented by human administrators, confined to the boundaries of the animals' exhibit area. With the exception of behavioural reactions to exhibit factors that human caretakers may interpret with varying degrees of accuracy, captive great apes typically have little-to-no control over the selection, quantity, or placement of environmental features. Moreover, given the resources, costs, and labor required to modify or replace exhibits' major structural features, the environmental changes implemented in captive facilities are often limited in scope (e.g., the addition, removal, or modification of ropes, swings, toys, or ground cover). The result for captive great apes can be entire lifetimes lived in relatively invariable environments, over which they have little to no control. The application of Animal-Computer Interaction (ACI) to captive animal facilities offers a unique and unparalleled opportunity to provide both a mechanism for choice and a means of environmental variability.

Animal-Computer Interaction (ACI)

Computer systems have improved human life, increasing users' access to information, safety, capabilities, performance, and well-being (Preece et al., 1993). This is especially true for exceptional users (i.e., the physically or cognitively disabled, the elderly, etc.) For example, tongue- and breath-controlled wheelchairs and accessible pedestrian signals have afforded mobility, safety, and independence to quadriplegic and visually impaired populations respectively (Ritvo & Allison, 2017); gloves have been developed to wirelessly translate American Sign-Language (ASL) into displayable text on smartphones (O'Connor et al., 2017); and vibrating baby monitors are in development that alert hearing impaired parents if a baby sounds hungry, bored, or tired (Fife, 2014). The examples are many, and their beneficial

influence on human life is extensive. There is every reason to believe that computer systems can be equally facilitating for animal users.

Accordingly, as computing technologies have become more flexible, mobile, inexpensive, and accessible to the layperson, software and hardware are increasingly being adapted and designed for domestic pets, farm animals, and captive wild animals (Ritvo & Allison, 2017). In homes, remote monitoring and food delivery systems for pets are becoming commonplace (Chang & Cheung, 2016); in the farming industry, computer devices are optimizing milk production (Rossing et al., 1997) and monitoring animal welfare (Caria et al., 2017); tracking and telemetric technologies are being used for wildlife conservation (Hebblewhite & Haydon, 2010; Huettelman & Bogie, 2009; McGowan et al., 2017; Simpfendorfer et al., 2010); and a variety of computer technologies including touchscreens and motion sensors are being employed to study animal behavior, cognition, physiology, and sensory systems (Butler & Kennerley, 2019; Hopper et al., 2018; Marsh & MacDonald, 2008; Ritvo & MacDonald, 2016; Schmidtke et al., 2018; Schweller, 2012; Vonk & MacDonald, 2004).

From these developments, a new rapidly evolving field of study has emerged called Animal-Computer Interaction (ACI). ACI comprises the study, design, and evaluation of computer interfaces that facilitate meaningful interactions between animals and computers (Ritvo & Allison, 2017). Drawing from subjects as diverse as computer science, cognitive science, human factors, psychology, software engineering, ergonomics, ethology, biology, zoology, and most directly, human-computer interaction (HCI), ACI is an interdisciplinary field. What differentiates ACI from ‘animal technology’, which includes any technology intended for animals, is that ACI systems involve an interaction between an animal and a computer (Ritvo & Allison, 2017). For example, let us consider the automatic milking system, a conventional

mechanized farming tool used with dairy cows (*Bos taurus*). Traditionally, this system has required a human to prepare, initiate, and facilitate milking. However, more recent models have incorporated a voluntary feature in which cows can initiate milking and self-determine the duration of a session through interaction with an interface (Heyden, 2015). Given that the former system is used with animals but requires a human's control, it would be considered an animal technology. Only the latter system qualifies as an ACI system because the interaction with a computer is controlled by the animal user (Ritvo & Allison, 2017).

Designing technology that supports animals' activities and improves animal welfare through interaction with computers is one of ACI's core aims (Mancini et al., 2017). In so doing, ACI practices what in HCI is termed 'user-centered design' (UCD). UCD is an iterative design process that focuses on users by acquiring a distinct understanding of intended 'inter-actors', (i.e., their tasks, environments, and contexts), and involving them in each phase of the design and development process (Mancini, 2017). UCD is essential for ACI which involves designing interfaces for users that: (a) belong to one of millions of highly diverse and unique species, (b) belong to a different species than the designer, (c) may be unable to understand instructions for system-use, and (d) cannot verbally or explicitly communicate design feedback. By including animals as design participants, their unique physiology, cognitive and sensory systems, as well as behavioral responses to prototypes can inform the design process, ensuring that deliverables are species-specific, highly accessible and functional, provide value for users, and meet users' unique requirements (Mancini 2017).

ACI as a Mechanism for Choice

Application of ACI to zoos that house great apes provides unique opportunities to transcend the limitations posed by captivity by enriching and expanding their perceptual,

conceptual, and physical worlds beyond the borders of their captive residences. The IPS' prescription for 'a complex, *responsive* environment' appears to be a task particularly well suited for ACI, a discipline that includes 'interaction' in its very name. What distinguishes ACI from traditional enrichment interventions is its responsive, flexible, and mutable nature that affords unparalleled opportunities for great ape control over their environments. ACI can address key enrichment issues and be easily adapted to diverse environments, situations, and group or individual preferences (Scheel, 2018). Human and animal research suggests that provision of environmental control through provision of choice is a promising means of enrichment, and therefore, likely an important factor in improved animal exhibit design (Lonsdorf et al., 2010). ACI systems have particular potential in this domain in their capacity to provide great apes with (a) a mechanism for choice (e.g., via joysticks, keyboards, touchscreen interfaces, auditory recognition, and accelerometers), (b) a delivery system for environmental change (e.g., via mutable visual displays and electro acoustics, remote control of atmospheric and situational features, and robotics), (c) a perceptual window into worlds beyond the borders of their captive homes (e.g., via video and acoustic recordings, and olfactory technology), and (d) a preference assessment tool (e.g., via collection and analysis of species-specific choice data). Imagine, for example, the ACI-equipped zoo that allows great ape residents choices of lighting, temperature, meal type and timing, computer-delivered games and puzzles, visual, auditory and olfactory displays, or access to sleeping quarters, the outdoors, and conspecifics. This exhibit could continuously and imperceptibly collect and analyze data on the choices great ape users make in various conditions (e.g., during various seasons or times of day, when animals are on or off exhibit, at different chronological ages, during estrous periods, or before, after, or in tandem with other activities, etc.). These data could inform exhibit and ACI design, enrichment programs, and

the study of great ape behavior and cognition. Such a choice-enriched environment would likely not only make for happier, healthier animals, but also for more entertaining exhibits for zoo-patrons.

Importantly, ACI systems have the potential to yield large impact via relatively simple and cost-effective designs with small footprints. Consequently, they do not necessitate affluent, privately funded, or spacious animal facilities. For example, the ACI system that allows animal users control over access to various areas of their enclosure or to manipulate temperature and lighting does not need to be complex in scope or scale. A single dial may suffice. But the environmental control afforded by something as straightforward as a dial has the potential to substantially improve animal users' emotional and physical welfare. Thus, great ape users, captive primate facilities, and ACI designers can benefit from a high impact-to-effort ratio of choice-facilitating ACI systems that provide a large user impact (i.e., improvement in animal welfare) relative to the minimal size, complexity, expense, and disturbance to captive animal protocols of the ACI design. Furthermore, in its capacity as both a mechanism and a delivery system for choice, ACI could inform future species-specific ACI design through great ape preference data analyses.

Choice Facilitating ACI Systems for Great Apes

Great apes have also been a primary focus of ACI applied to zoos (Ackerman, 2012; Clay et al., 2011; Fernandez-Blance, 2012; Hsu, 2012; Nijholt, 2015; Perdue et al., 2012; Ravignani et al., 2013; Ritvo & MacDonald, 2016; Scheel, 2018; Schweller, 2012; Schweller, 2014; Tarou et al., 2004; Wirman, 2013). At Bristol Zoo Gardens in the United Kingdom, Clark et al. (2019) designed a modular cuboid puzzle maze for Western lowland gorillas (*Gorilla gorilla gorilla*). At Melbourne Zoo in Australia, Webber et al. (2017) developed a game for resident orangutans

using a motion sensing Xbox Kinect that features a projected sphere that ‘explodes’ when touched. At the Indianapolis Zoo in the United States, orangutans are encouraged to engage in naturalistic climbing behaviors by push button-activated electronic feeders located at the top of 90 ft towers (Martin & Shumaker, 2018). At Zoo Atlanta in the United States, a computer touchscreen simultaneously provides orangutan enrichment, allows cognitive research to take place on exhibit, and elicits highly positive reactions from zoo patrons (Perdue et al., 2012). In addition to the enrichment requirements discussed above, this marked interest in great apes is likely due to a combination of factors including their: (a) phylogenetic proximity and similar physiological, cognitive, and sensory systems to humans, (b) cognitive capacities, (c) visual and colour acuity (Adams et al., 2017; Anderson, 2011; Marsh & MacDonald, 2008; Tigges, 1963), and (d) motivation to participate in computer-delivered studies (Anderson, 2011; Marsh et al., 2011; Marsh & MacDonald, 2008; Perdue et al., 2012; Renner et al., 2016; Vonk, 2002). These factors make the design of ACI systems for great apes easier and more likely to be successful. By the same token, great apes make promising candidates for choice facilitating ACI technology.

However, although preferences for and the positive effects of choice have been empirically confirmed in humans and monkeys, investigations of these effects in great apes have been both limited in number and scope and have yielded mixed behavioral results that are vulnerable to a variety of selective interpretation (Bloomsmith et al., 2000; Kurtycz et al., 2014; Lonsdorf et al., 2010; Morimura, 2003). Moreover, these studies have sought to evaluate great apes’ reactions to choices, but have not directly assessed preferences for choice itself. Despite the fact that great apes’ relationship with choice is undetermined, given that humans and monkeys such as macaques and capuchins have demonstrated a preference for and benefit from choice, there has been carry-over beliefs in equivalent value for great apes (Lonsdorf et al.,

2010). Importantly, because computers have traditionally been designed by humans for humans, ACI systems are at risk of suffering from anthropomorphic bias (Ritvo & Allison, 2017). Thus, it is critically important to ensure that in developing ACI systems, we do not assume that what is true for humans (or any species for that matter) is also true for other species. Doing so can result in not only biased systems that are ill-suited for the intended user species, but more importantly, unintentional deleterious effects on animal welfare. For example, music is pervasively used as auditory enrichment in captive nonhuman primate facilities under the assumption it is as enriching for nonhuman primates (hereafter, primates) as it is for humans (Hinds et al., 2007; Lutz & Novak, 2005). However, Ritvo and MacDonald's (2016) investigation of orangutan music preference using an orangutan-controlled touchscreen program indicated that orangutans preferred silence to music or were indifferent. These results suggest that the music played for captive orangutans may not be as enriching as previously thought or could even be aversive. Thus, in keeping with a UCD focus, the first step in the development of choice-facilitating ACI systems for great apes is to determine (a) if great apes value and benefit from choice, (b) if computer interfaces are an effective means of delivery of choice, and (c) the best type of interface or application for providing computer-provided choices.

Species of Investigation

Sumatran orangutans (*Pongo abelii*) (hereafter, orangutans) were selected as subjects for the experiments that follow for several reasons. First, orangutans are phylogenetically close to and physiologically similar to humans. Sharing 97% of human DNA, orangutans are one of our most closely related species (Locke et al., 2011). Like humans, orangutans mature slowly, are long-lived, experience a protracted period of physiological and mental development, are dietary generalists, and have long inter-birth intervals (Kaplan & Rogers, 2000; Milton & May, 1976).

These qualities makes orangutans an attractive comparison species for the study of comparative cognition involving investigation of: (a) behavioral traits, (b) cognitive capacities, (c) life stages from juvenility to adulthood, and (d) consideration of the timing of orangutans' evolutionary divergence from humans and the implications thereof.

Second, orangutans make ideal subjects in great ape research involving computers. Orangutans are intelligent (Damerius et al., 2019), consistently scoring among the highest for primates on cognitive tasks, and possess a variety of cognitive abilities only shared with other great apes, including planning, causal and logical reasoning, mirror self-recognition, deception, and role reversal (Delgado & Van Schaik, 2000). Additionally, wild and captive orangutans have demonstrated manufacturing and flexible use of tools (Russon et al., 2015; van Schaik et al., 1999). It is believed that orangutans' arboreal lifestyle in the unpredictable and unstable forest canopy has encouraged tool improvisation and innovation. Moreover, orangutans have demonstrated motivation to participate in human-directed empirical investigation and capacity to effectively operate touchscreen computers (Egelkamp & Ross, 2019; MacDonald & Ritvo, 2016).

Third, as discussed earlier, effective enrichment is an important means of management and preservation of captive species facing extinction. Orangutans are one of the two most critically endangered genera of great ape in the world. As a result of deforestation, their population has declined from 230,000 a century ago to only 13,846 today in an area of 16,775 km² of forest (IUCN, 2020). If this trend continues, orangutans could face extinction in the wild in as little as 10 years (Cross, 2019). Given that most captive animal reintroductions across taxa are unsuccessful (Beck et al., 1994), and how quickly palm oil plantations and logging are

driving orangutan habitat loss, reintroduction of orangutans into the wild is challenging (Campbell-Smith et al., 2011).

Finally, orangutans, unlike gorillas that live in troops of up to 30 individuals, are the most solitary great ape species (Goodall, 2005). With the exception of mother-offspring pairs and breeding relations, orangutans live semi-solitary lifestyles in which individuals often live alone but will associate in small groups for social benefits (Delgado & Van Schaik, 2000). Because zoos rarely have enough space to physically support this type of social system, and orangutans can be intolerant of living in close quarters with conspecifics, zoos often resort to separating captive orangutans into separate holding areas. Typically, zoos can afford a maximum of two exhibit areas (i.e., an indoor and outdoor area) per species. This combination of factors can result in captive orangutans spending long hours off exhibit in holding areas that are not only less spacious but also possess less variety of natural stimuli (i.e., natural light, sounds, and smells). Thus, exploration of effective modes of enrichment and environmental control for captive individuals is critical.

Thus, research and development of choice-facilitating ACI that can provide enrichment for orangutans via systems with small physical footprints is arguably more necessary and urgent than for other great ape species.

The Task at Hand

As a means of developing choice-facilitating ACI enrichment systems for great apes, as well as advancing our understanding of a relatively undefined area of comparative cognition, the research that follows is an investigation of a sample of orangutans' (a) preferences for computer touchscreen-delivered free-choice, and (b) abilities to recognize the content of 2-D pictures.

Studies are described in the order of data collection, and no concurrent research was undertaken with these studies.

Chapter 2 examined whether free choice is an intrinsic and independent motivator for orangutans when extraneous variables are highly controlled. Whereas humans (Bown et al., 2003; Suzuki, 1997) and monkeys (Suzuki, 1999) appear to value choice in and of itself, it is unclear if great apes do as well. If orangutans value choice, does that valuation depend on the benefit afforded by available choices or do orangutans intrinsically prefer choice itself? In the first systematic investigation of preference for free- or forced- choice in a great ape species, this question was examined by assessing participants' choice to take one of two nearly identical virtual routes (i.e., one that provided a choice of reward keys and one that did not) to an identical food reward via a touchscreen computer program. Importantly, selection of the 'free-choice' alternative did not provide a variety of choice options or outcomes. In this way, as an attempt to evaluate inherent preference for free-choice in and of itself, the study described in Chapter 2 assessed preference for a largely illusory 'free-choice' because the selection of either route had no impact on outcome (i.e., resulted in identical outcomes).

Orangutans demonstrated marked difficulty learning associations between the colour of icons and food rewards in the software program employed in Chapter 2. Motivated by this observation, Chapter 3 explored if orangutans recognized the content of pictures presented by either digital or printed mediums. From infancy, humans have proven capable of recognizing picture content (Barrera & Maurer, 1981). Whether primates share this competency is less clear, but is critically important for how they use ACI systems that provide choices through presentation of 2-D images. Although successful use of pictorial stimuli in primate research is quite common, prior to experimental testing subjects are usually exposed to picture stimuli

during task training. For this reason, it's difficult to know if primates' recognition of pictures during experimental testing is a result of (a) conditioning (i.e., a picture amounts to a symbol that is associated with a specific outcome), or (b) recognition of picture content (identifying a real world object from a picture). A series of three experiments explored if orangutans' can spontaneously recognize the content of novel pictorial stimuli and if this capacity is affected by either presentation medium (i.e., digital or print) or format (i.e., size, composition, and number of displays). Specifically, Experiment 1 and Experiment 3 investigated if orangutans could recognize novel pictures of food presented in several formats and on several types of digital displays. Experiment 2 and Experiment 3 investigated if the same subjects could recognize food images, in the same formats, presented in prints of various sizes.

Having confirmed that orangutans were able to recognize touchscreen-displayed food images in at least one format, the study described in Chapter 4 used this format to continue examination of orangutans' preference for computer-delivered choice. In the study presented in Chapter 2, orangutans demonstrated preferences for free-choice that were weaker than expected given that long-tailed macaques (*Macaca fascicularis*) (Suzuki, 1999) and pigeons (*Columba livia domestica*) (Catania, 1975; Catania & Sagvolden, 1980) have demonstrated more consistent selections in nearly identical conditions. Motivated by the hypothesis that the experimental paradigm employed to evaluate preference for choice may not have provided enough variation to be interpreted as a 'free-choice' by a cognitively complex species like orangutans, Chapter 4 explored whether increasing the fidelity (i.e., verisimilitude) of the paradigm, by providing more choice variation, elicited stronger choice preferences. This question was investigated in a stepwise manner. In Chapter 2, the 'free-choice' alternative did not provide a variety of choice options or outcomes. However, in Experiment 1 of Chapter 4, selection of the 'free-choice

alternative' provided access to a variety of choice options, while holding the outcomes of choices constant (i.e., selection of any option led to the same outcome). In Experiment 2, the fidelity of the choice paradigm was increased further by providing a variety of choice options and outcomes.

Finally, Chapter 5 discusses research results and the implications of findings for both the field of comparative cognition and ACI, particularly in relation to choice-facilitating computer systems. Limitations and future research directions are also discussed.

References

Abramson, L. Y., Seligman, M. E., & Teasdale, J. D. (1978). Learned helplessness in humans: Critique and reformulation. *Journal of Abnormal Psychology, 87*(1), 49–74.

<https://doi.org/10.1037/0021-843X.87.1.49>

Ackerman, E. (2012). RoboBonobo: Giving apes control of their own robot. *IEEE Spectrum, 49*(7), 38–45.

Adams, L., Wilkinson, F., & MacDonald, S. (2017). Limits of spatial vision in Sumatran orangutans (*Pongo abelii*). *Animal Behavior and Cognition, 4*(3), 204–222.

<https://doi.org/10.26451/abc.04.03.02.2017>

Anderson, U. (2011). *Color, shape, and number identity-nonidentity responding and concept formation in orangutans* [Dissertation, Georgia Institute of Technology].

<http://search.proquest.com/docview/926207977>

Averill, J. R. (1973). Personal control over aversive stimuli and its relationship to stress.

Psychological Bulletin, 80(4), 286–303. <https://doi.org/10.1037/h0034845>

AZA Ape Taxon Advisory Group. (2017). *Orangutan (Pongo) care manual*. Association of Zoos and Aquariums.

<https://ams.aza.org/iweb/upload/Orangutan%20Care%20Manual%20DRAFT-0a71e9d2.pdf>

Bandura, A. (2010). Self-efficacy. In I. B. Weiner & W. E. Craighead (Eds.), *The Corsini Encyclopedia of Psychology*. John Wiley & Sons, Inc.

<https://doi.org/10.1002/9780470479216.corpsy0836>

Bandura, A., Taylor, C. B., Williams, S. L., Mefford, I. N., & Barchas, J. D. (1985).

Catecholamine secretion as a function of perceived coping self-efficacy. *Journal of Consulting and Clinical Psychology*, *53*(3), 406–414. <https://doi.org/10.1037/0022-006X.53.3.406>

Barrera, M. E., & Maurer, D. (1981). Recognition of mother's photographed face by the three-month-old infant. *Child Development*, *52*(2), 714–716. <https://doi.org/10.2307/1129196>

Bayne, K. A., Hurst, J. K., & Dexter, S. L. (1992). Evaluation of the preference to and behavioral effects of an enriched environment on male rhesus monkeys. *Laboratory Animal Science*, *42*(1), 38–45.

Bazerman, M. H. (1982). Impact of personal control on performance: Is added control always beneficial? *Journal of Applied Psychology*, *67*(4), 472–479. <https://doi.org/10.1037/0021-9010.67.4.472>

Beattie, V. E., O'Connell, N. E., Kilpatrick, D. J., & Moss, B. W. (2000). Influence of environmental enrichment on welfare-related behavioural and physiological parameters in growing pigs. *Animal Science*, *70*(3), 443–450.

<https://doi.org/10.1017/S1357729800051791>

Beck, B. B., Rapaport, L. G., Price, M. R. S., & Wilson, A. C. (1994). Reintroduction of captive-born animals. In P. J. S. Olney, G. M. Mace, & A. T. C. Feistner (Eds.), *Creative*

Conservation (pp. 265–286). Springer Netherlands. https://doi.org/10.1007/978-94-011-0721-1_13

Beran, M. J., Klein, M. D., Evans, T. A., Antworth, R., & Chan, B. (2007). Perceived control, motivation, and task performance in capuchin monkeys. In P. R. Zelick (Ed.), *Issues in the psychology of motivation* (pp. 171–175). New York: Nova Science Publishers. In R. Zelick (Ed.), *Issues in the psychology of motivation* (pp. 171–175). Nova Science.

Bloomsmith, M. A., Ross, K. C., & Baker, K. C. (2000). Control over computer-assisted enrichment for socially housed chimpanzees. *American Journal of Primatology*, *51*(5), 45.

Bobadilla-Suarez, S., Sunstein, C. R., & Sharot, T. (2017). The intrinsic value of choice: The propensity to under-delegate in the face of potential gains and losses. *Journal of Risk and Uncertainty*, *54*(3), 187–202. <https://doi.org/10.1007/s11166-017-9259-x>

Bown, N. J., Read, D., & Summers, B. (2003). The lure of choice. *Journal of Behavioral Decision Making*, *16*(4), 297–308. <https://doi.org/10.1002/bdm.447>

Brent, L., Lee, D. R., & Eichberg, J. W. (1989). Evaluation of two environment enrichment devices for singly caged chimpanzees (*Pan troglodytes*). *Am J Primatol Suppl*, *1*, 65–

Butler, J. L., & Kennerley, S. W. (2019). Mymou: A low-cost, wireless touchscreen system for automated training of nonhuman primates. *Behavior Research Methods*, *51*(6), 2559–2572. <https://doi.org/10.3758/s13428-018-1109-5>

Campbell-Smith, G., Campbell-Smith, M., Singleton, I., & Linkie, M. (2011). Apes in space: Saving an imperilled orangutan population in Sumatra. *PLoS ONE*, *6*(2), e17210.

<https://doi.org/10.1371/journal.pone.0017210>

- Caria, M., Schudrowitz, J., Jukan, A., & Kemper, N. (2017). Smart farm computing systems for animal welfare monitoring. *2017 40th International Convention on Information and Communication Technology, Electronics and Microelectronics (MIPRO)*, 152–157.
<https://doi.org/10.23919/MIPRO.2017.7973408>
- Carlstead, K., & Shepherdson, D. (2000). Alleviating stress in zoo animals with environmental enrichment. In G. P. Moberg & J. A. Mench (Eds.), *The biology of animal stress: Basic principles and implications for animal welfare*. CABI Pub.
<http://www.cabi.org/cabebooks/FullTextPDF/2000/20002215200.pdf>
- Carlstead, Kathy, & Shepherdson, D. (1994). Effects of environmental enrichment on reproduction. *Zoo Biology*, *13*(5), 447–458. <https://doi.org/10.1002/zoo.1430130507>
- Catania, A. C. (1975). Freedom and knowledge: An experimental analysis of preference in pigeons. *Journal of the Experimental Analysis of Behavior*, *24*(1), 89–106.
<https://doi.org/10.1901/jeab.1975.24-89>
- Catania, A. C., & Sagvolden, T. (1980). Preference for free choice over forced choice in pigeons. *Journal of the Experimental Analysis of Behavior*, *34*(1), 77–86.
<https://doi.org/10.1901/jeab.1980.34-77>
- Chamove, A. S., Anderson, J. R., Morgan-Jones, S. C., & Jones, S. P. (1982). Deep woodchip litter: Hygiene, feeding, and behavioral enhancement in eight primate species. *International Journal for the Study of Animal Problems*, *3*(4), 308–318.
- Chang, V., & Cheung, M. (2016). *Furbo Dog Nanny*. Tomofun. <https://furbo.com/>
- Clark, F. E., Gray, S. I., Bennett, P., Mason, L. J., & Burgess, K. V. (2019). High-tech and tactile: Cognitive enrichment for zoo-housed gorillas. *Frontiers in Psychology*, *10*, 1574.
<https://doi.org/10.3389/fpsyg.2019.01574>

- Clay, A. W., Perdue, B. M., Gaalema, D. E., Dolins, F. L., & Bloomsmith, M. A. (2011). The use of technology to enhance zoological parks. *Zoo Biology*, *30*(5), 487–497.
<https://doi.org/10.1002/zoo.20353>
- Cross, D. T. (2019). Deforestation will drive orangutans extinct ‘in a decade.’ *Sustainability Times*. <https://www.sustainability-times.com/environmental-protection/deforestation-will-drive-orangutans-extinct-in-a-decade/>
- Damerius, L. A., Burkart, J. M., van Noordwijk, M. A., Haun, D. B. M., Kosonen, Z. K., Galdikas, B. M. F., Saraswati, Y., Kurniawan, D., & van Schaik, C. P. (2019). General cognitive abilities in orangutans (*Pongo abelii* and *Pongo pygmaeus*). *Intelligence*, *74*, 3–11. <https://doi.org/10.1016/j.intell.2018.10.008>
- de Azevedo, C. S., Cipreste, C. F., & Young, R. J. (2007). Environmental enrichment: A GAP analysis. *Applied Animal Behaviour Science*, *102*(3–4), 329–343.
<https://doi.org/10.1016/j.applanim.2006.05.034>
- Deci, E. L., & Ryan, R. M. (2013). *Intrinsic motivation and self-determination in human behavior*. Springer Science + Business Media.
- DeGood, Douglas E. (1975). Cognitive control factors in vascular stress responses. *Psychophysiology*, *12*(4), 399–401. <https://doi.org/10.1111/j.1469-8986.1975.tb00010.x>
- Delgado, R. A., & Van Schaik, C. P. (2000). The behavioral ecology and conservation of the orangutan (*Pongo pygmaeus*): A tale of two islands. *Evolutionary Anthropology*, *9*(5), 201–218.
- Egelkamp, C. L., & Ross, S. R. (2019). A review of zoo-based cognitive research using touchscreen interfaces. *Zoo Biology*, *38*(2), 220–235. <https://doi.org/10.1002/zoo.21458>

- Faircloth, K. P. (1974). The importance of subject control in reinforcing brain stimulation. *Learning and Motivation*, 5(1), 16–23. [https://doi.org/10.1016/0023-9690\(74\)90034-4](https://doi.org/10.1016/0023-9690(74)90034-4)
- Fernandez-Blance, K. (2012, August 23). Toronto zoo orangutans go ape for iPad. *The Toronto Star*.
http://www.thestar.com/news/gta/2012/08/23/toronto_zoo_orangutans_go_ape_for_ipad.html
- Fife, E. (2014). Hands-on with Moneaul’s Babble. *Reviewed*.
<https://www.reviewed.com/health/news/moneuals-babble>
- Fujiwara, J., Usui, N., Park, S. Q., Williams, T., Iijima, T., Taira, M., Tsutsui, K.-I., & Tobler, P. N. (2013). Value of freedom to choose encoded by the human brain. *Journal of Neurophysiology*, 110(8), 1915–1929. <https://doi.org/10.1152/jn.01057.2012>
- Geer, J. H., Davison, G. C., & Gatchel, R. I. (1970). Reduction of stress in humans through nonveridical perceived control of aversive stimulation. *Journal of Personality and Social Psychology*, 16(4), 731–738. <https://doi.org/10.1037/h0030014>
- Glass, D. C., & Singer, J. E. (1972). Behavioral aftereffects of unpredictable and uncontrollable aversive events. *American Scientist*, 60(4), 457–465.
- Goodall, J. (2005). Great ape biology. In J. O. Caldecott, L. Miles & K. A. Annan (Eds.), *World atlas of great apes and their conservation* (pp. 29-30). University of California Press.
- Goodstein, L., MacKenzie, D. L., & Shotland, R. L. (1984). Personal control and inmate adjustment to prison. *Criminology*, 22(3), 343–369. <https://doi.org/10.1111/j.1745-9125.1984.tb00304.x>

- Greenberger, D. B., Strasser, S., Cummings, L. L., & Dunham, R. B. (1989). The impact of personal control on performance and satisfaction. *Organizational Behavior and Human Decision Processes*, 43(1), 29–51. [https://doi.org/10.1016/0749-5978\(89\)90056-3](https://doi.org/10.1016/0749-5978(89)90056-3)
- Hebblewhite, M., & Haydon, D. T. (2010). Distinguishing technology from biology: A critical review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1550), 2303–2312. <https://doi.org/10.1098/rstb.2010.0087>
- Helzer, E. G., & Jayawickreme, E. (2015). Control and the “good life”: Primary and secondary control as distinct indicators of well-being. *Social Psychological and Personality Science*, 6(6), 653–660. <https://doi.org/10.1177/1948550615576210>
- Henry, R. A., & Sniezek, J. A. (1993). Situational factors affecting judgments of future performance. *Organizational Behavior and Human Decision Processes*, 54(1), 104–132. <https://doi.org/10.1006/obhd.1993.1005>
- Heyden, T. (2015). The cows that queue up to milk themselves. *BBC News Magazine*. <https://www.bbc.com/news/magazine-32610257>
- Hokanson, J. E., DeGood, D. E., Forrest, M. S., & Brittain, T. M. (1971). Availability of avoidance behaviors in modulating vascular-stress responses. *Journal of Personality and Social Psychology*, 19(1), 60–68. <https://doi.org/10.1037/h0031052>
- Hopper, L. M., Egelkamp, C. L., Fidino, M., & Ross, S. R. (2018). An assessment of touchscreens for testing primate food preferences and valuations. *Behavior Research Methods*. <https://doi.org/10.3758/s13428-018-1065-0>
- Hsu, J. (2012, July 12). Talking apes project faces cash crisis. *Innovation News Daily*. <http://www.livescience.com/21560-talking-apes-project-crisis.html>

- Huettelman, D. A., & Bogie, H. (2009). Direct blood pressure monitoring in laboratory rodents via implantable radio telemetry. In K. DiPetrillo (Ed.), *Cardiovascular genomics* (Vol. 573, pp. 57–73). Humana Press. https://doi.org/10.1007/978-1-60761-247-6_4
- Hughes, B. O., & Duncan, I. J. H. (1988). The notion of ethological ‘need’, models of motivation and animal welfare. *Animal Behaviour*, *36*(6), 1696–1707. [https://doi.org/10.1016/S0003-3472\(88\)80110-6](https://doi.org/10.1016/S0003-3472(88)80110-6)
- IPS International Guidelines for the Acquisition Care and Breeding of Nonhuman Primates*. (2016). The International Primatological Society. http://www.internationalprimatologicalsociety.org/docs/ips_international_guidelines_for_the_acquisition_care_and_breeding_of_nonhuman_primates_second_edition_2007.pdf
- IUCN. (2020). The IUCN red list of threatened species. *Version 2020-2*. <https://www.iucnredlist.org>
- Kaplan, G. T., & Rogers, L. J. (2000). *The orangutans*. Perseus Pub. <http://catalog.hathitrust.org/api/volumes/oclc/44193818.html>
- Kessel, A. L., & Brent, L. (1998). Cage toys reduce abnormal behavior in individually housed pigtail macaques. *Journal of Applied Animal Welfare Science*, *1*(3), 227–234. https://doi.org/10.1207/s15327604jaws0103_3
- Kim-McCormack, N. N. E., Smith, C. L., & Behie, A. M. (2016). Is interactive technology a relevant and effective enrichment for captive great apes? *Applied Animal Behaviour Science*, *185*, 1–8. <https://doi.org/10.1016/j.applanim.2016.09.012>
- Kurtycz, L. M., Wagner, K. E., & Ross, S. R. (2014). The choice to access outdoor areas affects the behavior of great apes. *Journal of Applied Animal Welfare Science*, *17*(3), 185–197. <https://doi.org/10.1080/10888705.2014.896213>

- Langer, E. J., & Rodin, J. (1976). The effects of choice and enhanced personal responsibility for the aged: A field experiment in an institutional setting. *Journal of Personality and Social Psychology*, 34(2), 191–198. <https://doi.org/10.1037/0022-3514.34.2.191>
- Leotti, L. A., & Delgado, M. R. (2011). The inherent reward of choice. *Psychological Science*, 22(10), 1310–1318. <https://doi.org/10.1177/0956797611417005>
- Leotti, L. A., Iyengar, S. S., & Ochsner, K. N. (2010). Born to choose: The origins and value of the need for control. *Trends in Cognitive Sciences*, 14(10), 457–463. <https://doi.org/10.1016/j.tics.2010.08.001>
- Locke, D. P., Hillier, L. W., Warren, W. C., Worley, K. C., Nazareth, L. V., Muzny, D. M., Yang, S.-P., Wang, Z., Chinwalla, A. T., Minx, P., Mitreva, M., Cook, L., Delehaunty, K. D., Fronick, C., Schmidt, H., Fulton, L. A., Fulton, R. S., Nelson, J. O., Magrini, V., Wilson, R. K. (2011). Comparative and demographic analysis of orang-utan genomes. *Nature*, 469(7331), 529–533. <https://doi.org/10.1038/nature09687>
- Lonsdorf, E., Ross, S. R., Matsuzawa, T., & Goodall, J. (2010a). *The mind of the chimpanzee ecological and experimental perspectives*. University of Chicago Press. <http://public.eblib.com/choice/publicfullrecord.aspx?p=570547>
- Lundberg, U., & Frankenhaeuser, M. (1978). Psychophysiological reactions to noise as modified by personal control over noise intensity. *Biological Psychology*, 6(1), 51–59. [https://doi.org/10.1016/0301-0511\(78\)90006-6](https://doi.org/10.1016/0301-0511(78)90006-6)
- MacDonald, S. E., & Ritvo, S. (2016). Comparative cognition outside the laboratory. *Comparative Cognition & Behavior Reviews*, 11, 49–61. <https://doi.org/10.3819/ccbr.2016.110003>

- Maier, S. F., Laudenslager, M. L., & Ryan, S. M. (2014). Stressor controllability, immune function, and endogenous opiates. In J. B. Overmier & F. R. Brush (Eds.), *Affect, conditioning, and cognition: Essays on the determinants of behavior*. Psychology Press. <http://www.vlebooks.com/vleweb/product/openreader?id=none&isbn=9781317596165>
- Mancini, C., Lawson, S., & Juhlin, O. (2017). Animal-computer interaction: The emergence of a discipline. *International Journal of Human-Computer Studies*, 98, 129–134. <https://doi.org/10.1016/j.ijhcs.2016.10.003>
- Marsh, H. L., & MacDonald, S. E. (2008). The use of perceptual features in categorization by orangutans (*Pongo abelli*). *Animal Cognition*, 11(4), 569–585. <https://doi.org/10.1007/s10071-008-0148-1>
- Marsh, H. L., Spetch, M. L., & MacDonald, S. E. (2011). Strategies in landmark use by orangutans and human children. *Animal Cognition*, 14(4), 487–502. <https://doi.org/10.1007/s10071-011-0382-9>
- Martin, C. F., & Shumaker, R. W. (2018). Computer tasks for great apes promote functional naturalism in a zoo setting. *Proceedings of the Fifth International Conference on Animal-Computer Interaction - ACI '18*, 1–5. <https://doi.org/10.1145/3295598.3295605>
- Mason, G., Clubb, R., Latham, N., & Vickery, S. (2007). Why and how should we use environmental enrichment to tackle stereotypic behaviour? *Applied Animal Behaviour Science*, 102(3–4), 163–188. <https://doi.org/10.1016/j.applanim.2006.05.041>
- McGowan, J., Beger, M., Lewison, R. L., Harcourt, R., Campbell, H., Priest, M., Dwyer, R. G., Lin, H.-Y., Lentini, P., Dudgeon, C., McMahon, C., Watts, M., & Possingham, H. P. (2017). Integrating research using animal-borne telemetry with the needs of conservation

- management. *Journal of Applied Ecology*, 54(2), 423–429. <https://doi.org/10.1111/1365-2664.12755>
- Miller, S. M. (1979). Controllability and human stress: Method, evidence and theory. *Behaviour Research and Therapy*, 17(4), 287–304. [https://doi.org/10.1016/0005-7967\(79\)90001-9](https://doi.org/10.1016/0005-7967(79)90001-9)
- Milton, K., & May, M. L. (1976). Body weight, diet and home range area in primates. *Nature*, 259(5543), 459–462. <https://doi.org/10.1038/259459a0>
- Morimura, N. (2003). A note on enrichment for spontaneous tool use by chimpanzees (*Pan troglodytes*). *Applied Animal Behaviour Science*, 82(3), 241–247. [https://doi.org/10.1016/S0168-1591\(03\)00058-3](https://doi.org/10.1016/S0168-1591(03)00058-3)
- Nijholt, A. (2015). *More playful user interfaces: Interfaces that invite social and physical interaction*. <http://public.eblib.com/choice/publicfullrecord.aspx?p=2095945>
- O’Connell, N. E., & Beattie, V. E. (1999). Influence of environmental enrichment on aggressive behaviour and dominance relationships in growing pigs. *Animal Welfare*, 8(3), 269–279.
- O’Connor, T. F., Fach, M. E., Miller, R., Root, S. E., Mercier, P. P., & Lipomi, D. J. (2017). The language of glove: Wireless gesture decoder with low-power and stretchable hybrid electronics. *PLOS ONE*, 12(7), e0179766. <https://doi.org/10.1371/journal.pone.0179766>
- Overmier, J. Bruce, & Seligman, M. E. (1967). Effects of inescapable shock upon subsequent escape and avoidance responding. *Journal of Comparative and Physiological Psychology*, 63(1), 28–33. <https://doi.org/10.1037/h0024166>
- Owen, M. A., Swaisgood, R. R., Czekala, N. M., & Lindburg, D. G. (2005). Enclosure choice and well-being in giant pandas: Is it all about control? *Zoo Biology*, 24(5), 475–481. <https://doi.org/10.1002/zoo.20064>

- Patall, E. A., Cooper, H., & Robinson, J. C. (2008). The effects of choice on intrinsic motivation and related outcomes: A meta-analysis of research findings. *Psychological Bulletin*, *134*(2), 270–300. <https://doi.org/10.1037/0033-2909.134.2.270>
- Perdue, B. M., Clay, A. W., Gaalema, D. E., Maple, T. L., & Stoinski, T. S. (2012). Technology at the zoo: The influence of a touchscreen computer on orangutans and zoo visitors: technology at the zoo. *Zoo Biology*, *31*(1), 27–39. <https://doi.org/10.1002/zoo.20378>
- Perdue, B. M., Evans, T. A., Washburn, D. A., Rumbaugh, D. M., & Beran, M. J. (2014). Do monkeys choose to choose? *Learning & Behavior*, *42*(2), 164–175. <https://doi.org/10.3758/s13420-014-0135-0>
- Perlmutter, L., & Monty, R. (1977). The importance of perceived control: Fact or fantasy? Experiments with both humans and animals indicate that the mere illusion of control significantly improves performance in a variety of situations. *American Scientist*, *65*(6), 759–765.
- Phares, E. J. (1976). *Locus of control in personality*. General Learning Press.
- Preece, J., Benyon, D., & Open University (Eds.). (1993). *A Guide to usability: Human factors in computing*. Addison-Wesley.
- Ravignani, A., Olivera, V. M., Gingras, B., Hofer, R., Hernández, C. R., Sonnweber, R.-S., & Fitch, W. (2013). Primate drum kit: A system for studying acoustic pattern production by non-human primates using acceleration and strain sensors. *Sensors*, *13*(8), 9790–9820.
- Renner, E., Price, E. E., & Subiaul, F. (2016). Sequential recall of meaningful and arbitrary sequences by orangutans and human children: Does content matter? *Animal Cognition*, *19*(1), 39–52. <https://doi.org/10.1007/s10071-015-0911-z>

- Ritvo, S. E., & Allison, R. S. (2017). Designing for the exceptional user: Nonhuman animal-computer interaction (ACI). *Computers in Human Behavior*, 70, 222–233.
<https://doi.org/10.1016/j.chb.2016.12.062>
- Ritvo, S. E., & MacDonald, S. E. (2016). Music as enrichment for Sumatran orangutans (*Pongo abelii*). *Journal of Zoo and Aquarium Research*, 4(3).
<https://www.jzar.org/jzar/article/view/231/113>
- Rodin, J. (1983). Behavioral medicine: Beneficial effects of self control training in aging. *Applied Psychology*, 32(2), 153–181. <https://doi.org/10.1111/j.1464-0597.1983.tb00901.x>
- Rodin, J. (1986). Aging and health: Effects of the sense of control. *Science*, 233(4770), 1271–1276. <https://doi.org/10.1126/science.3749877>
- Ross, S. R. (2006). Issues of choice and control in the behaviour of a pair of captive polar bears (*Ursus maritimus*). *Behavioural Processes*, 73(1), 117–120.
<https://doi.org/10.1016/j.beproc.2006.04.003>
- Rossing, W., Hogewerf, P. H., Ipema, A. H., Ketelaar-De Lauwere, C. C., & De Koning, C. J. A. M. (1997). Robotic milking in dairy farming. *Netherlands Journal of Agricultural Science*, 45(1), 15–31. <https://doi.org/10.18174/njas.v45i1.523>
- Russon, A. E., Kuncoro, P., & Ferisa, A. (2015). Tools for the trees. In *Animal Creativity and Innovation* (pp. 419–458). Elsevier. <https://doi.org/10.1016/B978-0-12-800648-1.00015-2>
- Scheel, B. (2018). Designing digital enrichment for orangutans. *Proceedings of the Fifth International Conference on Animal-Computer Interaction - ACI '18*, 1–11.
<https://doi.org/10.1145/3295598.3295603>

- Schmidtke, D., Ammersdörfer, S., Joly, M., & Zimmermann, E. (2018). First comparative approach to touchscreen-based visual object–location paired-associates learning in humans (*Homo sapiens*) and a nonhuman primate (*Microcebus murinus*). *Journal of Comparative Psychology*, *132*(3), 315–325. <https://doi.org/10.1037/com0000116>
- Schweller, K. (2012). Apes with apps. *IEEE Spectrum*, *49*(7), 38–45.
<https://doi.org/10.1109/MSPEC.2012.6221081>
- Schweller, Ken. (2014, March 15). *Of Apes and Apps*. Buena Vista University.
<https://www.bvu.edu/campaign/faculty/detail.dot?id=19a8f70e-935a-44c9-8c90-62c5960019c3>
- Seligman, M. E. P. (1972). Learned helplessness. *Annual Review of Medicine*, *23*, 407–412.
- Seligman, Martin E. P. (1992). *Helplessness: On depression, development, and death*. W. H. Freeman.
- Shepherdson, D. J., Carlstead, K., Mellen, J. D., & Seidensticker, J. (1993). The influence of food presentation on the behavior of small cats in confined environments. *Zoo Biology*, *12*(2), 203–216. <https://doi.org/10.1002/zoo.1430120206>
- Shepherdson, D. J., Mellen, J. D., & Hutchins, M. (2012). *Second Nature: Environmental Enrichment for Captive Animals*. Random House Publisher Services.
<https://public.ebookcentral.proquest.com/choice/publicfullrecord.aspx?p=5337768>
- Simpfendorfer, C. A., Wiley, T. R., & Yeiser, B. G. (2010). Improving conservation planning for an endangered sawfish using data from acoustic telemetry. *Biological Conservation*, *143*(6), 1460–1469. <https://doi.org/10.1016/j.biocon.2010.03.021>

- Singh, D. (1970). Preference for bar pressing to obtain reward over freeloading in rats and children. *Journal of Comparative and Physiological Psychology*, 73(2), 320–327.
<https://doi.org/10.1037/h0030222>
- Staub, E., Tursky, B., & Schwartz, G. E. (1971). Self-control and predictability: Their effects on reactions to aversive stimulation. *Journal of Personality and Social Psychology*, 18(2), 157–162. <https://doi.org/10.1037/h0030851>
- Stotland, E., & Blumenthal, A. L. (1964). The reduction of anxiety as a result of the expectation of making a choice. *Canadian Journal of Psychology/Revue Canadienne de Psychologie*, 18(2), 139–145. <https://doi.org/10.1037/h0083492>
- Sullivan, M. W., & Lewis, M. (2003). Contextual determinants of anger and other negative expressions in young infants. *Developmental Psychology*, 39(4), 693–705.
<https://doi.org/10.1037/0012-1649.39.4.693>
- Suzuki, S. (1997). Effects of number of alternatives on choice in humans. *Behavioural Processes*, 39(2), 205–214. [https://doi.org/10.1016/S0376-6357\(96\)00049-6](https://doi.org/10.1016/S0376-6357(96)00049-6)
- Suzuki, S. (1999). Selection of forced- and free-choice by monkeys (*Macaca fascicularis*). *Perceptual and Motor Skills*, 88(1), 242–250. <https://doi.org/10.2466/pms.1999.88.1.242>
- Swaigood, R. R. (2007). Current status and future directions of applied behavioral research for animal welfare and conservation. *Applied Animal Behaviour Science*, 102(3–4), 139–162.
<https://doi.org/10.1016/j.applanim.2006.05.027>
- Swaigood, R. R., & Shepherdson, D. J. (2005). Scientific approaches to enrichment and stereotypies in zoo animals: What's been done and where should we go next? *Zoo Biology*, 24(6), 499–518. <https://doi.org/10.1002/zoo.20066>

- Swaisgood, R. R., White, A. M., Zhou, X., Zhang, H., Zhang, G., Wei, R., Hare, V. J., Tepper, E. M., & Lindburg, D. G. (2001). A quantitative assessment of the efficacy of an environmental enrichment programme for giant pandas. *Animal Behaviour*, *61*(2), 447–457. <https://doi.org/10.1006/anbe.2000.1610>
- Tafarodi, R. W., Milne, A. B., & Smith, A. J. (1999). The confidence of choice: Evidence for an augmentation effect on self-perceived performance. *Personality and Social Psychology Bulletin*, *25*(11), 1405–1416. <https://doi.org/10.1177/0146167299259006>
- Tarou, L. R., Kuhar, C. W., Adcock, D., Bloomsmith, M. A., & Maple, T. L. (2004). Computer-assisted enrichment for zoo-housed orangutans. *Animal Welfare*, *13*(4), 445–453.
- Thompson, S. C. (1981). Will it hurt less if i can control it? A complex answer to a simple question. *Psychological Bulletin*, *90*(1), 89–101.
- Tigges, J. (1963). On color vision in gibbon and orangutan. *Folia Primatologica*, *1*(3–4), 188–198. <https://doi.org/10.1159/000165794>
- Tricomi, E. M., Delgado, M. R., & Fiez, J. A. (2004). Modulation of caudate activity by action contingency. *Neuron*, *41*(2), 281–292. [https://doi.org/10.1016/S0896-6273\(03\)00848-1](https://doi.org/10.1016/S0896-6273(03)00848-1)
- van Schaik, C. P., Deaner, R. O., & Merrill, M. Y. (1999). The conditions for tool use in primates: Implications for the evolution of material culture. *Journal of Human Evolution*, *36*(6), 719–741. <https://doi.org/10.1006/jhev.1999.0304>
- Vonk, J., & MacDonald, S. E. (2004). Levels of abstraction in orangutan (*Pongo abelii*) Categorization. *Journal of Comparative Psychology*, *118*(1), 3–13. <https://doi.org/10.1037/0735-7036.118.1.3>

- Vonk, Jennifer. (2002). Can orangutans and gorillas acquire concepts for social relationships? *International Journal of Comparative Psychology*, 15(4).
<http://escholarship.org/uc/item/5r52391b>
- Voss, S. C., & Homzie, M. J. (1970). Choice as a value. *Psychological Reports*, 26(3), 912–914.
<https://doi.org/10.2466/pr0.1970.26.3.912>
- Washburn, D. A., Hopkins, W. D., & Rumbaugh, D. M. (1991). Perceived control in rhesus monkeys (*Macaca mulatta*): Enhanced video-task performance. *Journal of Experimental Psychology. Animal Behavior Processes*, 17(2), 123–129.
- Webber, S., Carter, M., Sherwen, S., Smith, W., Joukhadar, Z., & Vetere, F. (2017). Kinecting with orangutans: Zoo visitors' empathetic responses to animals' use of interactive technology. *Proceedings of the 2017 CHI Conference on Human Factors in Computing Systems*, 6075–6088. <https://doi.org/10.1145/3025453.3025729>
- White, R. W. (1959). Motivation reconsidered: The concept of competence. *Psychological Review*, 66(5), 297–333. <https://doi.org/10.1037/h0040934>
- Winocur, G., Moscovitch, M., & Freedman, J. (1987). An investigation of cognitive function in relation to psychosocial variables in institutionalized old people. *Canadian Journal of Psychology/Revue Canadienne de Psychologie*, 41(2), 257–269.
<https://doi.org/10.1037/h0084156>
- Wirman, H. (2013). Orangutan play on and beyond a touchscreen. *19th International Symposium on Electronic Art*, 1212–1215. <http://hdl.handle.net/2123/9678>
- Young, D., Lawlor, P. A., Leone, P., Dragunow, M., & During, M. J. (1999). Environmental enrichment inhibits spontaneous apoptosis, prevents seizures and is neuroprotective. *Nature Medicine*, 5(4), 448–453. <https://doi.org/10.1038/7449>

- Young, R. J. (2003). *Environmental enrichment for captive animals*. Blackwell Science.
- Zebunke, M., Puppe, B., & Langbein, J. (2013). Effects of cognitive enrichment on behavioural and physiological reactions of pigs. *Physiology & Behavior*, *118*, 70–79.
<https://doi.org/10.1016/j.physbeh.2013.05.005>
- Zuckerman, M., Porac, J., Lathin, D., & Deci, E. L. (1978). On the importance of self-determination for intrinsically-motivated behavior. *Personality and Social Psychology Bulletin*, *4*(3), 443–446. <https://doi.org/10.1177/014616727800400317>

CHAPTER 2: DO ORANGUTANS PREFER FREE-CHOICE WHEN CHOICE OPTIONS AND OUTCOMES DO NOT VARY?

Enrichment is important for critically endangered captive orangutans. Choice-facilitating ACI systems have great potential in this regard. Given that zoos and other captive great ape facilities put a great deal of time, effort, and consideration into animal care plans (e.g., food and activity type, quantity, and timing), changes to established routines or protocols can be disruptive, difficult to acquire approval for, and challenging to implement. For this reason, ideal great ape enrichment interventions are those that provide a large impact on animal welfare, with as little disruption to established captive animal protocols as possible. If, like humans, orangutans benefit from even an illusion of control (Perlmutter & Monty, 1977), a system that has no true effect on the great apes' diet, environment, or schedule (i.e., the 'choices' provided do not affect outcome), and therefore does not disrupt established animal care protocols, could still provide appreciable welfare payoffs. However, orangutans' preference for choice has yet to be established. To this end, the experiment that follows investigates orangutans' preference for a largely illusory free-choice in which, apart from the position of reward keys, both choice options and the outcomes of choices do not vary.

PREFERENCE FOR FREE- OR FORCED- CHOICE IN SUMATRAN ORANGUTANS

(*PONGO ABELII*)*

Empirical investigations of humans, pigeons, rats, and monkeys have indicated that these species will select free- over forced- choice, even when faced with identical outcomes. However, the same has yet to be quantitatively confirmed in nonhuman great apes. This experiment is the first systematic investigation of preference for free- or forced- choice in great apes using a paradigm in which extraneous variables are highly controlled. Three orangutans were given a choice of one of two virtual routes, one that provided a choice and one that did not via a touchscreen computer program. Choice of either route was rewarded with the same type and quantity of food. Initial results indicated a preference for free-choice across all three participants. However, in two control conditions, orangutans' preferences varied, suggesting a weaker tendency to exercise choice than species previously tested. We suggest further investigation of preference for free- and forced- choice in orangutans and other great apes through alternative experimental paradigms that focus on increasing the fidelity of free- and forced- choice options.

* This manuscript has been previously published in the *Journal of Experimental Analysis of Behavior*: Ritvo, S. E., & MacDonald, S. E. (2020). Preference for free- or forced- choice in orangutans (*Pongo abelii*). *Journal of Experimental Analysis of Behavior*, 113(2), 419–434. <https://doi.org/10.1002/jeab.584>

Introduction

Cross-cultural preference for free-choice has been extensively demonstrated in humans. Results suggest that choice, or even the illusion of choice, has affective, cognitive, motivational, behavioural, and physiological benefits (Greenberger et al., 1989; Iyengar & Lepper, 2000; Lonsdorf et al., 2010a; Winocur et al., 1987; Zukerman et al., 1978). As a corollary, there is evidence that an external locus of control and *lack* of free-choice can be detrimental (Benassi et al., 1988; Goodstein et al., 1984; Hill et al., 2015; Mineka & Hendersen, 1985; Moore & Cox, 1988; Roddenberry & Renk, 2010; Ruback et al., 1986). In fact, human preference for choice is so strong that it does not appear to be contingent on reward outcomes. Despite the additional energy required to consider and make choices, when presented with equivalent option outcomes, humans choose options that lead to *more* choice (Bown et al., 2003; Leotti et al., 2010; Shuji Suzuki, 1997). Thus, it appears that for humans, choice is an independent motivator (Leotti et al., 2010) and reinforcer (Bown et al., 2003; Shuji Suzuki, 1997). Even when choice has no discernible benefit, humans still prefer to choose.

Origins of Control

Converging evidence indicates that preference for free choice has been adaptively selected for evolutionary survival (Leotti et al., 2010). Environmental control, exercised via conscious and unconscious decision-making, functions as a means of responding to and managing the environment (Perlmutter & Monty, 1977). Moreover, the perception of control buffers stress responses to the environment. In turn, environmental control is believed to reinforce an adaptive perception of *self-efficacy*, defined by Bandura (1977) as, 'one's personal expectations of their ability to succeed' (Leotti et al., 2010). In other words, control of the environment through choice-making affirms personal beliefs in one's ability to achieve desired

outcomes. The opposite is also true. A lack of choice challenges self-efficacy beliefs, generating doubt in one's ability to bring about desired results, a state of mind correlated with hopelessness and depression (Blackburn & Owens, 2015; Botti & McGill, 2006; Deci & Ryan, 2000; Devins & et al, 1982; Kwasky & Groh, 2014; Leotti et al., 2010; Maddux & Meier, 1995; Pu et al., 2016; Ryan & Deci, 2000; Sacco et al., 2005; Schwarzer, 2014; M. E. P. Seligman, 1975; Shnek et al., 1997).

Nonhuman Animals (NHAs), Choice and Control

Although analogous investigations of choice and control in nonhuman animals' (NHAs) are comparatively sparse, existing data indicate that several NHA species also prefer to control their environment by exercising choice (Perdue et al., 2012). Catania (1975b) and Catania and Sagvolden (1980) found that when given the option between two keys, one that led to a free-choice, the other to a forced-choice, pigeons (*Columba livia domestica*) reliably chose the free-choice option even when food reward outcomes were equated. Similarly, when offered either a direct route, or a choice of maze routes, Voss and Homzie (1970) found that laboratory Sprague-Dawley rats (*Rattus norvegicus*) reliably selected the option that allowed choice despite the fact that both paths led to the same destination. Moreover, Singh (1970) found that rats demonstrated a preference to work for rewards by bar pressing rather than to 'free-load' (i.e., receive unearned rewards), thereby demonstrating a preference to control the environment by choosing *when* food becomes available. This behavior persisted even when the amount of bar pressing required to access food was varied or when food could be obtained faster by free-loading.

There is also indication that choice-- or the lack thereof-- has affective, motivational, and physiological effects on NHAs (Beran et al., n.d.; Catania, 1975a; Catania & Sagvolden, 1980; Lonsdorf et al., 2010b; S. Suzuki, 1999a; Voss & Homzie, 1970; Washburn et al., 1991a). When

giant pandas (*Ailuropoda melanoleuca*) were provided a choice to access alternative exhibit areas, they exhibited fewer signs of behavioral agitation and lower urinary cortisol than when they were not provided such choice (Owen et al., 2005). Likewise, when captive polar bears (*Ursus maritimus*) were provided the choice to access an indoor enclosure during the daytime, they demonstrated decreased stereotypies and increased social play, behaviours associated with decreased anxiety and psychological distress (Ross, 2006). Faircloth (1974) found that for rats receiving pleasant electrical stimulation, the effectiveness of the intervention was enhanced when rats controlled treatment onset. Inversely, Weiss (1971) found that ulceration was more frequent and extensive in rats subjected to electric shock over which they had no control. Perhaps most famously, in classic studies by Seligman (1975; 1992a), both laboratory rats and domesticated dogs (*Canis familiaris*) exposed to uncontrollable aversive conditions developed ‘helpless’ behaviour, termed *learned helplessness* (Overmier & Seligman, 1967). After receiving shock treatment that they could not control, when these NHAs were provided the opportunity to ‘escape’ the electric shocks, they no longer attempted to do so. Seligman and Overmier (1967; 1992) concluded that once NHAs learn that their responses have no effect on avoiding aversive stimuli (e.g., after failing to avoid electric shocks), they stop attempting to do so, even when explicitly provided an opportunity.

Several species of monkeys have also demonstrated preference for free-choice. Suzuki (1999b) observed that long-tailed macaques (*Macaca fascicularis*) reliably chose a free-choice option with multiple alternatives over a forced-choice with a preferred alternative. Likewise, Perdue et al. (2014a) found that both capuchin monkeys (*Cebus apella*) and rhesus macaques (*Macaca mulatta*) showed a preference for choosing task-order over having task order randomly assigned. This preference held even when the assigned task was made tangibly attractive in other

respects. For example, several monkeys in Perdue et al.'s (2014b) study maintained a preference to choose task order, even when the alternative was assignment to a task they had previously *preferred* over others.

Research also indicates that choice improves NHP performance on cognitive tasks. When capuchin monkeys were provided control over the order of computer-delivered tasks, they performed significantly better on several aspects than when task order was predetermined (Beran et al., 2007). Likewise, in a computer-delivered study, rhesus macaques performed better when provided a choice of *which* tasks to perform than when they were assigned tasks (Washburn et al., 1991b).

Together these findings suggest that, like humans, several NHA species from varying genera, (a) value control, (b) seek opportunities to choose, and (c) benefit from exercising environmental control via provision of choice (Perdue et al., 2014a).

Great Apes

Investigation of great apes' preferences for choice and environmental control have generated more diverse results. Morimura (2003) found that chimpanzees (*Pan troglodytes*) spontaneously elected to use tools to access tube feeders when they were available, irrespective of the fact that they also intermittently used their mouth and hands to access the feeders instead. Morimura (2003) argued that these results indicate chimpanzee preference for employing all choices available (i.e., mouth, hands, *and* tools). Lonsdorf et al. (2010b) have reported that providing chimpanzees a choice of enrichment videos resulted in lower frequencies of anxiety-induced scratching than when this choice was not provided. Similarly, Kurtycz, Wagner, and Ross (2014) found that providing chimpanzees the choice to access outdoor enclosures resulted in more frequent social and self-directed behaviours (i.e., grooming and playing) and higher

levels of activity. This held true even when the chimpanzees did not exploit the choice provided. Wagner and Ross (2014) contend that these behavioural observations are collectively indicative of a general increase in chimpanzee arousal levels. Kummer (1968) has also drawn links between decision making and increased self-directed behaviours in his field studies of Hamadryas Baboons (*Papio hamadryas*). However, it is important to consider that heightened arousal can also be a negative indicator of affect (e.g., anxiety is also considered a heightened state of arousal), and in great apes, self-directed behaviours can indicate distress. Therefore, Wagner and Ross' (2004) and Kummer' (1968) results could alternatively suggest that this type of choice or decision making was anxiety-provoking for the NHAs observed. Intriguingly, when Kurtycz, Wagner, and Ross (2014) tested gorillas (*Gorilla gorilla gorilla*) in the same conditions, more frequent inactivity and lower levels of feeding and object manipulation were observed in the free choice condition. Again, these behavioural observations are open to selective interpretation. Inactivity could be construed as indicators of either boredom or relaxation. In contrast, Bloomsmith et al. (2000) found that provision of chimpanzee choice had no observable effects. When chimpanzees that were provided control over a computer task were compared to a yoked group who could see the same display and received the same rewards, but were only passively involved in the task, no differences in behavioural measures of well-being (i.e., levels of activity, self-directed behaviours, scratching, or stereotypes) were observed between the two groups.

Together these results suggest that humans and monkeys exhibit a preference for choice and that the ability to choose can have beneficial effects. However, great ape preferences for choice and the effects of choice on great apes remains unclear.

Modelled after Catania and Sagvolden's (1980) concurrent-chain paradigm, the purpose of this study was to explore whether orangutans prefer free- or forced-choice when the outcome

of their choices is held constant. Orangutans have proven motivated to participate in computer-delivered empirical investigation, capable of color vision, and show sufficient visual acuity for the required study tasks, making them an ideal species for this line of enquiry (Adams, 2017, Anderson, 2012; Tigges, 1963). This is the first systematic investigation of preference for free-choice in great apes using a paradigm in which extraneous variables were highly controlled.

Method

Participants

The study group consisted of 3 Sumatran orangutans (*Pongo abelli*) housed at the Toronto Zoo: Two females (Ramai, 32 years old, and Sekali, 25 years old), and one male: (Budi, 11 years old). Participants were not related to one another and had been trained to use a dowel to operate a touchscreen computer for previous studies investigating music and visual preferences (Adams et al., 2016; Ritvo & MacDonald, 2016); however, none had participated in investigations of environmental control or choice. Research participation was voluntary and participants were not deprived of food or water at any time. Instead, food rewards were provided as positive reinforcement for participation. Studies were conducted under the oversight of the York University Animal Care Committee, the Toronto Zoo Animal Care Committee, and followed the guidelines of the Canadian Council on Animal Care.

Apparatus and Materials

Experimental sessions were administered and recorded using an HP Desktop 260-A129 PC (“HP Desktop”, 2019) and a 21” color PC computer monitor with a Keytec Magic Touch touchscreen (*Magic Touch*, 2016) unit attached. Orangutans’ choice preferences were assessed via a custom touchscreen-delivered program written in Java. Computer hardware was mounted in a mobile wooden housing that allowed the entire unit to be positioned in front of a participant’s

enclosure. Touchscreen selections were made using a wooden dowel. To motivate participation, participants received a single preferred food reward (i.e., one blueberry) for every trial that ended in a correct response.

Design

Data were collected in orangutan holding areas accessible only to zookeepers and experimenters. Participants were physically separated from one another during testing but had some auditory contact through adjoining enclosures. Participants could leave the testing area at any time. Absence from the testing area for more than 10 minutes resulted in the termination of that session. Experimental sessions consisted of 64 trials, and each participant completed 1-2 sessions per day, 3-4 days per week.

Test sessions were initiated by positioning the touchscreen in front of a participants' enclosure. Participants initiated test sessions by approaching the experimental apparatus. Upon approach, the experimenter offered a wooden dowel to the participant and activated the touchscreen program to initiate the first trial.

Only a single selection per task parameter was accepted and participants received a single food reward for successful completion of a trial. To prevent the experimenter from cuing participants, she was positioned behind the housing unit, facing the participant, such that she could not see the display and was prompted to reward the participant appropriately via auditory chime. The experimenter delivered rewards to participants by hand over the top-center of the apparatus so as to avoid inadvertently indicating that rewards were related to one side of the apparatus versus the other.

Orangutans' preference for free or forced choice was assessed via a touchscreen-delivered program that mimicked Catania and Sagvolden's (1980) six-key pigeon chamber

concurrent-chain paradigm. This program allowed orangutans to choose one of two virtual routes (i.e., one that provided a free-choice and one that did not). Orangutans were provided a choice of selection of one of two white circular touchscreen-displayed keys, called ‘initial link keys’.

Initial link keys were located on the same plane, equidistant from the central axis. Selection of one initial link key led to a forced-choice of a single terminal link key to the food reward, while selection of the other initial link key allowed a free-choice of several terminal link keys to arrive at the same food reward (see Figure 1 for visual example of a trial). More specifically, selection of one of the two initial link keys produced one of two terminal links:

- *Free-choice terminal link*: Three reward keys and one neutral key displayed in a row at the center of the touchscreen.
- *Forced-choice terminal link*: One reward key and three neutral keys displayed in a row at the center of the touchscreen.

In both terminal links:

- If an orangutan selected a *reward* key (i.e., a correct response) they received an auditory bridge followed by a standardized food reward before the next trial was initiated. During the 3 second ITI, the touchscreen display was black.
- If an orangutan selected a *neutral* key (i.e., an incorrect response), the next trial initiated after a 3 second ITI without an auditory bridge or reward.

To control for the potentially confounding effect of the position of the initial link keys on the display, two control conditions were also employed in which the position of the free choice initial link key was changed from the left to the right of the display, and from the right to the top of the display (see Table 1). Furthermore, as identified by Catania and Sagvolden (1980), investigations of preference for free over forced choice are vulnerable to being confounded by

the number, variety, and information value of stimuli. This paradigm controlled for these extraneous variables by making terminal link stimuli equivalent in number, variety, and bits of information (Catania & Sagvolden, 1980). Each terminal link included four keys, one of which was a different color than the other keys in both the free- and forced- choice terminal links. Therefore, the free and forced choice conditions were matched for stimulus number (i.e., four keys), stimulus variety (i.e., one odd colored key among four keys), and bits of information (i.e., two bits of information to select either one of four keys or three of four keys). In addition, to control for color preference confounds, assigned reward key colors, and key color pairs were randomized and counterbalanced per participant, so that an equal number of participants were rewarded for selecting red, green, or yellow keys. Budi was rewarded for selecting yellow keys amongst blue keys, Ramai was rewarded for selecting blue keys amongst yellow keys, and Sekali and was rewarded for selecting red keys amongst green keys. The position of the odd key was also randomized and counterbalanced across trials (e.g., BAAA, ABAA, AABA, or AAAB) to control for side preference confounds.

Reward Color Training.

Color training consisted of sessions in which a single reward key and a single neutral key were displayed in a row at the center of the touchscreen. If the participant selected the reward key (i.e., a correct response), they received an auditory bridge followed by a standardized food reward before the next trial initiated. During the 3 second ITI, the touchscreen display was black. If the participant selected the *neutral* key (i.e., an incorrect response), the next trial initiated after a 3 second ITI without a bridge or reward (see Figure 2 for visual example of a trial). Color training was complete, and participants were graduated to concurrent-chains training, when each met an 80% correct criterion for 3 training sessions.

Terminal Link Keys Color Training.

Concurrent-chains training started with multiple key color training. In these sessions, free choice terminal links (i.e., three reward keys, and one neutral key) and forced choice terminal links (i.e., one reward key, and three neutral keys) were presented individually in a randomized and counterbalanced sequence. For both terminal links, selection of reward keys were reinforced with an auditory bridge and a food reward and selection of neutral keys ended a trial with no bridge or reward. Terminal link keys color training was complete when each participant met an 80% correct criterion for three training sessions (see Figure 3 for visual example of a trial).

Initial Link Keys Side Training.

For the concurrent-chains initial link training, a single initial link key was presented at the beginning of each trial. Depending on the side of the screen that the initial link key was presented on, selection of the initial link key initiated a free-choice terminal link or a forced-choice terminal link respectively. As indicated previously, position of the reward- and neutral-colored terminal link keys were randomized and counterbalanced across trials. To control for the potential confounding effect of the display side that free- and forced- choice initial link keys were presented on (i.e., to ensure that participant side-preferences did not confound results), three initial link key orientation conditions were trained and tested: (a) free-choice left, forced-choice right (free-left), (b) free-choice right, forced choice left (free-right), and (c) free-choice top, forced-choice bottom (free-top). In the free-top condition, the top and bottom keys were displaced 5 cm above and below the horizontal plane where initial link keys were located in the free-left and free-right conditions. Participants were required to meet an 80% correct criterion over 3 sessions in each training condition before moving onto testing in the same condition type.

Once testing was complete in that condition, the participant was trained and then tested in the next condition, and so on (see Table 1 for order of training and testing stages).

Testing.

In the testing condition, both the free- and forced- choice keys were presented in the initial link at the beginning of each trial. Selection of the initial link key on one side of the display initiated a free-choice terminal link and selection of the initial link key on the other side of the display initiated a forced- choice terminal link respectively. As in previous conditions, position of the reward- and neutral- colored terminal link keys were randomized and counterbalanced across trials. Preference for free over forced choice was assessed by relative choice percentages in respective initial link keys. There were 16 distinct trial conditions (i.e., combinations of free-choice terminal link key order, and forced-choice terminal link key order). Each experimental session consisted of 4 blocks of 16-trials, for a total of 64 trials per session. Each participant completed 1-2 sessions per day. Testing was terminated when a participant reached an 80% preference criterion for either the free- or forced- choice initial link key over 4 test sessions.

Results

All orangutans participated in test sessions consistently and reliably. The few instances in which orangutans declined to participate in a test session occurred during periods of unusual environmental disruption (e.g., construction to the enclosure). Results are discussed for each study condition and analyzed by individual. General trends are also reported.

Test Condition: Free-Choice Left, Forced-Choice Right (free-left)

Relative choice percentages from sessions in which the free-choice initial link key was accessed via the left side of the display and forced-choice initial link key was accessed via the

right side of the display are provided in Figure 4. All participants demonstrated a preference for the free-choice initial link key. Budi and Sekali showed the strongest and most consistent preference for the free-choice condition. Both met the 80% free-choice preference criterion rate in session 1 and continued to do so in every subsequent session. Although Ramai also met the free-choice preference criterion, she took three sessions to do so and showed less consistency in her choices.

Free-Choice Right, Forced-Choice Left Condition (free-right)

As a control condition, the positions of the free- and forced- choice initial link keys on the display were reversed. If participants' preference for the free-choice terminal link was robust, we would expect them to stop selecting the left initial link key as observed in the free-left condition, and to instead start selecting the right initial link key. Relative choice percentages from free-right sessions are provided in Figure 5. Although Budi demonstrated a continued preference for free-choice, both Ramai and Sekali did not. Specifically, Budi met the free-choice preference criterion in session 2, then dipped below criterion and briefly reached the forced-choice preference criterion in sessions 5 and 6, before climbing back to criterion for free choice in sessions 10 to 12. For the most part, Ramai and Sekali continued selecting the left initial link key as they had in the free-left condition, thereby selecting the forced choice initial link in the free-right condition. Ramai met the preference criterion for forced-choice by session 4 and like in the free-right condition, showed less consistency in her choices than the other two orangutans. Notably, Ramai demonstrated a slight shift towards selection of the free-choice initial link key in sessions 12 to 14, nearly meeting the free-choice criterion in session 13. Although in Sekali's first test session, she chose the free-choice initial link key more often than the forced-choice initial link key, from session 2 onward, she chose the forced-choice initial link key 50% of the

time or more. By session 10, Sekali reached the forced-choice preference criterion and continued to do so in subsequent sessions.

Free-Choice Top, Forced-Choice Bottom Condition (free-top)

Given the contrasting results from the free-left and free-right conditions, and the hypothesis that learned side preference from the free-left condition may have confounded results in the free-right condition, a second control condition was tested to minimize the impact of the side of the display on which the free- and forced- choice initial link keys were located. In the free-top condition, initial link keys were changed from a horizontal to a vertical orientation, so that the free-choice initial link key was displayed above the forced-choice initial link key. Relative choice percentages from free-top sessions are provided in Figure 6. As hypothesized, once right-left side preferences were controlled for, both Ramai and Sekali demonstrated a strong and relatively consistent preference for free-choice terminal link as they had in the first free-left condition. Sekali met the 80% for free-choice preference criterion in session 3 and continued to do so for subsequent sessions. Ramai met the free-choice preference criterion immediately in session 1, and showed fairly consistent preference for free-choice thereafter, meeting criterion in sessions 3, 5, and 6, and only dipping slightly below criterion in sessions 2 and 4. Budi, in contrast to his observed preference for free-choice in the free-left and free-right conditions however, demonstrated an immediate and fairly consistent preference for forced choice in the free-top condition, meeting the forced-choice preference criterion in session 1, and sessions 3 to 5.

Discussion

In this study, Sumatran orangutans were assessed with an experimental choice paradigm modeled on that employed by Catania and Sagvolden (1980) with pigeons. Catania and

Sagvolden (1980) reported that with the exception of the early conditions for one participant, each shift of the free-choice initial link key from one side of the display to the other, was consistently followed by a corresponding shift in initial link key preference. However, one of the four pigeons tested (Pigeon 18), only demonstrated this behaviour in the last two conditions tested. In the present study, although all of the orangutans initially demonstrated a preference for free-choice in the first condition (free-left), in the second (free-right) and third (free-top) conditions, the orangutans' preferences varied. Ramai and Sekali both displayed a preference for forced-choice in the second condition, and free-choice in the third condition, and Budi maintained his preference for free-choice in the second condition but preferred the forced-choice option in the third condition (see Table 2). Compared to Catania and Sagvolden's (1980) study, Ramai and Sekali's results bears some semblance to Pigeon 18's behavior. However the behaviour of all three orangutans differs from the behavior of the other 3 pigeons tested (i.e., the majority of participants). The results of this study also differ from other investigations of choice that have found that humans, NHPs, and rats will reliably select a free-choice option when provided the opportunity even when both options lead to equivalent outcomes (Bown et al., 2003; Catania, 1975; Catania & Sagvolden, 1980; Morimura, 2003; Perdue et al., 2014; Suzuki, 1997; Suzuki, 1999; Voss and Homzie, 1970).

If these results indicate some degree of indifference in orangutans to free- or forced-choice when outcomes are held constant, this conclusion would be supported by Bloomsmith et al.'s (2000) observations that provision of choice in a chimpanzee computer task did not affect behavioural measures of well-being. However, given that all three orangutans preferred the free-choice option in the first (free-left) condition, it seems unlikely that indifference is the most appropriate explanation.

Side biases often arise when participants are unsure of what is required of them, or when the rate of reinforcement is the same regardless of the participant's performance. Therefore, side bias could explain why, in this paradigm, participants selected an initial link key on one side of the display more often than the other. However, this would not explain why *all* three orangutans preferred the initial link key located on the *same* side of the display in the free-left condition. Comparative results of population-level handedness in nonhuman primates have been inconsistent between and within species (Hopkins, 2014). For this reason, and given how close in proximity the initial link keys were positioned, it is unlikely that handedness is a likely explanation either. Instead, given that all three participants demonstrated a strong left initial link key preference in the *first* free-left condition (i.e., when they were naïve to the paradigm), these results suggest a weak preference for free-choice when outcomes are held constant.

In Ramai and Sekali's case, it is reasonable to suppose that a side bias, developed through the selection of, and positive association with, the free-choice initial link key in the first (free-left) condition, carried over into the second (free-right) condition. That is, when the location of the free-choice initial link key was moved from the left to the right side of the display for the second (free-right) condition, the left side bias that Ramai and Sekali learned from selecting the free-choice initial link key in the first (free-left) condition, conflicted with, and eventually outweighed their preference for the free-choice terminal link in the free-right condition. This conflict may be evidenced by several test sessions in the free-right condition in which both participants responded at near chance levels for both initial link keys (see Figure 5 b-c). Notably, the same type of conflict in response was not observed as often for Ramai, or at all for Sekali in the first free-left condition. This explanation is supported by the fact that when left vs. right side preferences were controlled for in the third condition (free-top) by changing the initial link keys

to a vertical orientation, both Ramai and Sekali again exhibited a preference for free-choice, by selecting the top free-choice initial link key. According to this explanation, it would appear that Ramai and Sekali preferred the free-choice option when outcomes were equated but that this preference was not strong enough to overcome a learned side bias.

Alternatively, Ramai and Sekali's conflicting results may be accounted for by orangutans' documented difficulty with single transposition scenarios. Barth and Call (2006) reported that Bornean orangutans (*Pongo pygmaeus*) did not perform as well as chimpanzees and bonobos in single spatial transpositions of baited cups. If this finding also applies to Sumatran orangutans, it could have made the transposition of the free-choice initial link key from the left of the display (in the free-left condition) to the right of the display (in the free-right condition) difficult for Ramai and Sekali to navigate appropriately. In other words, Ramai and Sekali may not have been able to follow a hidden reward (i.e., the free-choice initial link key) as it switched locations with an adjacent identical stimulus (i.e., the forced-choice initial link key).

Unlike Ramai and Sekali, Budi demonstrated a preference for free-choice in both the first (free-left) and second (free-right) conditions, but not in the third (free-top) condition. These results suggest that if Budi developed a left side bias in the first (free-left) condition, it was weaker than his preference for free choice, because in the second (free-right) condition, he quickly switched from selecting the left initial link key to selecting the right initial link key. Alternatively, if difficulty with transpositions was at issue in this paradigm, Budi may have experienced less difficulty in this regard given that he was younger and therefore likely more cognitively flexible than Ramai and Sekali.

Curiously, in the last (free-top) condition, Budi demonstrated a preference for forced choice by selecting the bottom initial link key. Again, because Budi demonstrated a strong

preference for free-choice in both the first and second conditions, it is unlikely that these results suggest indifference to free- or forced-choice. Given that this was the third condition, this behavior could be indicative of boredom or confusion with the paradigm. Budi may have been engaging in what has been termed 'hypothesis testing' in which a participant will test alternative solutions to a task as means of determining if their hypothesis about the task solution is correct. However, why Budi continually selected the forced choice initial link key for the duration of the free-top condition, is uncertain. It's also possible that, after growing accustomed to the paradigm in the first two conditions, Budi sought out the forced choice terminal link because of the challenge it offered - locating and selecting, a single reward key, rather than selecting any of three reward keys in the free-choice terminal link. As reported above, Budi was the most engaged participant, completing test sessions more quickly and consistently than Ramai and Sekali. This behavior may be indicative of more interest in, and attention to, the paradigm and could have attributed to boredom in the free-top condition that Ramai and Sekali did not experience. Although the reasoning behind Budi's forced-choice selection in the third condition is uncertain, at the very least, like Ramai and Sekali, Budi's results as a whole, also suggest at least a weak preference for free choice.

Overall, results of all three participants suggest an inclination towards free-choice (in the first free-left condition), but one that can be easily influenced by competing factors (in the subsequent free-right or free-top conditions). Given that Catania and Sagvolden (1980) observed a stronger, more consistent preference for free choice in the majority of pigeons tested using a similar paradigm, this is an unexpected result.

One potential factor in accounting for these differences is participants' experience with environmental control. In previous research, environmental control, exercised through decision-

making, has been observed to reinforce an adaptive perception of what Bandura (1977) terms *self-efficacy*, ‘one’s personal expectations of the ability to succeed’ (Leotti et al., 2010). The more environmental control exercised through choice-making, the stronger one’s personal beliefs in their ability to achieve desired outcomes. This amounts to a conditioning effect wherein the more extensive the individual’s prior experience in choice-making, the stronger the individual’s motivation to continue exercising choice. The opposite is also true. A lack of choice challenges self-efficacy beliefs, generating a perceived inability to bring about desired results, a state Seligman (1975) describes as *learned helplessness* (Blackburn & Owens, 2015; Botti & McGill, 2006; Deci & Ryan, 2000; Devins & et al, 1982; Kwasky & Groh, 2014; Leotti et al., 2010; Maddux & Meier, 1995; Pu, Hou, & Ma, 2016; Ryan & Deci, 2000; Sacco et al., 2005; Schwarzer, 2014; Shnek et al., 1997). Therefore, prior experiences in applying environmental control can strengthen or weaken tendencies to exercise choice.

The orangutans tested in this study have lived in a captive zoo setting for their lifetimes. Although enrichment is incorporated by captive animal facilities as an important part of animal care, by their very nature these facilities are limited in their ability to afford residents control over captive environments equal to that found in natural environments. Living in an environment where free-choice is limited, theoretically may have reduced these orangutans’ tendencies to exercise free-choice in situations where it is possible to do so. But, why would that not also hold true for pigeons (Catania and Sagvolden, 1980), rats (Voss and Homzie, 1970) or monkeys (Suzuki, 1999) that have been found to reliably demonstrate a preference for free-choice over forced-choice?

The fidelity of the choice paradigm employed here and by Catania and Sagvolden (1980) may have been a factor. In this choice paradigm, both the choice options and the reward

outcomes are identical. The free choice terminal link offers a choice between three identical keys and selection of any reward key in both the free- and forced- choice terminal links is rewarded with the same quantity and type of food. Thus, apart from reward key position, selection of the ‘free choice’ link does not provide a variety of choice options or outcomes. It’s possible that for orangutans, the free choice link in this paradigm did not provide enough tangible ‘free-choice’ (Russon, 1998). In other words, this paradigm may not provide enough variation to be interpreted as a ‘free choice’ by orangutans and could account for the observed weak preferences for the free-choice condition. For this reason, it would be interesting to investigate if (a) similar results are observed using this paradigm with other great ape species, including chimpanzees, gorillas, bonobos and human children and (b) if a choice paradigm that provides more tangible variability in either choice options or outcomes, elicits stronger preference for free- or forced-choice in orangutans.

Based on the present research, we cannot speculate whether Sumatran orangutans display a weaker preference for free-choice than pigeons and monkeys, or whether their preference selections reflect the inappropriateness of Catania and Sagvolden’s (1980) choice paradigm for this species and other great apes. It is possible that the differences observed between this experiment and others that employed the same paradigm reflect a difference in understanding of what ‘free-choice’ constitutes between species. Regardless, as the first systematic investigation of preference for free- or forced- choice in great apes using a paradigm in which extraneous variables are highly controlled, the present research builds on knowledge of an important area of comparative cognition that can be applied to captive animal welfare.

References

- Adams, L., Wilkinson, F. E., & MacDonald, S. E. (2016). Limits of spatial vision in Sumatran orangutans (*Pongo abelli*). *Animal Behavior and Cognition*.
- Bandura, A. (1977). Self-efficacy: Toward a unifying theory of behavioral change. *Psychological Review*, *84*(2), 191–215. <https://doi.org/10.1037/0033-295X.84.2.191>
- Benassi, V. A., Sweeney, P. D., & Dufour, C. L. (1988). Is there a relation between locus of control orientation and depression? *Journal of Abnormal Psychology*, *97*(3), 357–367. <https://doi.org/10.1037/0021-843X.97.3.357>
- Beran, M. J., Klein, M. D., Evans, T. A., Antworth, R., & Chan, B. (2007). Perceived control, motivation, and task performance in capuchin monkeys. In P. R. Zelick (Ed.), *Issues in the psychology of motivation* (pp. 171–175). New York: Nova Science Publishers.
- Blackburn, L., & Owens, G. P. (2015). The effect of self efficacy and meaning in life on posttraumatic stress disorder and depression severity among veterans: Self-efficacy and meaning. *Journal of Clinical Psychology*, *71*(3), 219–228. <https://doi.org/10.1002/jclp.22133>
- Bloomsmith, M. A., Ross, K. C., & Baker, K. C. (2000). Control over computer-assisted enrichment for socially housed chimpanzees. *American Journal of Primatology*, *51*(1), 45.
- Botti, S., & McGill, A. L. (2006). When choosing is not deciding: The effect of perceived responsibility on choice outcome satisfaction. *Journal of Consumer Research*, *33*, 512–513.
- Bown, N. J., Read, D., & Summers, B. (2003). The lure of choice. *Journal of Behavioral Decision Making*, *16*(4), 297–308. <https://doi.org/10.1002/bdm.447>

- Catania, A. C. (1975). Freedom and knowledge: An experimental analysis of preference in pigeons. *Journal of the Experimental Analysis of Behavior*, 24(1), 89–106.
<https://doi.org/10.1901/jeab.1975.24-89>
- Catania, A. C., & Sagvolden, T. (1980). Preference for free choice over forced choice in pigeons. *Journal of the Experimental Analysis of Behavior*, 34(1), 77–86.
<https://doi.org/10.1901/jeab.1980.34-77>
- Clay, A. W., Perdue, B. M., Gaalema, D. E., Dolins, F. L., & Bloomsmith, M. A. (2011). The use of technology to enhance zoological parks. *Zoo Biology*, 30(5), 487–497.
<https://doi.org/10.1002/zoo.20353>
- Deci, E. L., & Ryan, R. M. (2000). The “what” and “why” of goal pursuits: Human needs and the self-determination of behavior. *Psychological Inquiry*, 11(4), 227–268.
- Devins, G. M., & et al. (1982). Perceived self-efficacy, outcome expectancies, and negative mood states in end-stage renal disease. *Journal of Abnormal Psychology*, 91(4), 241–244.
<https://doi.org/10.1037/0021-843X.91.4.241>
- Faircloth, K. P. (1974). The importance of subject control in reinforcing brain stimulation. *Learning and Motivation*, 5(1), 16–23. [https://doi.org/10.1016/0023-9690\(74\)90034-4](https://doi.org/10.1016/0023-9690(74)90034-4)
- Goodstein, L., MacKenzie, D. L., & Shotland, R. L. (1984). Personal control and inmate adjustment to prison. *Criminology: An Interdisciplinary Journal*, 22(3), 343–369.
- Greenberger, D. B., Strasser, S., Cummings, L. L., & Dunham, R. B. (1989). The impact of personal control on performance and satisfaction. *Organizational Behavior and Human Decision Processes*, 43(1), 29–51. [https://doi.org/10.1016/0749-5978\(89\)90056-3](https://doi.org/10.1016/0749-5978(89)90056-3)

- Hill, R. P., Rapp, J. M., & Capella, M. L. (2015). Consumption restriction in a total control institution: Participatory action research in a maximum security prison. *Journal of Public Policy & Marketing, 34*(2), 156–172. <https://doi.org/10.1509/jppm.14.101>
- Iyengar, S. S., & Lepper, M. R. (2000). When choice is demotivating: Can one desire too much of a good thing? *Journal of Personality and Social Psychology, 79*(6), 995–1006.
- Kurtycz, L. M., Wagner, K. E., & Ross, S. R. (2014). The choice to access outdoor areas affects the behavior of great apes. *Journal of Applied Animal Welfare Science, 17*(3), 185–197. <https://doi.org/10.1080/10888705.2014.896213>
- Kwasky, A. N., & Groh, C. J. (2014). Vitamin D, depression and coping self-efficacy in young women: Longitudinal study. *Archives of Psychiatric Nursing, 28*(6), 362–367. <https://doi.org/10.1016/j.apnu.2014.08.010>
- Leotti, L. A., Iyengar, S. S., & Ochsner, K. N. (2010). Born to choose: The origins and value of the need for control. *Trends in Cognitive Sciences, 14*(10), 457–463. <https://doi.org/10.1016/j.tics.2010.08.001>
- Lonsdorf, E., Ross, S. R., Matsuzawa, T., & Goodall, J. (2010). *The mind of the chimpanzee ecological and experimental perspectives*. Chicago: University of Chicago Press. Retrieved from <http://public.eblib.com/choice/publicfullrecord.aspx?p=570547>
- Maddux, J. E., & Meier, L. J. (1995). Self-efficacy and depression. In J. E. Maddux (Ed.), *Self-efficacy, adaptation, and adjustment* (pp. 143–169). Boston, MA: Springer US. Retrieved from http://link.springer.com/10.1007/978-1-4419-6868-5_5
- Magic Touch Add-On Touchscreen. (2018). [Incorporation]. Retrieved from <http://www.magictouch.com/addon-1.html>

- Mineka, S., & Hendersen, R. W. (1985). Controllability and predictability in acquired motivation. *Annual Review of Psychology*, *36*(1), 495–529.
<https://doi.org/10.1146/annurev.ps.36.020185.002431>
- Moore, J. Z., & Cox, J. (1988). Health locus of control of female inmates from the Virginia Correctional Center for Women (VCCW) measured by the Multidimensional Health Locus of Control (MHLC) Scale. *Journal of Prison & Jail Health*, *7*(2), 98–108.
- Morimura, N. (2003). A note on enrichment for spontaneous tool use by chimpanzees (*Pan troglodytes*). *Applied Animal Behaviour Science*, *82*(3), 241–247.
[https://doi.org/10.1016/S0168-1591\(03\)00058-3](https://doi.org/10.1016/S0168-1591(03)00058-3)
- Overmier, J. B., & Seligman, M. E. (1967). Effects of inescapable shock upon subsequent escape and avoidance responding. *Journal of Comparative and Physiological Psychology*, *63*(1), 28–33.
- Owen, M. A., Swaisgood, R. R., Czekala, N. M., & Lindburg, D. G. (2005). Enclosure choice and well-being in giant pandas: Is it all about control? *Zoo Biology*, *24*(5), 475–481.
<https://doi.org/10.1002/zoo.20064>
- Perdue, B. M., Evans, T. A., Washburn, D. A., Rumbaugh, D. M., & Beran, M. J. (2014). Do monkeys choose to choose? *Learning & Behavior*, *42*(2), 164–175.
<https://doi.org/10.3758/s13420-014-0135-0>
- Perlmutter, L. C., & Monty, R. A. (1977). The importance of perceived control: Fact or fantasy? *American Scientist*, *65*(6), 759–765.
- Pu, J., Hou, H., & Ma, R. (2016). Direct and indirect effects of self-efficacy on depression: The mediating role of dispositional optimism. *Current Psychology*.
<https://doi.org/10.1007/s12144-016-9429-z>

- Ritvo, S. E., & MacDonald, S. E. (2016). Music as enrichment for Sumatran orangutans (*Pongo abelii*). *Journal of Zoo and Aquarium Research*, (3).
<https://doi.org/10.19227/jzar.v4i3.231>
- Roddenberry, A., & Renk, K. (2010). Locus of control and self-efficacy: Potential mediators of stress, illness, and utilization of health services in college students. *Child Psychiatry & Human Development*, 41(4), 353–370. <https://doi.org/10.1007/s10578-010-0173-6>
- Ross, S. R. (2006). Issues of choice and control in the behaviour of a pair of captive polar bears (*Ursus maritimus*). *Behavioural Processes*, 73(1), 117–120.
<https://doi.org/10.1016/j.beproc.2006.04.003>
- Ruback, R. B., Carr, T. S., & Hopper, C. H. (1986). Perceived control in prison: Its relation to reported crowding, stress, and symptoms. *Journal of Applied Social Psychology*, 16(5), 375–386. <https://doi.org/10.1111/j.1559-1816.1986.tb01147.x>
- Russon, A. E. (1998). The nature and evolution of intelligence in orangutans (*Pongo pygmaeus*). *Primates*, 39(4), 485-503.
- Ryan, R. M., & Deci, E. L. (2000). Self-determination theory and the facilitation of intrinsic motivation, social development, and well-being. *The American Psychologist*, 55(1), 68–78.
- Sacco, W. P., Wells, K. J., Vaughan, C. A., Friedman, A., Perez, S., & Matthew, R. (2005). Depression in adults with type 2 diabetes: The role of adherence, body mass index, and self-efficacy. *Health Psychology*, 24(6), 630–634. <https://doi.org/10.1037/0278-6133.24.6.630>
- Schwarzer, R. (2014). *Self-efficacy thought control of action*. London: Routledge, Taylor and Francis. Retrieved from <http://public.eblib.com/choice/publicfullrecord.aspx?p=1710802>

- Seligman, M. E., & Beagley, G. (1975). Learned helplessness in the rat. *Journal of Comparative and Physiological Psychology*, 88(2), 534–541. <https://doi.org/10.1037/h0076430>
- Seligman, M. E. P. (1992). *Helplessness: on depression, development, and death*. New York: W. H. Freeman.
- Shnek, Z. M., Foley, F. W., LaRocca, N. G., Gordon, W. A., DeLuca, J., Schwartzman, H. G., ... Irvine, J. (1997). Helplessness, self-efficacy, cognitive distortions, and depression in multiple sclerosis and spinal cord injury. *Annals of Behavioral Medicine*, 19(3), 287–294. <https://doi.org/10.1007/BF02892293>
- Suzuki, S. (1997). Effects of number of alternatives on choice in humans. *Behavioural Processes*, 39(2), 205–214. [https://doi.org/10.1016/S0376-6357\(96\)00049-6](https://doi.org/10.1016/S0376-6357(96)00049-6)
- Suzuki, S. (1999). Choice between forced- and free-choice by monkeys (*Macaca fascicularis*). *Perceptual and Motor Skills*, (88), 242–250.
- Vonk, J. (2002). Can orangutans and gorillas acquire concepts for social relationships? *International Journal of Comparative Psychology*, 15(4). Retrieved from <http://escholarship.org/uc/item/5r52391b>
- Vonk, J. (2014). Quantity matching by an orangutan (*Pongo abelii*). *Animal Cognition*, 17(2), 297–306. <https://doi.org/10.1007/s10071-013-0662-7>
- Voss, S. C., & Homzie, M. J. (1970). Choice as a value. *Psychological Reports*, (26), 912–914.
- Washburn, D. A., Hopkins, W. D., & Rumbaugh, D. M. (1991). Perceived control in rhesus monkeys (*Macaca mulatta*): Enhanced video-task performance. *Journal of Experimental Psychology. Animal Behavior Processes*, 17(2), 123–129.
- Weiss, J. M. (1971). Effects of coping behavior in different warning signal conditions on stress pathology in rats. *Journal of Comparative and Physiological Psychology*, 77(1), 1–13.

Winocur, G., Moscovitch, M., & Freedman, J. (1987). An investigation of cognitive function in relation to psychosocial variables in institutionalized old people. *Canadian Journal of Psychology, 41*(2), 257–269.

Zukerman, M., Porac, J., Lathin, D., Smith, R., & Deci, E. L. (1978). On the importance of self-determination for intrinsically motivated behavior. *Personality and Social Psychology Bulletin, 4*(4), 443-446.

Tables

Table 1.1

Order of Delivery of Training and Testing Stages

Chronological Order	Stage
1	Reward Color Training
2	Terminal Link Keys Color Training
3	Free-Left ^a Initial Link Keys Side Training Testing
4	Free-Right (Control 1) ^b Initial Link Keys Side Training Testing
5	Free-Top (Control 2) ^c Initial Link Keys Side Training Testing

^a Free-choice initial link key located on the left side of the display. Forced-choice initial link key located on the right side of the display.

^b Free-choice initial link key located on the right side of the display. Forced-choice initial link key located on the left side of the display.

^c Free-choice initial link key located at the top of the display. Forced-choice initial link key located at the bottom of the display.

Table 1.2

Free- vs. forced- Choice Observed Preference Results in Each Condition Per Subject

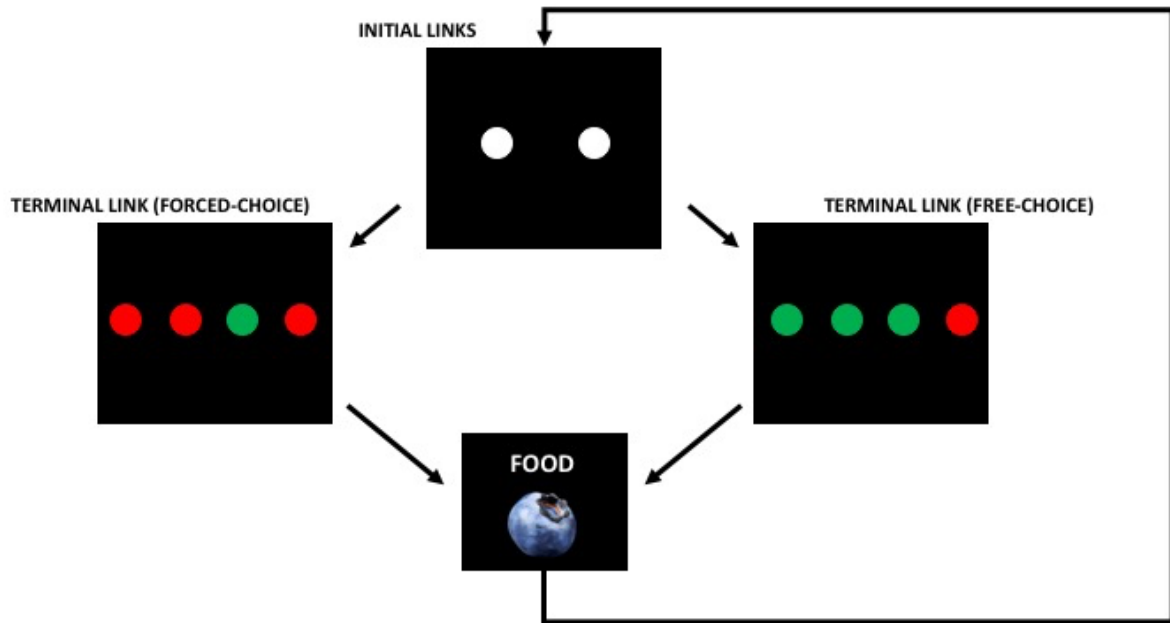
	Free Choice Left	Free Choice Right	Free Choice Top
Budi	Free Choice	Free Choice	Forced Choice
Ramai	Free Choice	Forced Choice	Free Choice
Sekali	Free Choice	Forced Choice	Free Choice

Note: Cells are color-coded to aid in data visualization

Figures

Figure 1.1

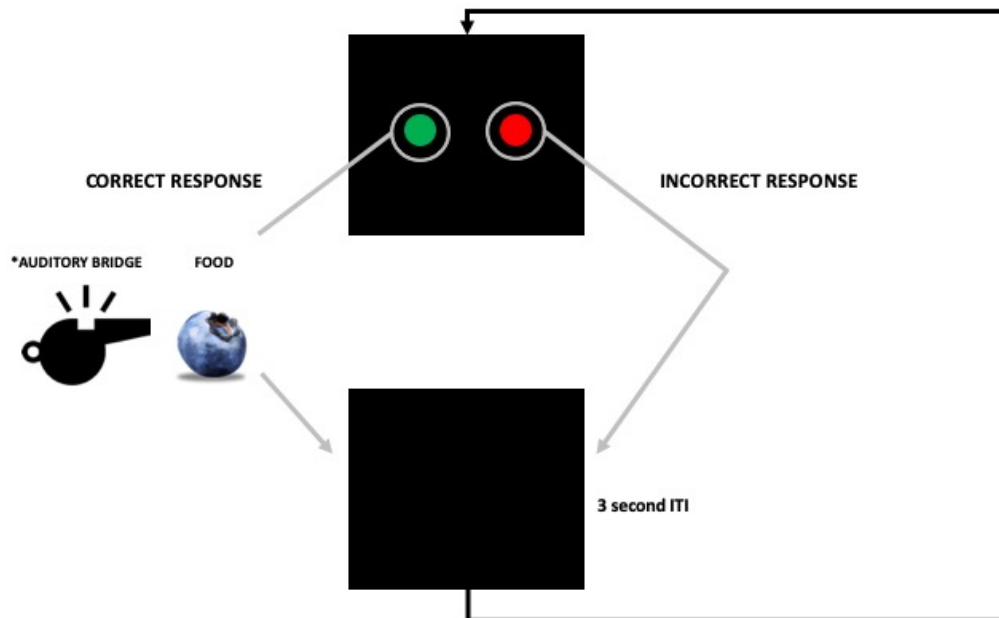
Example of a Testing Trial in the Free-Choice Right Condition



Note. In the example, the participant's reward key color is green and neutral key color is red. In the initial link (top square), two white keys are displayed. The free-choice terminal link is accessed via selection of the right initial link key, and the forced-choice terminal link is accessed via selection of the left initial link key. In the forced-choice terminal link (left square), three keys are red and one key is green. In the free-choice terminal link (right square), three keys are green and one key is red. Selection of a green key in either terminal link produced an auditory bridge, a standardized food reward (i.e., selection of a green key in either terminal link lead to the same food reward), and initiation of a new trial. Selection of a red key initiated a new trial, with no reward.

Figure 1.2

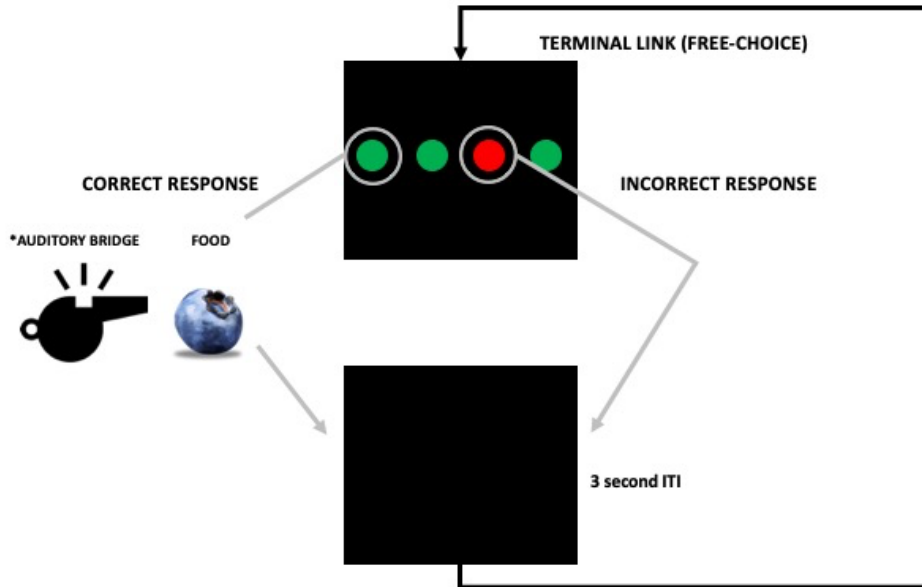
Example of Color Training Procedure



Note. A single reward key and a single neutral key are displayed in a row at the center of the first display (top square). In the example, the participant's reward key color is green and neutral key color is red. If the participant selects the reward key, they receive an auditory bridge and a single food reward during the 3 second ITI. If the participant selects the neutral key, they do not receive a reward during the 3 second ITI.

Figure 1.3

Example of Terminal Link Keys Color Training Procedure

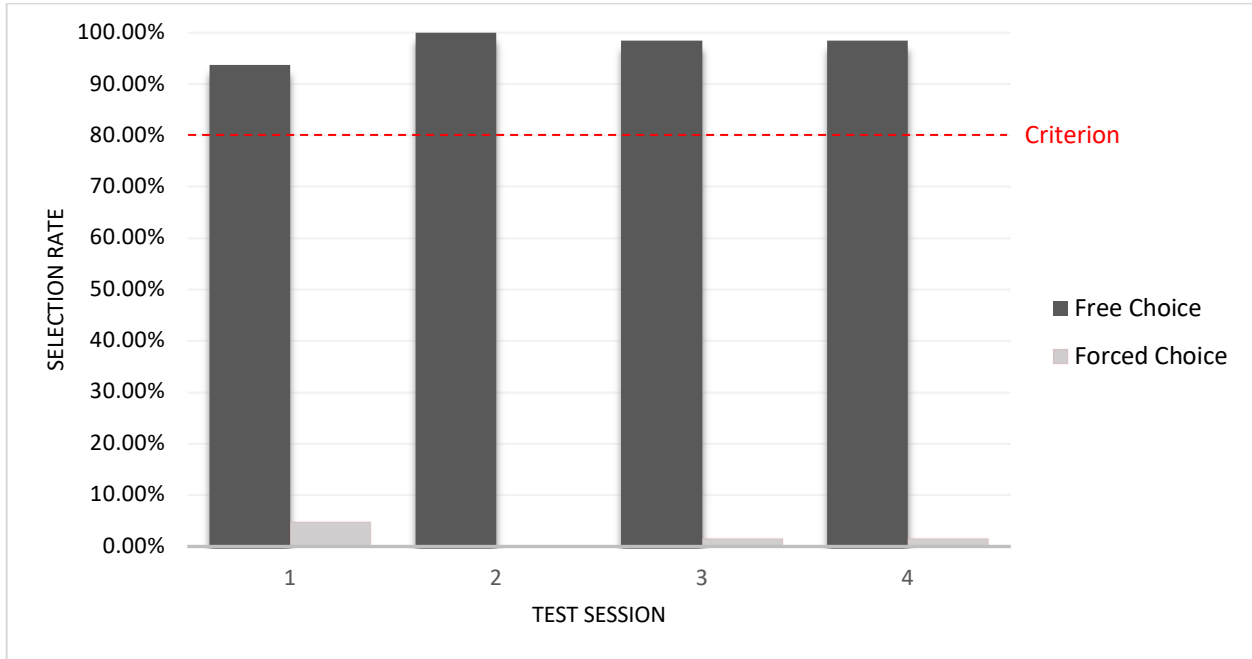


Note. In the example, a free-choice terminal link is displayed, and the participant's reward key color is green and neutral key color is red. Free choice terminal links (i.e., three reward keys, and one neutral key) and forced choice terminal links (i.e., one reward key, and three neutral keys) were presented in a randomized and counterbalanced sequence. In both conditions, selection of reward-color keys were reinforced with an auditory bridge and a food reward and selection of neutral keys ended a trial with no reward.

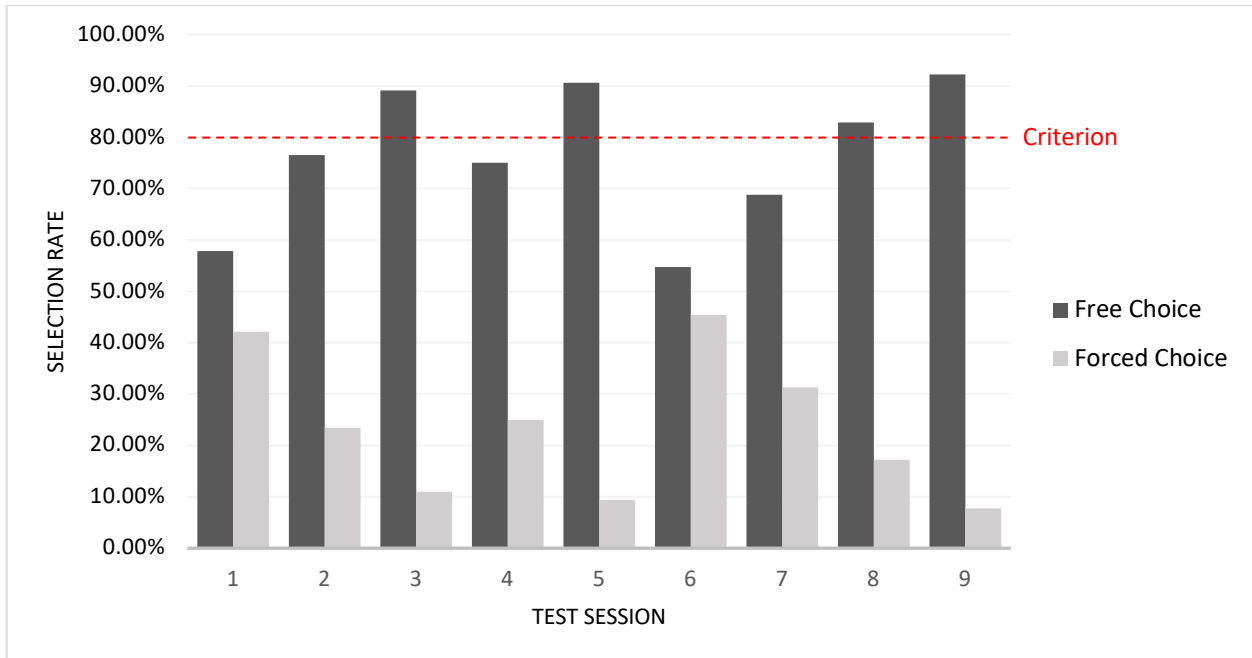
Figure 1.4a, 1.4b, and 1.4c

Frequency of Free- and Forced- Choice Initial Link Key Selections

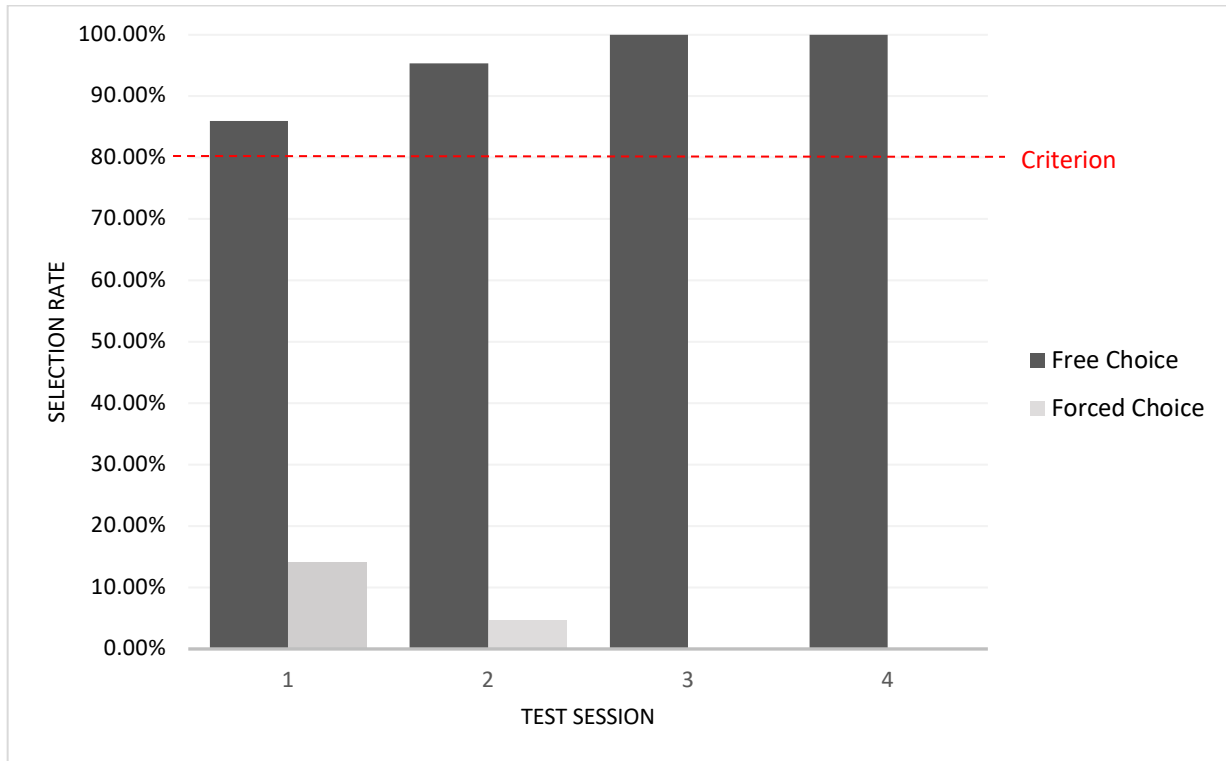
a) Budi



b) Ramai



c) Sekali

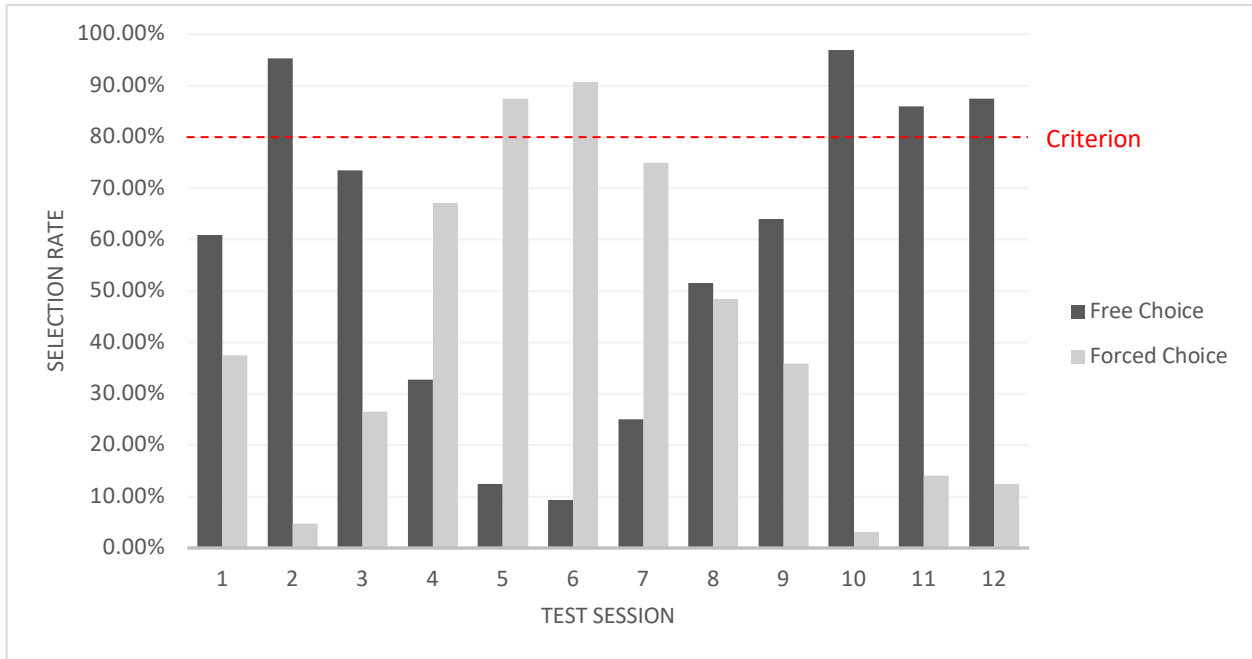


Note. Based on 64-trials per session, in comparison to preference criterion for each orangutan, in the first condition: Free-Choice Left, Forced-Choice Right.

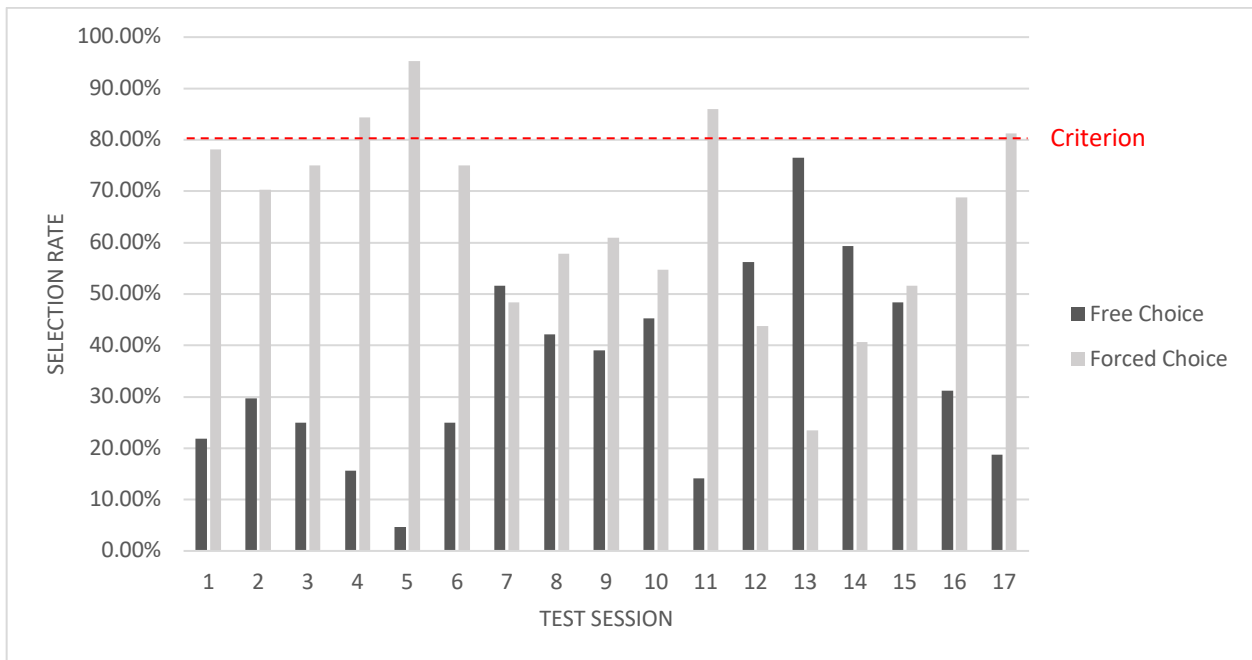
Figure 1.5a, 1.5b, and 1.5c

Frequency of Free- and Forced- Choice Initial Link Key Selections

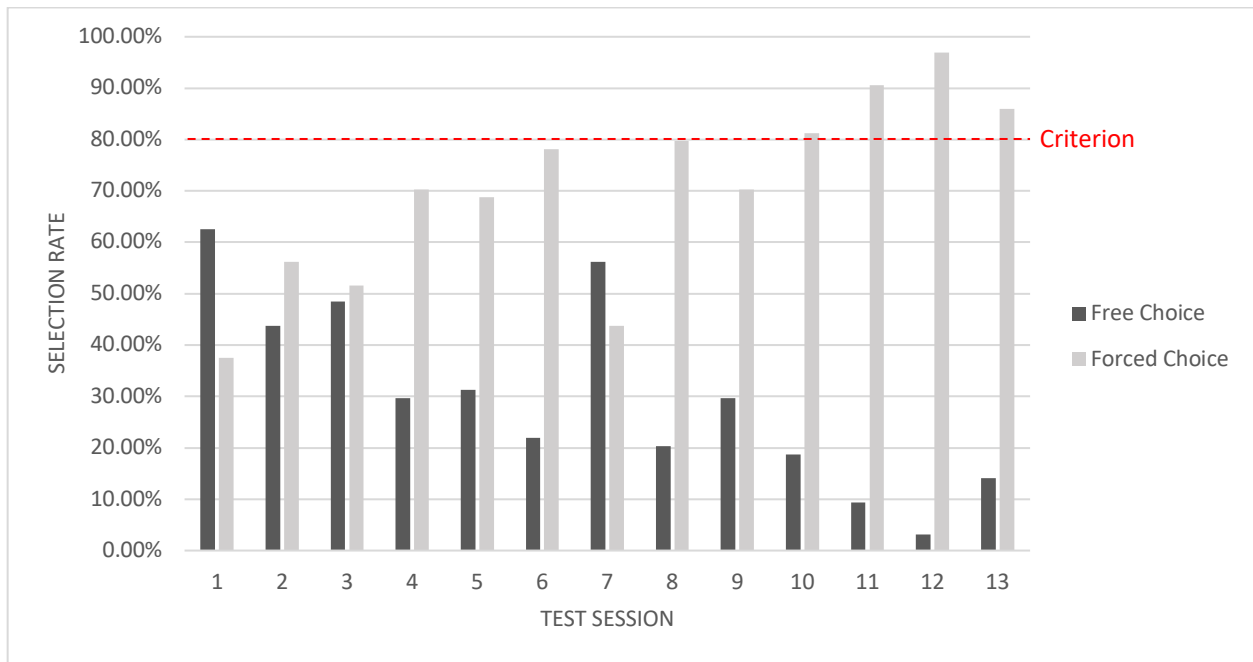
a) Budi



b) Ramai



c) Sekali

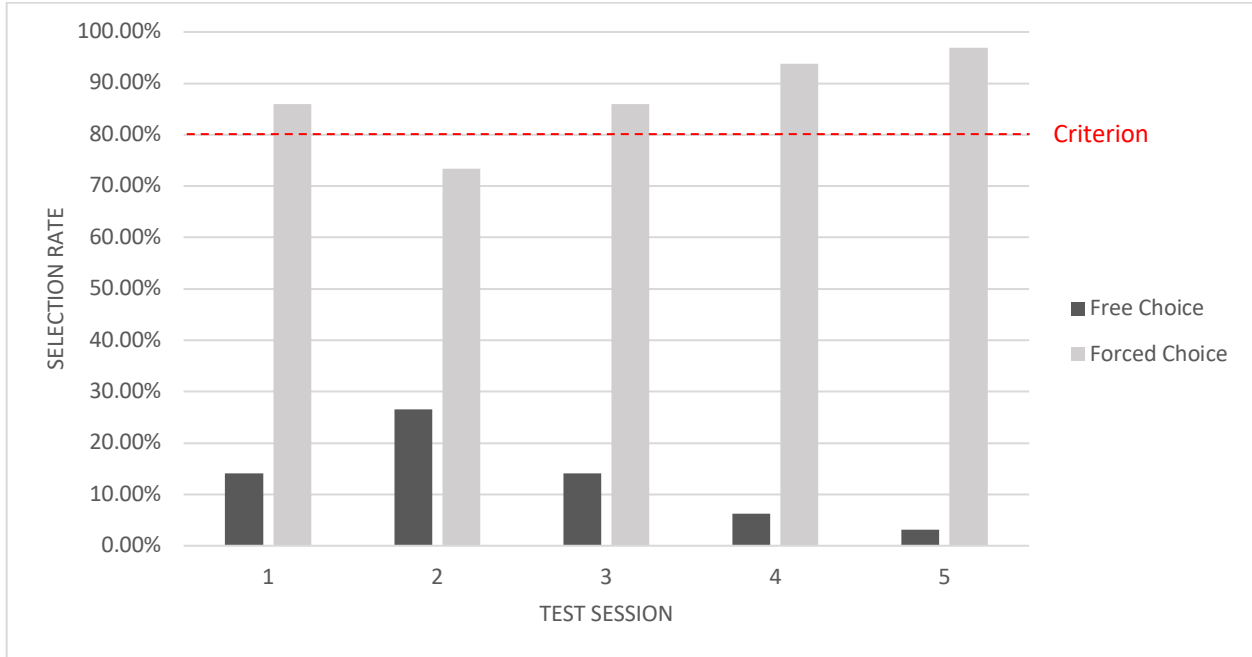


Note. Based on 64-trials per session, in comparison to preference criterion for each orangutan, in the second condition: Free-Choice Right, Forced-Choice Left.

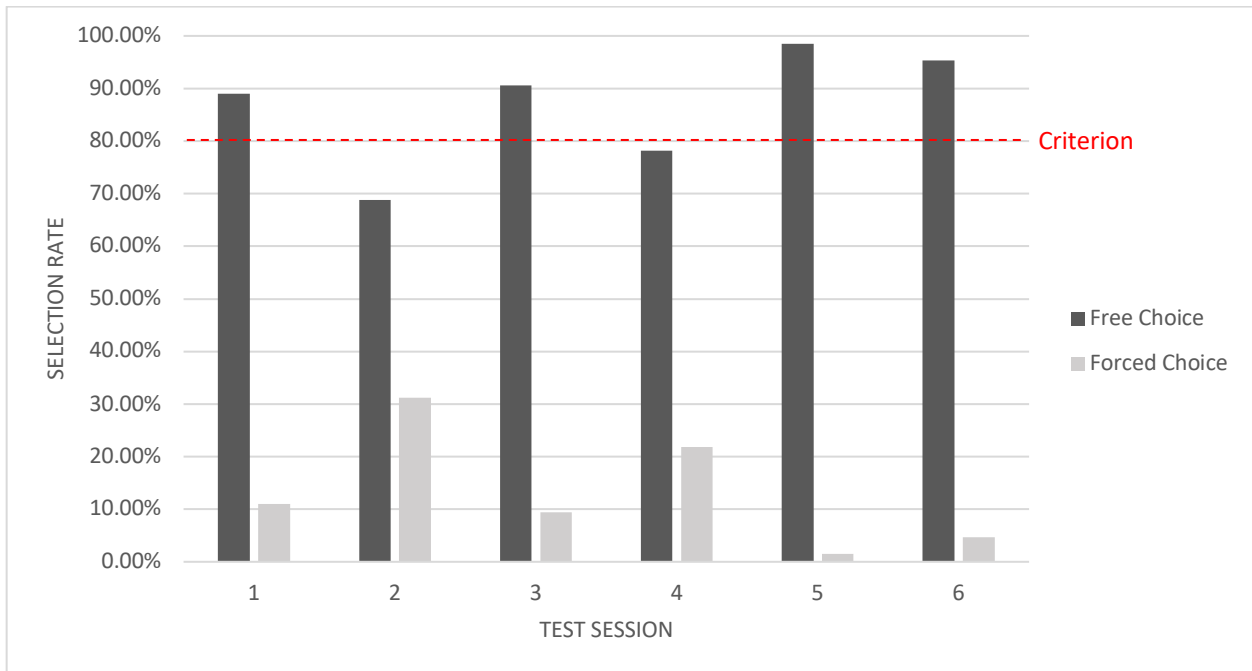
Figure 1.6a, 1.6b, and 1.6c

Frequency of Free- and Forced- Choice Initial Link Key Selections

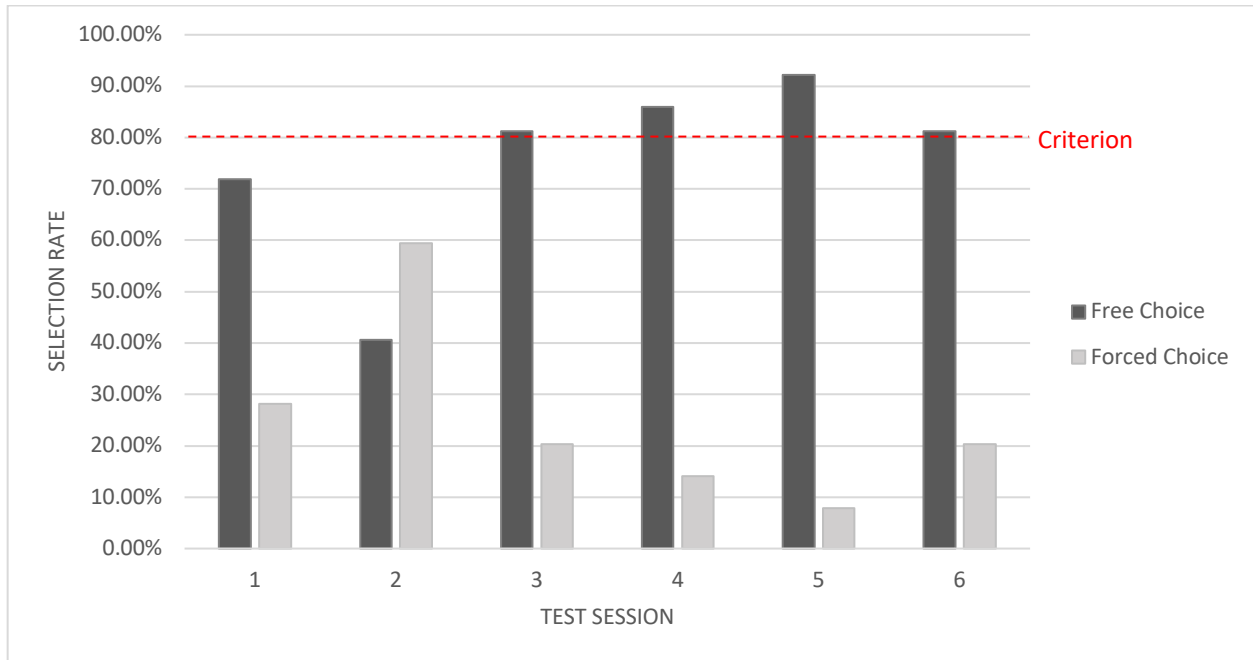
a) Budi



b) Ramai



c) Sekali



Note. Based on 64-trials per session, per orangutan in the third condition: Free-Choice Top, Forced-Choice Bottom.

CHAPTER 3: CAN ORANGUTANS RECOGNIZE PICTURE CONTENT?

Before continuing the investigation of orangutans' preference for computer-provided choice, it was important to ensure that the manner in which choices were presented and communicated was appropriate for this species. During training for the study described in Chapter 2, the orangutans demonstrated marked difficulty during the reward color phase of training, learning associations between colored computer software icons and food rewards. Five orangutans were initially recruited for the study and participated in the reward color phase of training in which they were rewarded with food for selecting a reward-colored key from among two keys displayed on a touchscreen. However, after over a year of training, three to four days a week, only three orangutans met the criterion required to graduate to the next phase of training. In other words, following a minimum of 9,828 trials, two orangutans did not learn to select a reward colored button over a neutral colored button displayed on a touchscreen. Given that orangutans have proven capable of (a) color vision (Tigges, 1963), and (b) learning a same-different color concept with 2-dimensional objects (King, 1973), this difficulty suggested that touchscreen displayed pictures, or more broadly, pictures in general, may be challenging for orangutans to interpret. Thus, motivated by this observation, the three experiments that follow explored if orangutans can spontaneously recognize the content of novel pictorial stimuli, and if this capacity is affected by either presentation format (i.e., size, composition, number of displays, etc.) or presentation medium (i.e., digital or print).

RECOGNITION OF NOVEL PICTURES BY SUMATRAN ORANGUTANS (*PONGO ABELII*): AN INVESTIGATION OF DIGITAL AND PRINTED MEDIUMS*

By three months of age, human infants can recognize picture content. Whether the same can be said of nonhuman primates (hereafter, primates) is unclear. In many primate studies that use pictures, subjects are trained on experimental tasks through reinforced exposure to the stimuli. However, training of this type circumvents investigation of primates' basic capacity to autonomously identify picture content. The purpose of this series of experiments was to investigate the ability of orangutans to spontaneously recognize the content of novel pictorial stimuli. Following establishment of food preference hierarchies, we tested whether subjects demonstrated the same hierarchical food preferences for food pictures in both digital (Experiments 1 and 3) and printed mediums (Experiments 2 and 3). Experimental conditions varied based on presentation format and mode. Stimuli comprised slices of food and whole foods, pictured both with and without backgrounds, presented on several types of digital displays and in prints of various sizes. Results indicate that orangutans only recognized food picture content in certain formats, and that they were slightly more proficient in print mediums than in digital ones. This was especially true for one of the youngest subjects who excelled at recognizing printed images, suggesting that the capacity to recognize picture content may vary across individuals and does not necessarily improve with age.

* This manuscript is currently under revision for publication in *Animal Cognition*.

Introduction

Since Herrnstein and Loveland (1964) tested the capacity of pigeons to discriminate between slides, two-dimensional photographic representations (i.e., pictures) have become one of the most predominant types of stimuli employed in studying nonhuman animal cognition (Parron et al., 2008). However, the nature of how animals perceive pictures is not entirely understood. In order to recognize a pictorially represented object, an observer must either: (a) make a perceptual error, mistaking the picture for the real object (Fagot et al., 1999; Herrnstein & Loveland, 1964), or (b), distinguish the picture as a referential stimulus, mentally associating the picture and its abstract relation to the object it represents (DeLoache, 2004; Herrnstein & Loveland, 1964).

Research suggests that previous experience with pictures may determine which approach is employed. Humans' ability to recognize the content of pictures is evident early in life (Bovet & Vauclair, 2000). Newborns can discriminate real objects from their pictorial representations, and three month old infants who have no experience with pictures can recognize a photograph of their mother's face (Barrera & Maurer, 1981). However, the ability to process a pictures as a representations appears to be affected by experience. Nine month-old infants investigate two-dimensional images by touching and feeling pictured objects and trying to pick them off the page, suggesting that they confuse the picture and its referent (DeLoache et al., 1998). However, by nineteen months of age, children begin pointing at pictured objects instead, indicating that through experience, they have learned that a picture is both an object itself, and a referent. Moreover, adults from cultures that have no experience with photographs have demonstrated difficulty perceiving photographs as representations of real objects (Segall et al., 1966), and recognizing objects or people in photographs and drawings (Miller, 1973). Interestingly, when the details of the pictures were pointed out, the same people were then able to recognize the

picture's content (Miller, 1973). Given infants' ability to recognize picture content described above, Bovet and Vauclair (2000) have hypothesized that this capacity is innate in humans but diminishes if an individual matures without exposure to pictures.

Which cognitive approach primates use to recognize pictured objects is unclear. Evidence suggests that at least some primate species can perceive pictures as representations and can transfer learned associations between real objects to pictured objects. Zimmerman and Hoch (1970) reported that rhesus monkeys (*Macaca mulatta*) transferred learned discriminations from objects to both photographs and line drawings of the objects. Likewise, Savage-Rumbaugh et al. (1980) found that when two encultured chimpanzees (*Pan troglodytes*) were trained to categorize edible food items vs. inedible tool items with lexigram labels, they transferred this training to photographs of food and tools. Moreover, Itakura (1994) found that a single chimpanzee with extensive experience in the use of visual symbols that was trained to identify conspecifics, humans, and an orangutan with an alphabetical letter, was able to correctly label computer displayed line drawings of the same individuals. It has been suggested that these findings indicate that rhesus monkeys and chimpanzees understand photographs or line drawings as representational of the objects they depicted. However, it is also possible that the primates in these studies simply generalized the photographic images to the appropriate line drawings based on their similarity. In a similar study Davenport and Rogers (1971) successfully trained one orangutan and two chimpanzees to cross-modally match a photograph to a haptic object. Subjects were required to select one of two three-dimensional objects that they could feel but not see, to a matched photograph of the object. All of the apes in this experiment performed above chance, and as successfully as they had in a previous experiment in which they were required to match two real objects in the same manner (Davenport & Rogers, 1971). Because subjects proved

capable of perceiving a photograph of an object as accurately as the object itself and could match-to-sample across sensory modalities, the authors concluded that (a) a cross-modal representational process exists in both orangutans and chimpanzees, and (b) these species are capable of immediately recognizing photographs of objects. However, Winner and Ettliger (1979) argue that because Davenport and Rogers (1971) did not systematically pair objects by size, a size strategy could have been used to solve the cross-modal matching task by selecting the largest object. Indeed, when Winner and Ettliger (1979) controlled for size, they failed to replicate Davenport and Rogers' (1971) findings. Chimpanzee subjects were unable to match an object to its photographic representation, even after several days of experience. Moreover, although subjects proved capable of discriminating between pairs of objects that were felt but not seen, performance fell to chance level when photographs were introduced. Based on these results, Winner and Ettliger (1979) concluded that the chimpanzees interpreted photographs as meaningless two-dimensional objects rather than a visual representation of a real object.

Several other investigations of primates' perception of pictures also suggest that they do not process pictures as representations. Sackett (1966) observed that macaques raised in isolation reacted to pictures in a way that would be appropriate when presented with the object pictured, but would be inappropriate when presented with a picture of the object. The macaques displayed 'disturbance' behaviours in response to 'threat' pictures of monkeys, suggesting that these animals confused the real objects with their representations. Parron, et al. (2008) reported similar results when they trained baboons (*Papio anubis*) and gorillas (*Gorilla, gorilla*) in a two alternative forced choice task between (a) a picture of a banana vs. a real banana, (b) a picture of a banana vs. a real pebble, and (c) a picture of a banana vs. a picture of a pebble. Although both species displayed a preference for the picture of food, they also responded by attempting to

remove the banana and eat it. These results suggest that the subjects confused the pictorial stimulus for the referent object, mistaking a real piece of banana for its 2D depiction.

Chimpanzees tested with the same scenario did not attempt to eat the picture of the banana and did not exhibit a preference for either the picture of the pebble or the picture of the banana, suggesting that the chimpanzees did not mistake the food for its pictorial referent. However, these results do not necessarily indicate that chimpanzee subjects understood the pictures as referential stimuli either (Parron et al., 2008). When Herrmann et al. (2006) tested if several great ape species could locate hidden food using only pictorial cues from a color photo of either the location of the food, or the food itself, they performed at chance levels, indicating that these subjects could not use pictures as referents in the task.

Given the role learning plays in human picture perception, limited experience with pictures could explain discrepant primate results. For example, select chimpanzee populations used in research are more likely than other chimpanzees and monkeys, to be trained or at the very least, familiar with pictorial representations of real-life objects (Parron et al., 2008). When Parron et al. (2008) tested this hypothesis, they found that young baboons tended to confuse a real object with its referent more than adult baboons by eating a picture of a banana more often than adult counterparts. However, given the highly rewarding nature of sweet fruit, if younger baboons were truly experiencing greater picture-referent confusion than adults, they should also exhibit a stronger preference for a picture of a banana over a real pebble. This result was not observed suggesting that the young baboons did not necessarily mistake the banana picture for a banana itself.

In many primate studies that employ pictures, subjects are trained on a task before testing through reinforced exposure to the stimuli. For example, for Hopper, et al.'s (2018) investigation

of the efficacy of using touchscreen interfaces to assess primate pairwise food preferences, subjects were provided 50 training trials for each of six food pairings. Training of this type is intended to allow subjects to learn the association between selection of an item's picture and receiving that item. However, it also circumvents investigation of primates' basic capacity to autonomously recognize and interpret pictures, a capacity that has important practical, theoretical, and evolutionary implications in the understanding of how primates perceive pictorial representations (Bovet & Vauclair, 2000). An alternative to this approach is to test subjects' ability to recognize the content of novel pictures without training. Investigations of this type have suggested that monkeys' likely recognize picture content evidenced by the fact that they spontaneously (i.e., at first sight) display adaptive behavioural responses to pictures of predators and prey, conspecifics (Pokorny & de Waal, 2009; Rosenfeld & Van Hoesen, 1979), and other primate species pictures (Kyes et al., 1992; Kyes & Candland, 1987). However, Morton et al. (2016) have failed to replicate these findings in monkeys, even with subjects with previous photo experience (Morton et al., 2016). Equivalent investigations of great ape species are comparatively sparse. In one of the few investigation of great apes' response to novel photographs, Parron et al. (2008) tested pictorially naïve chimpanzees and gorillas in a two alternative forced choice task between a pebble, a slice of banana, and pictures of each. Gorillas exhibited preference for the banana pictures, suggesting that they recognized the objects pictured. However, the chimpanzees expressed no preference for either picture, suggesting that the pictures of the banana and pebble were equally attractive to them. Given the well-known reinforcing strength of sweet fruit for primates, it is very likely that the chimpanzees preferred to receive a slice of banana over a pebble. Thus, these chimpanzees' lack of preference for the banana picture may indicate that they were not able to recognize what the pictures denoted.

In order to determine if primates recognize pictures as referential stimuli, we must first establish if they can recognize picture content at all. One of the main conclusions of Bovet and Vauclair's (2000) review of investigations of primates' capacity to interpret pictures, is that pictures of visual stimuli are not necessarily instantly recognized by nonhuman or human subjects. These capacities therefore, cannot be assumed in any primate species, even those that have similar visual psychophysics to humans (Fagot & Parron, 2010). Pictures are bi-dimensional abstract objects, and for that reason, do not provide the same number or quantity of visual cues as real objects. A picture of an object can differ from the referent object according to size, color, contrast, and stereoscopic and motion parallax depth cues. Depending on which of these cues an animal uses for object identification, these differences can make recognition of the pictured stimuli challenging. Some species may attend to object defining cues, while others may be distracted by other extraneous cues that indicate that the picture is not three-dimensional (Fagot & Parron, 2010).

Thus, given disparate results in relation to how primates interpret pictures, a scarcity of investigation of great apes' capacity to recognize pictures, as well as preliminary indications that chimpanzees do not recognize pictured objects (Parron et al., 2008), the present series of experiments investigated the ability of orangutans to spontaneously identify novel pictorial content. A criterion for assessing if subjects can establish a correspondence between objects and their pictorial representations suggested by Wilkie et al. (2016) is whether knowledge gained with the real object affects subjects' reactions to the picture of that object (or vice versa). Using this criterion, we assessed if knowledge of how specific foods taste would affect subjects' reaction to pictures of the same foods. After using an alternative forced choice task to establish 3-item food preference hierarchies common across all subjects, we tested whether subjects

demonstrated the same hierarchical food preferences for pictures of the food hierarchy items on digital displays (Experiments 1 and 3) and in printed photographs (Experiments 2 and 3). Experimental conditions varied based on how food was pictured, and the mode of presentation. Stimuli included images of food slices and whole foods pictured both with, and without backgrounds. These stimuli were presented on several types of digital displays and in prints of various sizes.

Method

Subjects

Five captive-born Sumatran orangutans (*Pongo abelii*), housed at the Toronto Zoo participated, including three females (Sekali 26 years old, Ramai 33 years old, and Jingga, 12 years old) and two males (Budi 12 years old, and Kembali 12 years old). All subjects had previously participated in studies employing picture stimuli of various types (i.e., images of food, objects, and animals), and of various colors and sizes, that were presented on both computer displays and in print. However, none had participated in investigations of spontaneous recognition of novel picture content, nor had they been exposed to the images used as stimuli in this study. Experiments were part of an enrichment programme for animals that were off-exhibit, and participation was voluntary. A subject indicated intention to participate by approaching the testing apparatus. Animals were not food or water deprived during testing.

Real Food: Establishing Food Hierarchies

Apparatus and Stimuli. Food preference hierarchies were established using a wooden tray approximately 76.2 cm in length, with two platforms 13cm apart, angled at 80 degrees, with a hinged cover. A round cookie cutter was used to cut food rewards into a uniform size and shape.

Design. Two 3-item food hierarchies common across all subjects were established using an alternative forced choice task in which each orangutan chose one of two equally-sized food slices presented simultaneously on the wooden tray. A hinged cover blocked the subjects' view of the platforms as they were baited. Initial selection of food types were based on subjects' food preferences as observed and reported by orangutan zoo keepers. Pairs of foods (e.g., carrot-celery, celery-banana, and banana-carrot) and the order in which food pairs were presented were randomized and counterbalanced to avoid order effects. The side of the display that each type of fruit was presented on was also randomized and counterbalanced to control for side preference confounds. Because we were interested in subjects' spontaneous food preferences, each subject was presented with each fruit pair x side combination only twice per session, resulting in a total of 12 trials per session. Subjects selected one of two foods presented per trial by touching the food with a wooden dowel 40.5 cm in length and 2.5 cm in diameter. Subjects were rewarded with a slice of the food-type selected. Four three-item food hierarchies were tested, but only two were selected for inclusion in the study. The food preference hierarchies selected for inclusion were ones in which all subjects selected these foods in the same ranked order in 100% of trials.

Results. Hierarchy 1 included banana > carrot > celery. Hierarchy 2 included tofu > beet > zucchini.

Experiment 1: Digital

Apparatus and Stimuli. Stimuli were presented using three types of digital displays: (a) a PC computer attached to a 46.99 cm colour PC monitor (Acer, 2010) mounted in a mobile wooden housing, (b) a 4th generation Apple iPad with 24.64 cm display, and (c) two Apple iPhone 8+ with 11.94 cm displays. Stimuli consisted of photographs of the food items used in food hierarchy trials (see Figure 2.1 and 2.2). These photos were taken in the same location in

which real food had been presented, at the same time of day, using the same camera to control for light, color, and contrast levels. Photographs were a minimum of ~ 3cm x 3cm, making them large enough to be easily seen by orangutans (Adams et al., 2017). Subjects' selected a food picture by touching the image using the same wooden dowel used during real food hierarchy trials.

In Experiment 1, images from Hierarchy 1 were digitally presented as stimuli (i.e., banana, carrot, and celery). Images included (a) equally sized pictures of *slices* of food hierarchy items, and (b) equally sized pictures of the same *whole* food items (e.g., a whole banana, a whole carrot, and a whole stalk of celery). The type of food pictures (i.e., food slices vs. whole food), the background of the food pictures, and the type, and number of digital displays food images were presented on, varied per condition (see Table 2.1 for summary of condition features; see Figure 2.3 for visual example of conditions):

- *Condition 1-A*: Two food slices pictured on a black background, presented on a desktop computer monitor.
- *Condition 1-B*: Two whole foods pictured on a black background, presented on a desktop computer monitor.
- *Condition 1-C*: Two food slices pictured on a black background, presented on an iPad resting on the wooden tray used for real food preference trials.
- *Condition 1-D*: Two food slices pictured on a black background presented on two iPhones (i.e., one food slice picture per iPhone) resting on the wooden tray used for real food preference trials.
- *Condition 1-E*: Two food slices pictured on the wooden tray used for real food preference trials, presented on a desktop computer monitor.

A number of presentation formats and modes were tested to explore several hypotheses: (a) In four of five conditions, pictures of the same food slices used in real food testing were used as stimuli to make the picture conditions as similar to the real food scenario as possible. However, in Condition 1-B whole food images were employed to explore if providing more visual cues about the type of food pictured would affect picture recognition; (b) In four of five conditions, food images were pictured against a black background to focus subjects' attention on food images and to limit potential confounds of variable backgrounds. However, in Condition 1-E, the wooden tray that had been used to present real food was pictured as a background to examine if providing a familiar context for food selection would affect picture recognition; (c) In three of five conditions, food images were presented on a single desktop monitor. However, in Condition 1-C images were presented on an iPad resting on the wooden tray used to present real food to examine if providing a familiar context for food selection would affect picture recognition. Additionally, in Condition 1-D, food images were presented on two iPhone displays to explore if presenting a single object per display, would affect picture recognition performance.

Design. Data were collected in orangutan holding areas accessible only to zookeepers and experimenters. Subjects were physically separated from one another but had some auditory contact through adjoining enclosures and could leave the testing area at any time. Absence for more than 10 minutes was interpreted as disinterest in participation and resulted in the termination of that session. Experimental sessions consisted of 12 trials, and each subject completed 1-2 sessions per day, 3 days per week.

Orangutans' ability to spontaneously recognize digital representations of food was assessed by testing if subjects, without training, and with a limited opportunity to learn through trial and error, would make alternative forced choice task selections of digital images of Hierarchy 1 items

in the same rank order as real food. Five electronic display conditions were employed to determine if display format would affect results (see Figure 2.3). To avoid learning effects, each possible food pair and side combination was presented only twice per condition (3 fruit pairs * 2 display sides * 2 occasions, for a total of 12 presentations). Additionally, the side of the display that each food type was presented on and the order in which food pairs were presented was counterbalanced and randomized within the constraints of counterbalancing to avoid order effects and side preference confounds. The order of conditions was also counterbalanced across subjects. Similar to the real food scenario, subjects selected one of the two foods presented per trial by touching the picture of the selected food with a wooden dowel. Only a single selection per task parameter was accepted and subjects were rewarded with a single uniformly sized slice of the food-type selected. The rewards were delivered by hand over the top-center of the apparatus.

Data Analysis. Cohen's Kappa statistics were calculated to assess if, at the group level, subjects selected digital images of food types in the same rank order as real food types above chance levels. The number of times each subject made one of six possible selections (e.g., banana > carrot, banana < carrot, banana > celery, banana < celery, carrot > celery, and carrot < celery) was compared between a real food condition and five digital food image conditions. Statistical analyses were conducted using IBM SPSS Statistics version 25.0. An alpha level of 0.05 and both Landis and Koch's (1977) and Altman's (1999) guidelines for interpreting magnitude of agreement was used for all statistical analyses. Additionally, to examine results per subject, a percent-agreement between rank order selections of real food and digital food images was calculated per condition.

Results and Discussion. Cohen's Kappa tests revealed that as a group, subjects did not show consistency between rank order selections of real food, and rank order selections of digital

food images significantly above chance levels in any of the experimental conditions. These results are summarized in Table 2.2. Individual percent-agreement results indicate that subjects' scores ranged from 41.67% to 66.67%, with an average of 53.00% ($SD = 0.09\%$) (see Table 2.7). Together these results suggest that when deprived of training, or the opportunity to learn through trial and error, subjects did not make selections of digital images of food types in the same rank order as real food types. Moreover, results suggest that subjects did not recognize the content of novel digital images of food, despite the fact that the foods types pictured were ones they eat regularly.

Experiment 2: Print

Apparatus and Stimuli. Experiment 2 stimuli replicated those used in Experiment 1 as closely as possible with the exception that Hierarchy 1 images were inkjet printed with Epson ink on matte Epson photo paper rather than presented digitally. The size and number of prints varied per condition (see Table 2.3 for summary of condition features; see Figure 2.4 for visual example of conditions):

- *Condition 2-A:* Two food slices pictured on a black background in a single 44.1 cm x 27.8 cm print. Presented by the experimenter holding the print vertically in front of subject (Equivalent to Condition 1-A).
- *Condition 2-B:* Two whole foods pictured on a black background in a single 44.1 cm x 27.8 cm print. Presented by the experimenter holding the print vertically in front of subject (Equivalent to Condition 1-B).
- *Condition 2-C:* Two food slices pictured on a black background in a single 23.9 cm x 16.8 cm print. Presented on the wooden tray used for real food trials (Equivalent to Condition 1-C).

- *Condition 2-D*: Two ~3 cm x 3 cm cut-outs of printed food slices (i.e., with no background). Presented on the wooden tray used for real food trials (Equivalent to Condition 1-D).
- *Condition 2-E*: Two food slices pictured on wooden tray used for real food trials in a single 44.1 cm x 27.8 cm print. Presented by the experimenter holding the print vertically in front of subject (Equivalent to Condition 1-E).

Design. To determine if orangutans' proficiency for spontaneously recognizing pictures of food would be affected by presentation medium, we tested if subjects made alternative forced choice selections of printed images of Hierarchy 1 items in the same rank order as real food. Experiment 2 replicated Experiment 1 with the exception that food images were presented in print rather than displayed digitally. Five print conditions were tested that were intended to mimic the five digital display conditions employed in Experiment 1 as closely as possible (e.g., display size, number of displays, background, etc.) (see Figure 2.4).

Data Analysis. Data analysis was the same as Experiment 1.

Results and Discussion. Cohen's Kappa tests revealed that as a group, there was consistency between subjects' rank order selections of real food, and rank order selections of printed food images significantly above chance levels for Conditions 2-B, 2-D, and 2-E, but not for conditions 2-A or 2-C. The magnitude of agreement score for Condition 2-D was fair (Altman, 1999; Landis & Koch, 1977) and the magnitude of agreement score for Conditions 2-B and 2-E was poor (Altman, 1999) or slight (Landis & Koch, 1977) (see Table 2.4). These results suggest that when deprived of training, and with very limited opportunity to learn through trial and error, subjects were able to recognize the content of printed images of food in some formats, but not in others.

On an individual level, subjects' percent-agreement scores ranged from 33.33% to 100.00% with an average of 63.67% ($SD = 0.22\%$) (see Table 2.7). Notably, Budi performed better than the other subjects in all conditions (2-A: 83.33%; 2-B: 91.67%; 2-C: 91.67%; 2-D: 100.00% and 2-E: 91.67%). Although Jingga (83.33%) and Ramai (100.00%), performed exceptionally well in condition 2-B and 2-D respectively, they did not do so in other conditions.

In comparison to digital images tested in Experiment 1, subjects' performance improved with printed images tested in Experiment 2. However, given that images of the same foods were tested in Experiment 1 and 2, learned associations between food images and food rewards could have been responsible for improved scores in Experiment 2. For this reason, the results from Experiment 1 and 2 cannot be directly compared. To provide a direct comparison of performance in digital and printed mediums, Experiment 3 re-tested four conditions that subjects performed best in in Experiment 1 (conditions 2-A, 2-B, 2-C, and 2-D), and three conditions that subjects performed best in in Experiment 2 (conditions 2-B, 2-D, and 2-E) with novel food images. If learning affected the results of Experiment 2, we would expect to see lower accuracy scores in Experiment 3 than in Experiment 2 across matched conditions. If learning was not a factor, the orangutans tested appear more proficient at recognizing image content in print displays than in digital ones.

Experiment 3: Digital and print

Apparatus and Stimuli. Stimuli were identical to respective conditions in Experiment 1 and Experiment 2, with the exception that food from Hierarchy 2, rather than Hierarchy 1 were pictured. Stimuli were presented on both digital display and printed on matte photo paper (see Table 2.5 for summary of condition features; see Figure 2.5 for visual example of conditions):

- *Condition 3-A*: Two food slices pictured on a black background, presented on a desktop computer monitor (Identical to Condition 1-A, with food images of Hierarchy 2).
- *Condition 3-B*: Two whole foods pictured on a black background, presented on a desktop computer monitor (Identical to Condition 1-B, with food images of Hierarchy 2).
- *Condition 3-C*: Two food slices pictured on a black background, presented on an iPad resting on the wooden tray used for real food preference trials (Identical to Condition 1-C, with food images of Hierarchy 2).
- *Condition 3-D*: Two food slices pictured on a black background presented on two iPhones (i.e., one food slice picture per iPhone) resting on the wooden tray used for real food preference trials (Identical to Condition 1-D, with food images of Hierarchy 2).
- *Condition 3-E*: Two whole foods pictured on a black background in a single 44.1 cm x 27.8 cm print. Presented by the experimenter holding the print vertically in front of subject (Identical to Condition 2-B, with food images of Hierarchy 2).
- *Condition 3-F*: Two ~3 cm x 3 cm cut-outs of printed food slices (i.e., with no background). Presented on the wooden tray used for real food trials (Identical to Condition 2-D, with food images of Hierarchy 2).
- *Condition 3-G*: Two food slices pictured on the wooden tray used for real food preference trials in a single 44.1 cm x 27.8 cm print. Presented by the experimenter holding print vertically in front of subject (Identical to Condition 2-E, with food images of Hierarchy 2).

Design. Because the same food images were tested in Experiment 1 and 2, learning in Experiment 1 could have resulted in superior aptitude in Experiment 2. For this reason, the results from Experiment 1 and 2 could not be directly compared. To provide a direct comparison,

Experiment 3 re-tested four conditions that subjects performed best in in Experiment 1, and three conditions that subjects performed best in in Experiment 2 using novel food images. These seven conditions were identical to respective conditions in Experiment 1 and 2 with the exception that food from Hierarchy 2, rather than Hierarchy 1 were pictured as stimuli (see Figure 2.5).

Data Analysis. Data analysis was the same as Experiment 1 and 2.

Results and Discussion. Cohen's Kappa tests revealed that as a group, there was consistency between subjects' rank order selections of real food, and rank order selections of:

- a. digital food images significantly above chance levels for condition 3-A but not for conditions 3-B, 3-C, or 3-D.
- b. printed food images for conditions 3-E and 3-F, but not for condition 3-G.

The magnitude of agreement for Condition 3-A, 3-E and 3-F is considered slight (Landis & Kock, 1977) or poor (Altman, 1999). These results, summarized in Table 2.6, indicate that without training, and very little opportunity to learn through experience, subjects were able to recognize the content of digital and printed images of food in certain formats, but not in others. Individual percent-agreement scores ranged from 33.33% to 91.67% with an average of 62.38% ($SD = 0.16\%$) (see Table 2.7). Sekali (83.33%) performed exceptionally in Condition 3-A; Sekali (83.33%), Budi (91.67%), and Jingga (83.33%) performed exceptionally in Condition 3-E; and Sekali, Budi, and Ramai performed exceptionally in condition 3-F, each scoring 83.33%.

General Discussion

Given previous disparate results concerning how primates interpret pictures, the purpose of this series of experiments was to investigate the ability of orangutans to spontaneously recognize the content of pictorial stimuli, and to compare that capacity in digital and printed mediums. Overall results indicate that orangutans of varying ages were only able to recognize food picture

content in certain formats, and that they were slightly more proficient in print mediums than in digital ones. This was especially true for one of the youngest subjects who excelled at recognizing printed image content, suggesting that the capacity to recognize picture content may vary across individuals and does not necessarily improve with age.

A single discrepancy was found between matched conditions in Experiment 1 and 3. In Experiment 1, as a group, subjects did not show consistency between selections of real food, and selections of digital food images above chance levels in any condition. However, in Experiment 3 subjects were able to recognize digital image content in Condition 3-A in which slices of food, pictured against a black background, were presented on a desktop computer monitor. Given that Condition 3-A was identical to Condition 1-A with the exception of food types pictured, this discrepancy suggests that as subjects became more experienced with the experimental paradigm, their performance at recognizing image content improved.

A single discrepancy was also found between matched conditions in Experiment 2 and 3. The results of Experiment 2 indicated that subjects recognized printed image content in Conditions 2-B, 2-D, and 2-E but not in Conditions 2-A, or 2-C. However, the results of Condition 2-E were not replicated in the mirror Condition 3-G in which subjects did not perform above chance levels. Consequently superior scores in Condition 2-E were likely a result of learning which pictures were associated with which food types after only 60 trials during Experiment 1. The results of the other print conditions in Experiment 3, Conditions 3-E and 3-F replicated the results of matched conditions in Experiment 2, Conditions 2-B and 2-D. Given that respective conditions only differed by the type of food pictured, it appears that subjects' capacity to recognize printed images in Conditions 2-B and 2-D were not a result of learning and constituted naïve recognition of the content of food images.

It is perhaps not surprising that subjects were successful in identifying picture content in Conditions 2-D, and its mirror condition 3-F as they most closely emulated real food trials (see Figure 2.4). In real food trials, subjects chose between two slices of food resting on a wooden platform. Similar to the real-life scenario, in Conditions 2-D and 3-F food was pictured in slices, in separate prints, with no background, resting on the wooden tray. Presenting food slice images on the same wooden tray used for real food selection may have acted as a memory cue to the real food scenario, improving performance. However, subjects did not recognize food slice images in Condition 3-G, in which food was pictured resting on the wooden tray in a single print, or in Condition 2-C when a print of food slices pictured against a black background was presented resting on the wooden tray. Likewise, subjects did not recognize food images in Condition 1-D when they were presented individually on iPhones resting on the wooden tray. This suggests that presenting food images on the same apparatus used for real food trials was not the only contributing factor.

Given that in both Conditions 2-D and 3-F each food image was presented on a separate print, success in recognizing the picture content in these conditions may also indicate that orangutans are better at discerning food image content when each food item is displayed separately or that subjects have difficulty interpreting a single display as including two distinct items. However, as stated above, when a single food image per display was presented digitally on iPhones, subjects did not recognize image content. As stated earlier, the fact that the prints in Condition 2-D and 3-F were cut-outs that did not include a background may have contributed to picture recognition. Alternatively, the print vs. digital presentation medium could have factored in as well. It may be the case that subjects found it easier to identify printed images of food items than digital ones. However this possibility will require further investigation.

Subjects were also able to recognize whole food pictures in Condition 2-B and in its mirror condition 3-E. In these conditions, images of whole foods likely provided subjects more visual cues about image content than images of food slices provided. It is interesting to note however, that subjects did not recognize whole foods when pictured on digital displays in Conditions 1-B and 3-B.

Importantly, as mentioned earlier, subjects were able to recognizing digital food images in the Condition 3-A, in which food slice images, pictured against a black background, were presented on a single desktop computer monitor. This result demonstrates that subjects were able to spontaneously recognize the content of food images in at least one digital format, and indicates that subjects did not necessarily require a single display per food item, a picture of the whole food, or the wooden platform used for real food presentation, to recognize the content of food images.

On an individual level, variance in percent-agreement results points to individual differences in subjects' capacity to spontaneously recognize image content in particular formats. For example, with the exception of Condition 3-G, Budi proved more proficient at recognizing image content in print displays than in digital ones despite the fact that print and digital conditions were formatted to mirror one another. Budi also proved more proficient at recognizing printed image content than the other orangutans tested. Although Ramai, Jingga and Sekali individually performed better in some conditions than others, this proficiency was not consistent per medium or per study. Given that Budi was one of the youngest subjects tested, this finding also indicates that picture content recognition did not necessarily improve with age.

As is the case in many studies of great apes, given the small sample size in these experiments, replication studies will be required to determine if findings are generalizable to other orangutans and other species of great ape. Moreover, the lack of competency in recognizing image

content of the orangutans tested here certainly warrants further investigation, particularly in digital mediums. Given evidence from human studies suggests that experience is important in learning to interpret pictures, and that subjects were more experienced with digital images than printed ones, it is surprising that subjects were more successful at recognizing printed image content than digital image content. Even more surprising was how poorly these orangutans performed in recognizing food pictures in any format. Although at the group level, subjects selected digital images of food types in the same rank order as real food types above chance levels in three formats, according to Landis and Koch's (1977) and Altman's (1999) guidelines, they achieved at most, a "fair" magnitude of agreement in condition 2-D and only a "poor" or "slight" magnitude of agreement in conditions 2-B, 2-E, 3-A, 3-E and 3-F. Moreover, examination of the percent-agreement scores for these conditions, suggests that most subjects did not recognize image content. For example, in Condition 2-E, three of five subjects scored below 50%. Thus for this condition, the scores of a minority of subjects were responsible for the statistically significant statistic. The same appears to be true to a lesser degree for conditions 2-B and 3-A.

With respect to the only previous investigation of spontaneous picture content recognition in primates, Parron et al. (2008) found that pictorially naïve baboons and gorillas exhibited preference for printed pictures of a banana over a printed picture of a pebble, and chimpanzees expressed no preference for either. This suggests that the baboons and gorillas recognized the objects pictured, and that the chimpanzees did not. As a group, the orangutans tested here did not exhibit the level of proficiency of the baboons and gorillas tested by Parron et al. (2008), nor the level of apparent lack of picture recognition observed in chimpanzees in either digital or printed mediums. Rather, orangutans' performance fell somewhere in between. On an individual level, although Budi exhibited proficiency in recognizing printed picture content akin to Parron et al.

(2008)'s baboons and gorillas, the other orangutans did not, suggesting that such proficiency can vary across individuals. Our results also indicate that, for orangutans, recognition of digital picture content may have been more challenging than recognition of printed picture content.

Phylogenetic psychophysical studies indicate that catarrhine monkeys are trichromatic, with cone receptors with the same wavelength sensitivities as humans, and possess similar flicker sensitivity and visual acuities to humans (De Valois & De Valois, 1988; Jacobs & Deagan, 1999). These findings suggest that the development of primate visual systems likely plateaued in this Old World primate species and that primates who evolved thereafter physically process pictures the same way humans do (Fobes & King, 1982). For this reason, psychophysical explanations of orangutans' difficulty with digital image content are unlikely. Differences between humans and orangutans capacity to recognize pictures are more likely attributable to cognitive factors. Having similar visual systems to humans means that primates likely process a picture's low level features in a similar way. However, pictures are bi-dimensional abstract objects that do not provide all the visual cues of the objects they represent. Therefore, in order to identify a pictured object, one must overcome the perceptual differences between pictures and objects (i.e., size, colour, stereoscopic, and motion parallax cues) (Bovet & Vauclair, 2000; Fagot & Parron, 2010). Doing so appears to be a cognitive task indeed. As Fagot and Parron (2010) have explained, "even subjects with identical visual systems may process pictures differently, either because they are not similarly proficient to solve referential cognition problems, or because they have not been exposed enough to pictures to develop a referential form of process" (p. 134).

There is evidence that interest in pictures can shape and facilitate picture recognition, and that interest can be facilitated by pictures of objects derived from an animal's natural or social environment (Bovet & Vauclair, 2000; Humphrey, 1974). Data supporting this premise have

revealed that for monkeys (Bovet & Vauclair, 1998; Dasser, 2010), birds (Evans & Marler, 1991; Watanabe, 1997), and sheep (Kendrick et al., 1995) images of food, predators, and conspecifics have proven to be the most effective stimuli for 2-D picture recognition. This is especially true for images of conspecifics. Several species of animals have been found to adaptively respond to pictures of conspecifics more easily than pictures of other categories of stimuli (Bovet & Vauclair, 2000). For this reason, in future investigations of orangutans' spontaneous recognition of picture content, it will be interesting to examine if performance improves when stimuli include socially derived images rather than food. Alternatively, another factor that could affect picture content recognition not examined here is the complexity of pictures. Simple stimuli like geometric shapes or object profiles may be more easily recognized than complex photographs (Bovet & Vauclair, 2000).

Given that pictures are one of the most predominant types of stimuli employed in the study of nonhuman primate cognition these results have important implications for their use, especially those presented digitally in the study of orangutans and perhaps great apes in general. Results suggest that for studies of orangutan cognition other than picture recognition, training on pictorial tasks before testing is important to ensure that subjects associate pictorial stimuli with their referents. As the first systematic investigation of orangutans' capacity to spontaneously recognize novel picture content in print and digital mediums, the present research contributes to our understanding of how primates perceive pictures. In order to determine if primates recognize pictures as referential stimuli, more research of this type is necessary to first establish if they can recognize picture content, and if so, in what capacity.

References

- Acer LCD Monitor (Model G18HV b)*. (2010). [LCD Monitor]. Acer, Inc.
- Adams, L. C., Wilkinson, F., & MacDonald, S. E. (2017). Limits of spatial vision in sumatran orangutans (*Pongo abelii*). *Animal Behavior and Cognition*, 4(3), 204–222.
<https://doi.org/10.26451/abc.04.03.02.2017>
- Altman, D. G. (1999). *Practical statistics for medical research*. Chapman & Hall/CRC Press.
- Barrera, M. E., & Maurer, D. (1981). Recognition of mother's photographed face by the three-month-old infant. *Child Development*, 52(2), 714–716. <https://doi.org/10.2307/1129196>
- Bovet, D., & Vauclair, J. (2000). Picture recognition in animals and humans. *Behavioural Brain Research*, 109(2), 143–165. [https://doi.org/10.1016/S0166-4328\(00\)00146-7](https://doi.org/10.1016/S0166-4328(00)00146-7)
- Bovet, D., & Vauclair, J. (1998). Functional categorization of objects and of their pictures in baboons (*Papio anubis*). *Learning and Motivation*, 29(3), 309–322.
<https://doi.org/10.1006/lmot.1998.1009>
- Dasser, V. (2010). Slides of group members as representations of the real animals (*Macaca fascicularis*). *Ethology*, 76(1), 65–73. <https://doi.org/10.1111/j.1439-0310.1987.tb00672.x>
- Davenport, R. K., & Rogers, C. M. (1971). Perception of photographs by apes. *Behaviour*, 39(2/4), 318–320.
- DeLoache, J. S. (2004). Becoming symbol-minded. *Trends in Cognitive Sciences*, 8(2), 66–70.
<https://doi.org/10.1016/j.tics.2003.12.004>
- DeLoache, J. S., Pierroutsakos, S. L., Uttal, D. H., Rosengren, K. S., & Gottlieb, A. (1998). Grasping the nature of pictures. *Psychological Science*, 9(3), 205–210.
<https://doi.org/10.1111/1467-9280.00039>

- De Valois, R., & De Valois, K. (1988). *Spatial Vision*. New York: Oxford University Press.
- Evans, C. S., & Marler, P. (1991). On the use of video images as social stimuli in birds: Audience effects on alarm calling. *Animal Behaviour*, *41*(1), 17–26.
[https://doi.org/10.1016/S0003-3472\(05\)80499-3](https://doi.org/10.1016/S0003-3472(05)80499-3)
- Fagot, J., Martin-Malivel, J., & Dépy, D. (1999). What is the evidence for an equivalence between objects and pictures in birds and nonhuman primates. *Annals of the New York Academy of Sciences: Cognitive/Current Psychology of Cognition*, *18*(5–6), 923–949.
- Fagot, J., & Parron, C. (2010). Picture perception in birds: Perspective from primatologists. *Comparative Cognition & Behavior*, *5*, 132–135.
<https://doi.org/doi:10.3819/ccbr.2010.50007>
- Fobes, J. L., & King, J. E. (1982). Vision: The dominant primate modality. In J. L. Fobes & J. E. King (Eds), *Primate Behavior* (pp. 219-243). New York: Academic Press.
- Herrmann, E., Melis, A. P., & Tomasello, M. (2006). Apes' use of iconic cues in the object-choice task. *Animal Cognition*, *9*(2), 118–130. <https://doi.org/10.1007/s10071-005-0013-4>
- Herrnstein, R. J., & Loveland, D. H. (1964). Complex visual concept in the pigeon. *Science*, *146*(3643), 549–551. <https://doi.org/10.1126/science.146.3643.549>
- Hopper, L. M., Egelkamp, C. L., Fidino, M., & Ross, S. R. (2018). An assessment of touchscreens for testing primate food preferences and valuations. *Behavior Research Methods*. <https://doi.org/10.3758/s13428-018-1065-0>
- Humphrey, N. K. (1974). Species and individuals in the perceptual world of monkeys. *Perception*, *3*(1), 105–114. <https://doi.org/10.1068/p030105>

- Itakura, S. (1994). Recognition of line-drawing representations by a chimpanzee (*Pan troglodytes*). *The Journal of General Psychology*, *121*(3), 189–197.
<https://doi.org/10.1080/00221309.1994.9921195>
- Jacobs, G. H., & Deagan, J. F. (1999). Uniformity of colour vision in Old World monkeys. *Proceedings of the Royal Society: Biological Sciences*, *266*, 2023–2028.
<https://doi.org/10.1098/rspb.1999.0881>
- Kendrick, K. M., Atkins, K., Hinton, M. R., Broad, K. D., Fabre-Nys, C., & Keverne, B. (1995). Facial and vocal discrimination in sheep. *Animal Behaviour*, *49*(6), 1665–1676.
[https://doi.org/10.1016/0003-3472\(95\)90088-8](https://doi.org/10.1016/0003-3472(95)90088-8)
- Kyes, R. C., Mayer, K. E., & Bunnell, B. N. (1992). Perception of stimuli presented as photographic slides in cynomolgus macaques (*Macaca fascicularis*). *Primates*, *33*, 407–412.
- Kyes, R. C., & Candland, D. K. (1987). Baboon (*Papio hamadryas*) visual preferences for regions of the face. *Journal of Comparative Psychology*, *101*(4), 345–348.
<https://doi.org/10.1037/0735-7036.101.4.345>
- Landis, J. R., & Koch, G. G. (1977). The measurement of observer agreement for categorical data. *Biometrics*, *33*(1), 159–174.
- Miller, R. J. (1973). Cross-cultural research in the perception of pictorial materials. *Psychological Bulletin*, *80*(2), 135–250. <https://doi.org/10.1037/h0034739>
- Morton, F. B., Brosnan, S. F., Prétôt, L., Buchanan-Smith, H. M., O’Sullivan, E., Stocker, M., D’Mello, D., & Wilson, V. A. D. (2016). Using photographs to study animal social cognition and behaviour: Do capuchins’ responses to photos reflect reality? *Behavioural Processes*, *124*, 38–46. <https://doi.org/10.1016/j.beproc.2015.10.005>

- Parron, C., Call, J., & Fagot, J. (2008). Behavioural responses to photographs by pictorially naïve baboons (*Papio anubis*), gorillas (*Gorilla gorilla*) and chimpanzees (*Pan troglodytes*). *Behavioural Processes*, 78(3), 351–357.
<https://doi.org/10.1016/j.beproc.2008.01.019>
- Pokorny, J. J., & de Waal, F. B. M. (2009). Face recognition in capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, 123(2), 151–160.
<https://doi.org/10.1037/a0014073>
- Rosenfeld, S. A., & Van Hoesen, G. W. (1979). Face recognition in the rhesus monkey. *Neuropsychologia*, 17(5), 503–509. [https://doi.org/10.1016/0028-3932\(79\)90057-5](https://doi.org/10.1016/0028-3932(79)90057-5)
- Sackett, G. P. (1966). Monkeys reared in isolation with pictures as visual input: Evidence for an innate releasing mechanism. *Science (New York, N.Y.)*, 154(3755), 1468–1473.
- Savage-Rumbaugh, E. S., Rumbaugh, D. M., Smith, S. T., & Lawson, J. (1980). Reference: The linguistic essential. *Science (New York, N.Y.)*, 210(4472), 922–925.
- Segall, M., Campbell, D. T., & Herskovits, M. J. (1966). *the influence of culture on visual perception*. Bobbs-Merill Co.
- Watanabe, S. (1997). Visual discrimination of real objects and pictures in pigeons. *Animal Learning & Behavior*, 25(2), 185–192. <https://doi.org/10.3758/BF03199057>
- Wilkie, D. M., Willson, R. J., & MacDonald, S. E. (2016). Animal's perception and memory for places. In W. K. Honig, J. G. Fetterman, & W. K. Honig (Eds.), *Cognitive Aspects of Stimulus Control* (pp. 89–112).
<http://www.vlebooks.com/vleweb/product/openreader?id=none&isbn=9781317728511>
- Winner, E., & Ettliger, G. (1979). Do chimpanzees recognize photographs as representations of objects? *Neuropsychologia*, 17, 413–420.

Zimmerman, R. R., & Hochberg, J. (1970). Responses of infant monkeys to pictorial representations of a learned visual discrimination. *Psychonomic Science*, *18*(5), 307–308

Tables

Table 2.1

Format and Mode of Conditions in Experiment 1

<i>Condition</i>	<i>Food Type</i>	<i>Background</i>	<i>Display Quantity</i>	<i>Display Type</i>	<i>Presentation Mode</i>
1-A	Slices	Black	1	Desktop computer monitor	Desktop computer stand
1-B	Whole	Black	1	Desktop computer monitor	Desktop computer stand
1-C	Slices	Black	1	iPad	Wooden tray
1-D	Slices	Black	2	iPhone	Wooden tray
1-E	Slices	Wooden tray	1	Desktop computer monitor	Desktop computer stand

Table 2.2*Consistency Among Rank Order Selections of Food and Digital Food Images in Experiment 1*

Condition	κ	95% CI	p	Magnitude of Agreement**
1-A	0.034	-0.013 to 0.0810	0.157	Poor/Slight
1-B	0.00	N/A	NS***	None
1-C	0.034	-0.013 to 0.0810	0.157	Poor/Slight
1-D	0.034	-0.013 to 0.0810	0.157	Poor/Slight
1-E	0.00	N/A	NS***	None

* $p < 0.05$

** Landis and Koch (1977)/Altman (1999)

*** Abbreviation: NS, not significant

Table 2.3*Format and Mode of Conditions in Experiment 2*

<i>Condition</i>	<i>Food Type</i>	<i>Background</i>	<i>Print Quantity</i>	<i>Print Type</i>	<i>Presentation Mode</i>
2-A	Slices	Black	1	44.1 cm x 27.8 cm print	Experimenter
2-B	Whole	Black	1	44.1 cm x 27.8 cm print	Experimenter
2-C	Slices	Black	1	23.9 cm x 16.8 cm print	Wooden tray
2-D	Slices	N/A	2	~3 cm x 3 cm print	Wooden tray
2-E	Slices	Wooden tray	1	44.1 cm x 27.8 cm print	Experimenter

Table 2.4*Consistency Among Rank Order Selections of Food and Print Food Images in Experiment 2*

Condition	κ	95% CI	p	Magnitude of Agreement**
2-A	-0.037	-0.125 to 0.051	0.414	Poor/Slight
2-B	0.111	0.023 to 0.199	0.014*	Poor/Slight
2-C	0.077	-0.029 to 0.183	0.157	Poor/Slight
2-D	0.273	0.102 to 0.443	0.003*	Fair/Fair
2-E	0.071	0.000 to 0.142	0.046*	Poor/Slight

* $p < 0.05$

** Landis and Koch (1977)/Altman (1999)

Table 2.5*Format and Mode of Conditions in Experiment 3*

<i>Condition</i>	<i>Food Type</i>	<i>Background</i>	<i>Display Quantity</i>	<i>Display/Print Type</i>	<i>Presentation Mode</i>
3-A	Slices	Black	1	Desktop computer monitor	Desktop computer stand
3-B	Whole	Black	1	Desktop computer monitor	Desktop computer stand
3-C	Slices	Black	1	iPad	Wooden tray
3-D	Slices	Black	2	iPhone	Wooden tray
3-E	Whole	Black	1	44.1 cm x 27.8 cm print	Experimenter
3-F	Slices	N/A	1	~3 cm x 3 cm print	Wooden tray
3-G	Slices	Wooden tray	1	44.1 cm x 27.8 cm	Experimenter

Table 2.6

Consistency Among Rank Order Selections of Food and Digital or Print Food Images in Experiment 3

Condition	Presentation Medium	κ	95% CI	p	Magnitude of Agreement**
3-A	Digital	0.091	(0.013 to 0.169)	0.025*	Poor/Slight
3-B	Digital	-0.034	(-0.013 to 0.081)	0.157	Poor/Poor
3-C	Digital	-0.034	(-0.013 to 0.081)	0.157	Poor/Poor
3-D	Print	0.000	(-0.071 to 0.071)	1.000	Poor/Slight
3-E	Print	0.200	(0.978 to 0.321)	0.002*	Poor/Slight
3-F	Print	0.184	(0.055 to 0.313)	0.007*	Poor/Slight
3-G	Digital	0.077	(-0.029 to 0.183)	0.157	Poor/Slight

* $p < 0.05$

** Landis and Koch (1977)/Altman (1999)

Table 2.7

Percent-Agreement Per Orangutan Between Selections of Food and Digital or Print Images of Food in Experiments 1-3

Condition	Participant	<i>Experiment 1: Digital</i>	<i>Experiment 2: Print</i>	<i>Experiment 3: Digital and Print</i>
A	Sekali	66.67%	41.67%	83.33%
	Kembali	58.33%	33.33%	41.67%
	Budi	50.00%	83.33%	66.67%
	Jingga	50.00%	58.33%	66.67%
	Ramai	50.00%	50.00%	58.33%
B	Sekali	58.33%	50.00%	75.00%
	Kembali	41.67%	66.67%	83.33%
	Budi	50.00%	91.67%	58.33%
	Jingga	66.67%	83.33%	33.33%
	Ramai	58.33%	66.67%	50.00%
C	Sekali	66.67%	41.67%	66.67%
	Kembali	41.67%	75.00%	41.67%
	Budi	41.67%	91.67%	58.33%
	Jingga	58.33%	58.33%	66.67%
	Ramai	50.00%	66.67%	58.33%
D	Sekali	50.00%	75.00%	58.33%
	Kembali	50.00%	33.33%	33.33%
	Budi	41.67%	100.00%	41.67%
	Jingga	50.00%	50.00%	58.33%
	Ramai	66.67%	100.00%	50.00%
E	Sekali	41.67%	41.67%	83.33%
	Kembali	50.00%	66.67%	50.00%
	Budi	41.67%	91.67%	91.67%
	Jingga	58.33%	33.33%	83.33%
	Ramai	66.67%	41.67%	75.00%
F	Sekali			83.33%
	Kembali			66.67%
	Budi	N/A	N/A	83.33%
	Jingga			66.67%
	Ramai			83.33%
G	Sekali			58.33%
	Kembali			50.00%
	Budi	N/A	N/A	50.00%
	Jingga			66.67%
	Ramai			41.67%

Figures

Figure 2.1

Photographs of Food Slices from Hierarchy 1 and Hierarchy 2 Respectively



Figure 2.2

Photographs of Whole Foods from Hierarchy 1 and Hierarchy 2 Respectively

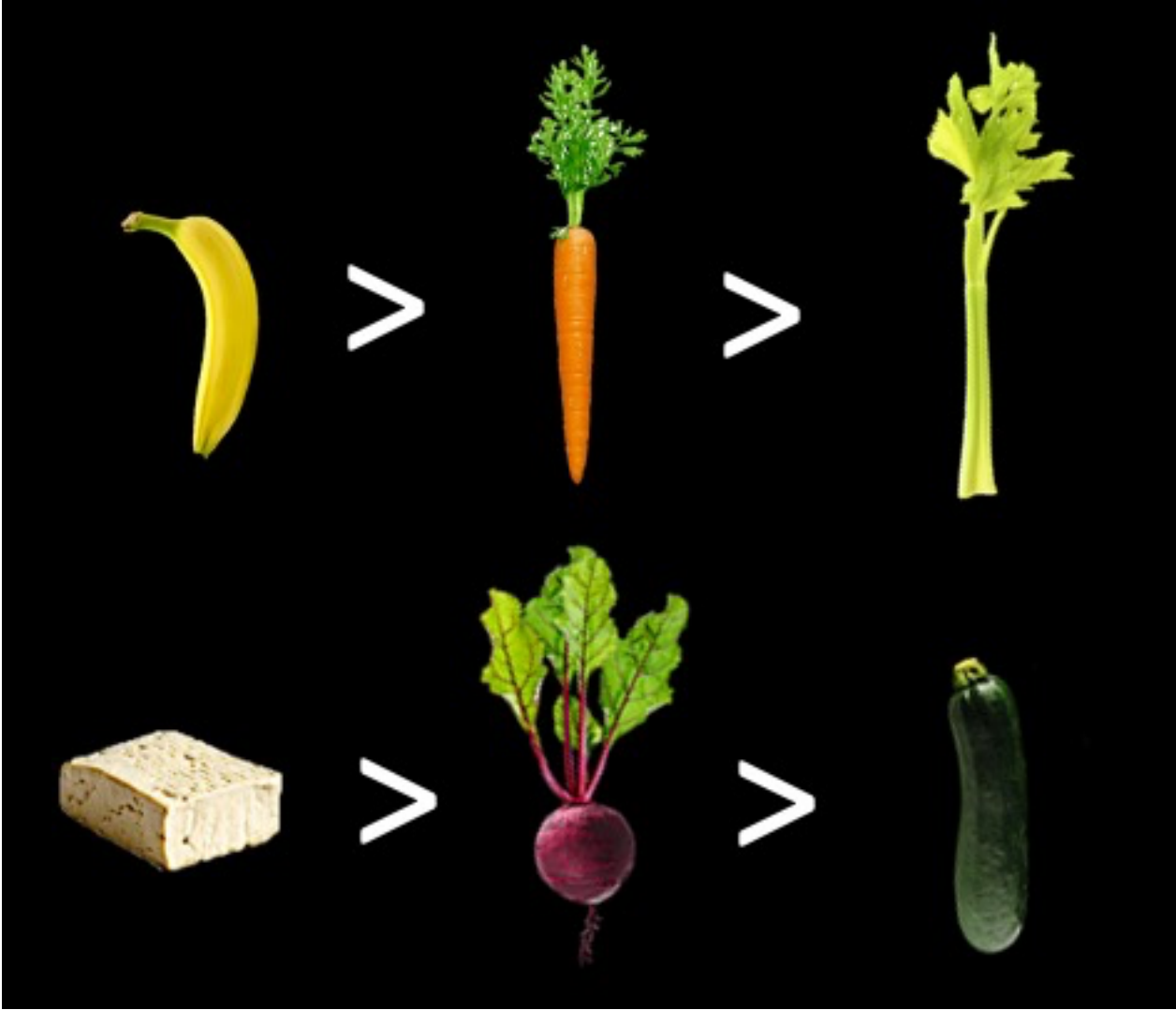


Figure 2.3

Experiment 1 Stimuli for Carrot-Celery Food Pairing in Conditions 1-A to 1-E

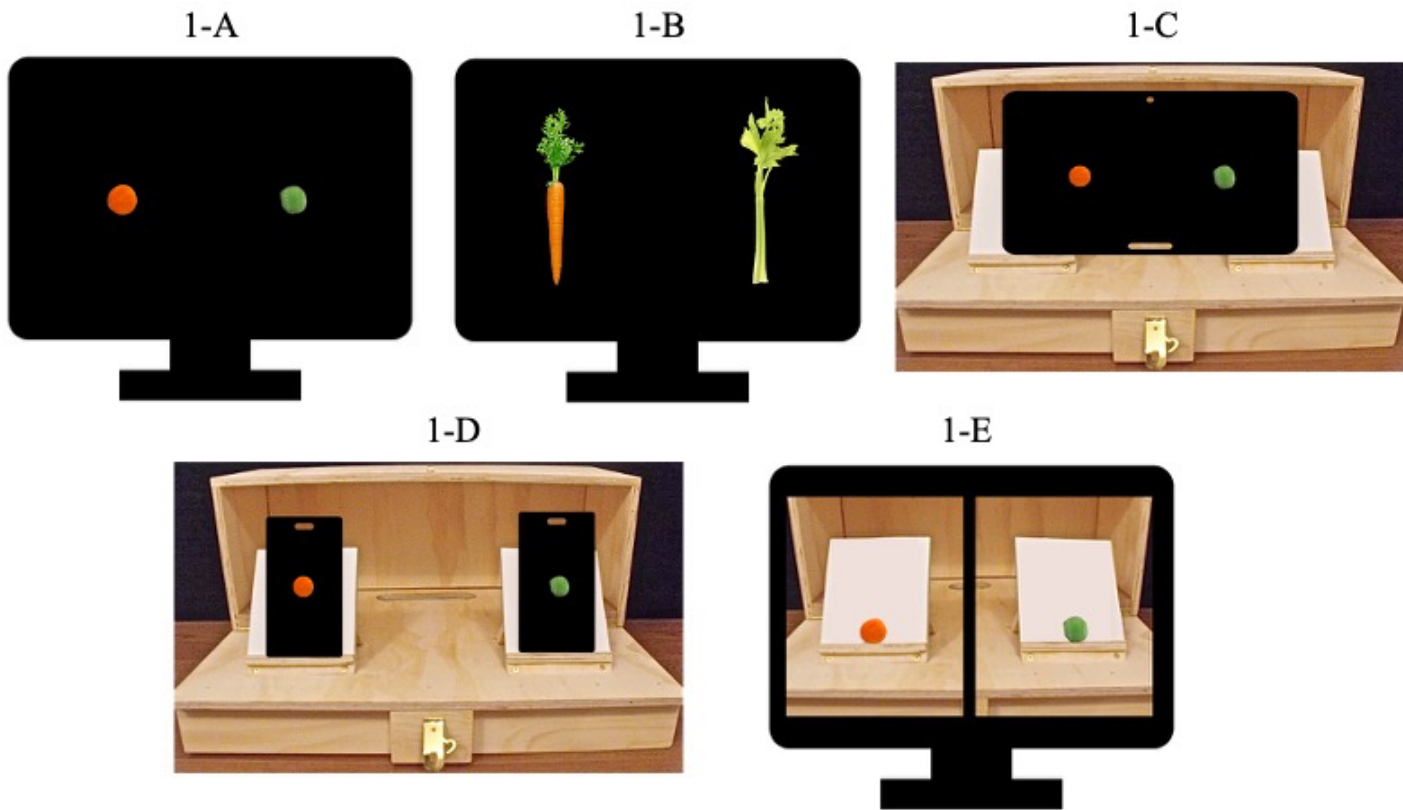


Figure 2.4

Experiment 2 Stimuli for Banana-Carrot Food Pairing in Conditions 2-A to 2-E

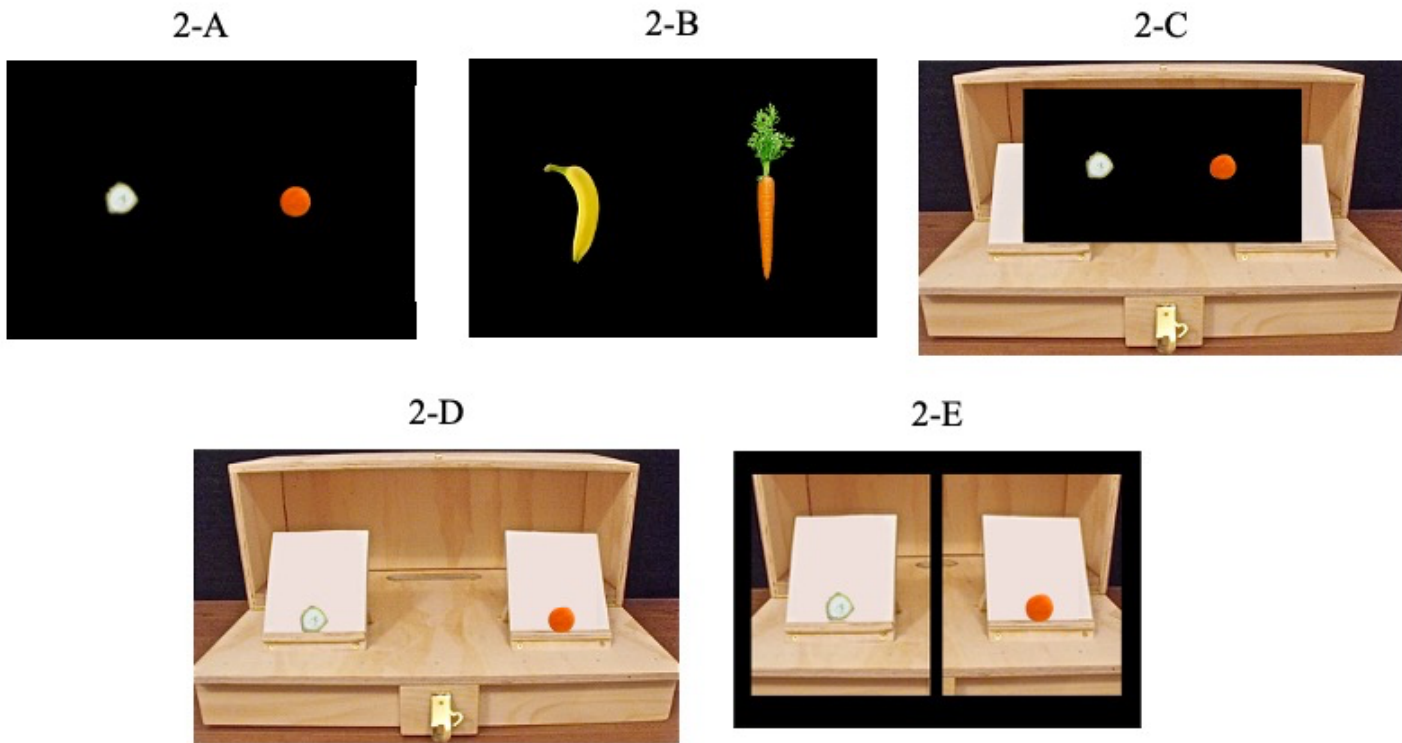
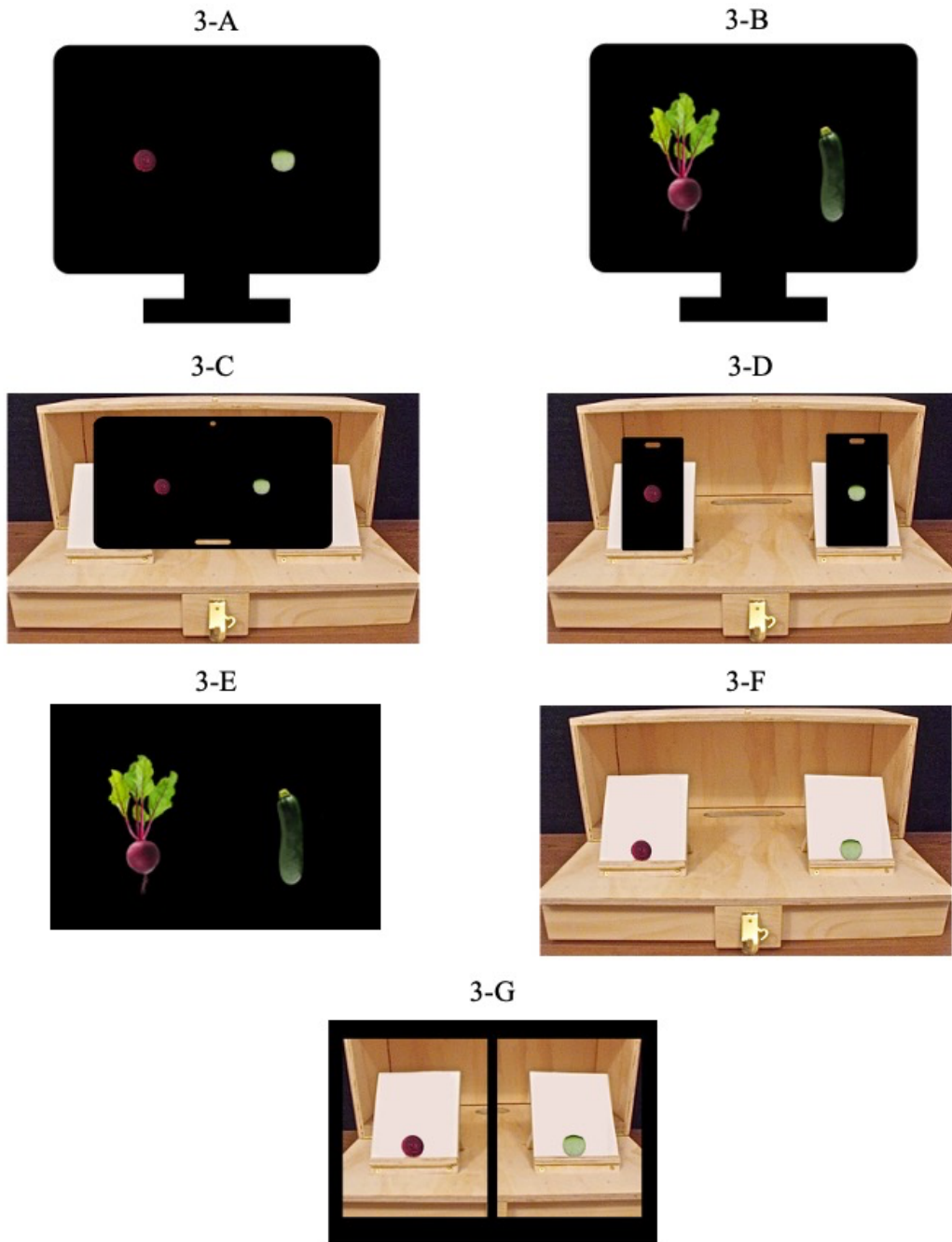


Figure 2.5

Experiment 3 Stimuli for Beet-Zucchini Food Pairing in Conditions 3-A to 3-G



CHAPTER 4: ARE ORANGUTANS' PREFERENCES FOR FREE-CHOICE STRONGER WHEN CHOICE OPTIONS OR OUTCOMES VARY?

Having confirmed in Chapter 3 that orangutans can recognize touchscreen-displayed food images in at least one format, in Chapter 4 this digital picture format was used to continue examination of orangutans' preference for computer-delivered choice. In Chapter 2 orangutans demonstrated preferences for free-choice that were weaker than expected given that long-tailed macaques (*Macaca fascicularis*) (Suzuki, 1999) and pigeons (*Columba livia domestica*) (Catania, 1975; Catania & Sagvolden, 1980) demonstrated more consistent selections in nearly identical conditions. Based on the hypothesis that a choice paradigm in which the choice options and outcomes are identical may not have provided enough variety to be interpreted as a true 'free choice' by a cognitively complex species like orangutans, the two experiments that follow explored if increasing the fidelity of the paradigm by providing more choice variety elicits stronger, more consistent choice preferences in four orangutans. This question was investigated in a stepwise manner. In Experiment 1, choice options were varied while holding the outcomes of choices constant. In Experiment 2, both the choice options and outcomes were varied.

AN ANALYSIS OF FREE-CHOICE PREFERENCE IN ORANGUTANS: DOES EXPERIMENTAL PARADIGM FIDELITY MATTER?*

The present study examined preference of Sumatran orangutans (*Pongo abelii*) for free- or forced- choice using a concurrent chain procedure presented on a touchscreen computer. Orangutans were given a choice between a free-choice alternative of three reward keys and a forced-choice alternative of a single reward key. Additionally, we explored if increasing the fidelity of the experimental choice paradigm, elicited stronger preferences. This was investigated in a stepwise manner: Experiment 1 provided a variety of choice options while holding choice outcomes constant. Experiment 2 provided a variety of both choice options *and* outcomes. Results indicated a preference for free-choice in orangutans, but one that can be overwhelmed by competing factors, and depend on the advantage afforded by it. We also found that for this species or great ape, the strength and quality of preference for free-choice can vary between individuals and can be affected by the fidelity of the choice paradigm. At least in part, free-choice preferences became stronger and more consistent as the fidelity of the choice paradigm was strengthened. We suggest that in light of these results, that preference for choice may be more accurately conceptualized along a spectrum rather than a simple dichotomy of preference for free-choice or lack thereof.

* This manuscript is currently under revision for publication in *Animal Cognition*.

Introduction

Converging evidence suggests that humans value choice and that this value is not necessarily contingent on reward outcomes or mitigated by the energy required to make choices (Bown et al., 2003; Leotti et al., 2010; Suzuki, 1997). Although learned socio-cultural values likely play an important role, there is also evidence of a biological explanation for the preference for choice (Leotti et al., 2010). Whether we are alone in this disposition is a topic of ongoing investigation; one that figures strongly in an understanding our own preoccupation with free-choice. Evidence suggests that rats, pigeons, and some species of monkeys also choose to choose even when there is no distinct benefit involved. Voss and Homzie (1970) observed that Sprague-Dawley rats (*Rattus norvegicus*) reliably selected a path that offered a choice of maze routes over a direct route to the same goal. Catania (1975) and Catania and Sagvolden (1980) found that when given the option between a free-choice of multiple reinforcement keys and a forced-choice of a single reinforcement key in a concurrent chains procedure, pigeons (*Columba livia domestica*) consistently selected the free-choice option despite matched reward outcomes. Importantly, Cerutti and Catania (1997) have demonstrated that pigeons' free-choice preferences in concurrent chains procedures are not reducible to preference for larger key areas. Although in some circumstances pigeons' preference for free-choice was found to be a joint function of key number and key area, it was also dependent on *separate* keys rather than *larger* key areas.

Three species of monkeys have exhibited similar behavior. In a concurrent chains procedure long-tailed macaques (*Macaca fascicularis*) reliably chose a free-choice option with multiple alternatives over a forced-choice option comprised of a single preferred alternative (Suzuki, 1999). Likewise, investigation of capuchin monkeys (*Cebus apella*) and rhesus macaques (*Macaca mulatta*) have revealed a preference for choosing task-order over random

assignment even when the assigned task was one they previously preferred over others (Perdue et al., 2014).

Whether the same can be said of some of our closest relatives, nonhuman great apes (hereafter, great apes), is unclear. Although several observational studies have investigated how free-choice opportunities affect well-being in great apes (Bloomsmith et al., 2000; Kurtycz et al., 2014; Lonsdorf et al., 2010), both the behavioral results and the interpretations of behavioral measures of well-being have varied. Only two studies have directly assessed great apes' preference for choice. Morimura (2003) found that when tools were made available to chimpanzees (*Pan troglodytes*) they elected to use them in addition to their mouths and hands to access tube feeders. Morimura (2003) argued that these results indicate a chimpanzee preference to use all available tool choices. In a more direct investigation of preference for choice in great apes using a paradigm in which extraneous variables were highly controlled, Ritvo and MacDonald (2020) tested Sumatran orangutans' (*Pongo abelii*) preference for free- or forced-choice. Orangutans were given a choice through a touchscreen computer program of one of two virtual routes to identical outcomes, one that provided a choice and one that did not. Although initial results indicated a preference for free-choice across all subjects, in two control conditions preferences varied, suggesting a weaker tendency to exercise choice than seen in nonhuman species previously tested.

In the experimental paradigm employed by Ritvo and MacDonald (2020), modeled on Catania and Sagvolden's (1980) six-key pigeon chamber concurrent-chain procedure, the free-choice alternative offered a choice of three identical reward keys and the forced-choice alternative offered a forced-choice of a single reward key. Selection of a reward key in either alternative was compensated with the same quantity and type of food. Apart from reward key

position, selection of the ‘free-choice’ alternative did not provide diverse choice options or outcomes. Ritvo and MacDonald hypothesized that this paradigm may not have provided enough variety to be interpreted as a ‘free-choice’ by orangutans, which could have accounted for the observed weak preferences for the free-choice alternative. The purpose of this study was to explore if increasing the fidelity (i.e., verisimilitude) of the choice paradigm by providing varied choice options or outcomes would elicit stronger preference for free- or forced- choice in orangutans. This was assessed in a stepwise manner to determine how increasing choice variety affected observed preferences. The first experiment marginally increased the free-choice paradigm fidelity by providing varied choice options while holding choice outcomes constant. The second experiment, went further by providing a variety of both choice options *and* outcomes.

Experiment 1: Varied Choices, Unvaried Outcomes

Method

Subjects. The study group consisted of 4 Sumatran orangutans (*Pongo abelli*) housed at the Toronto Zoo: Three females (Sekali 26 years old, Ramai 33 years old, and her daughter Jingga, 12 years old) and one male (Budi 12 years old). Subjects had been trained to use a dowel to operate a touchscreen computer for previous studies investigating music and visual preferences (Adams et al., 2016; Ritvo & MacDonald, 2016); as well as preference for free-choice (Ritvo & MacDonald, 2020). Research participation was voluntary and subjects were not deprived of food or water. Studies were conducted under the oversight of the York University Animal Care Committee, the Toronto Zoo Animal Care Committee, and followed the guidelines of the Canadian Council on Animal Care.

Apparatus and stimuli. Experimental sessions were administered and recorded using an HP Desktop 260-A129 PC (“HP Desktop”, 2019) and a 21” color PC computer monitor (Acer, 2010) with a Keytec Magic Touch touchscreen (Magic Touch, 2016) unit attached. Computer hardware was mounted in a mobile wooden housing positioned in front of a subject’s enclosure. Orangutans’ choice preferences were assessed with a custom touchscreen-delivered program written in Java. Subjects used a wooden dowel to make touchscreen selections and received a single food item for trials completed with a correct response. Stimuli consisted of size-matched photographs of 3 distinct banana slices and a purple sewing button (See Figure 1).

Design. Data were collected in orangutan holding areas accessible only to zookeepers and experimenters. Subjects were physically separated during test sessions but had some auditory contact through adjoining enclosures. Experimental sessions consisted of 64 trials, and each subject completed 1-2 sessions per day, 3-4 days per week. Test sessions and test trials were initiated by subjects making the first touchscreen selection. Only a single selection per task parameter was accepted and food rewards were delivered by hand over the top-center of the apparatus to avoid inadvertently motivating side biases. Subjects were not food or water deprived and could withdraw from a test session at any time. Absence from the testing area for more than 10 minutes terminated a session.

The experimental design was intended to reproduce that of Ritvo and MacDonald (2020) with select modifications. As in Ritvo and MacDonald (2020), preference for free or forced choice was assessed via a touchscreen-delivered program that offered orangutans one of two virtual routes, one that provided a free-choice and one that did not. Trials started with two white circular initial link keys displayed on the same plane, equidistant from the central axis. Selection of one initial link key led to a free-choice terminal link comprised of three reward keys and one

neutral key; while selection of the other initial link led to a forced-choice terminal link comprised of one reward key and three neutral keys. To control for side confounds, position of the odd key was randomized and counterbalanced across trials (e.g., BAAA, ABAA, AABA, or AAAB). In either terminal link, selection of a reward key resulted in an auditory bridge followed by delivery of a size-matched food reward before the next trial started. During the 3 second intertrial interval (ITI), the display was black. Selection of a neutral key resulted in initiation of the next trial after a 3 second ITI, with no bridge or food reward. To control for the effect of the position of the initial link keys, control conditions were also tested in which the position of the free-choice initial link key was changed from the left to the right of the display, or from the right to the top of the display.

In Ritvo and MacDonald (2020), reward keys were identical to one another and food type and size rewarded for a correct selection was consistent regardless of which terminal link subjects had selected. Thus, both the free-choice options (i.e., the reward keys) and outcome (i.e., the food reward) were unvaried. In the present experiment, to increase the fidelity of the choice paradigm, a variety of free-choice options were offered while keeping choice outcomes constant. To do so, in contrast to Ritvo and MacDonald (2020), the reward keys and the neutral keys consisted of circular real life objects rather than colored circles. Three reward key types were presented by three distinct slices of banana, and the neutral keys were represented by a single photograph of a purple sewing button. Thus, when subjects selected the free-choice initial link key, they were ostensibly provided a choice of one of three distinct banana slices in the free-choice terminal link. Every banana slice image was matched for size, but differed moderately in color, shape, etc., allowing subjects to select one that appealed to them. For example, if Budi preferred riper bananas he might opt for the darker colored banana. The banana slice image

displayed in the forced-choice terminal link was randomly selected from the three banana images and counterbalanced so that subjects had an equal chance of being offered any one of the three banana images in a terminal link selection. Choice outcomes still did not vary however, because regardless of the reward key chosen, subjects received an arbitrary slice of banana indiscriminately selected from a uniformly sized group. Selection of the of the neutral button key on the other hand, was considered an incorrect response and resulted in no reward (see Figure 1 for visual example of a trial).

Preliminary training. Prior to testing, subjects were trained on the experimental paradigm in a series of steps. For each step, subjects graduated to the next phase of training when they met an 80% correct criterion for 3 training sessions.

During reward key training, a single reward key and a single neutral key appeared in a row at the center of the touchscreen. When the subject touched the reward key, they received an auditory bridge and a banana slice, followed by a 3 second intertrial interval (ITI), before the next trial initiated. When the subject selected a *neutral* key (i.e., an incorrect response), the next trial initiated following the ITI without a bridge or reward.

In terminal link keys training, free-choice terminal links (i.e., three reward keys, and one neutral key) and forced choice terminal links (i.e., one reward key, and three neutral keys) were presented in a randomized and counterbalanced sequence. For each presentation, selection of reward keys were reinforced with an auditory bridge and a food reward and selection of neutral keys ended a trial with no bridge or reward.

For initial link training, a single initial link key was presented at the beginning of each trial on either the left or right side of the display. Depending on the side on which it appeared, selection initiated a free-choice terminal link or a forced- choice terminal link. As in other

training steps, in either terminal link selection of reward keys were reinforced and selection of neutral keys were not. To ensure that subject side-preferences did not confound results, three initial link key orientation conditions were trained and tested: (a) free-choice left, forced-choice right, (b) free-choice right, forced choice left, and (c) free-choice top, forced-choice bottom. In the free-top condition, the top and bottom keys were displaced 5 cm above and below the horizontal plane that initial link keys were located on in the free-left and free-right conditions. Subjects who met criterion moved onto testing in the same condition type. Once testing was complete in one condition, the subject was trained and tested in the next condition.

Testing. For testing both free- and forced- choice initial link keys appeared at the beginning of a trial. Selection of the initial link key on one side of the display initiated a free-choice terminal link and selection of the initial link key on the other side of the display initiated a forced- choice terminal link. Each experimental session consisted of 4 blocks of 16-trials (i.e., 16 combinations of free- and forced-choice terminal links key orders), for a total of 64 trials per session. Preference for free over forced choice was assessed by relative selection percentages of initial link keys. Testing was complete when a subject reached an 80% preference criterion for either the free- or forced- choice initial link key in 4 test sessions.

Results and Discussion

Free-choice left, forced choice-right (free-left 1). Relative choice percentages from sessions in which the free-choice initial link key was positioned on the left side of the display and the forced-choice initial link key was positioned on the right side of the display are provided in Figure 2. All subjects demonstrated a preference for free-choice. Budi and Jingga showed the most immediate preference for the free-choice initial link key, meeting the 80% free-choice

criterion by session 1 and 3 respectively. Although Ramai and Sekali took longer to meet criterion for free-choice preference, once they did so, they were consistent in that preference.

Free-choice right, forced-choice left condition (free-right 1). To ensure that the results of the free-left condition were not a result of a left side preference, the positions of the free- and forced- choice initial link keys were reversed. If subjects' preference for the free-choice terminal link was robust, we would expect them to stop selecting the left initial link key, which now lead to the forced-choice terminal link and to start selecting the right initial link key which now lead to the free-choice terminal link. Relative choice percentages from the free-right condition are provided in Figure 3. Although Budi, Ramai and Jingga demonstrated a continued preference for free-choice, Sekali did not.

Specifically, Budi, Ramai and Jingga met the free-choice preference criterion relatively quickly in sessions, 6, 5 and 3 respectively. Jingga exhibited the most consistent preference, remaining at, or near free-choice criterion for sessions 4-8. Although Budi dipped below criterion for free-choice in sessions 8-14 before climbing back to criterion in sessions 15-16. In the intermediate sessions he still selected the free-choice terminal link more often than forced. Likewise, after meeting criterion for forced-choice, thereafter Ramai consistently chose free-choice more often than forced with the exception of session 9.

Conversely, Sekali continued predominantly electing the left initial link key as she had in the free-left condition thereby selecting forced choice in the free-right condition. Although Sekali demonstrated some inclination for free-choice by selecting free-choice more often than forced-choice in sessions 1 and 6-9, she met criterion for forced-choice preference in sessions 2, 11, 13, and 15. This was not entirely surprising given that Ritvo and MacDonald's (Ritvo & MacDonald, 2020) investigation of free-choice preference, both Sekali and Ramai exhibited the

same behavior when the free-choice initial link key was transposed. Given that Sekali demonstrated a strong preference for free-choice in the free-left condition, we hypothesized that selection of the left initial link key may have inspired a left side preference that carried over into the free-right condition.

Free-choice top, forced-choice bottom condition (free-top 1). Sekali's selections contrasted in the free-left and free-right conditions. To determine if a left side preference that developed during the free-left condition may have confounded results in the free-right condition, Sekali was tested in a second control condition. Testing in this condition was not necessary for other subjects because they had demonstrated the same choice preferences in both the initial and control condition.

To circumvent the impact of a left-right side preference, in the free-top condition initial link keys were changed from a horizontal to a vertical orientation. Sekali's relative choice percentages from free-top sessions are provided in Figure 4. As observed in Ritvo and MacDonald (2020), once horizontal side preferences were controlled for, Sekali showed an immediate and consistent preference for free-choice. Sekali met the preference criterion for free-choice in sessions 1 and 3-5. Although she dipped below criterion in session 2, she still selected the free-choice link in 60% of those trials. These results would appear to confirm that Sekali's supposed preference for forced-choice is likely a result of a side preference she learned in the free-left condition by associating the left initial link key with the free-choice terminal link that she preferred. If this is true, it would also suggest that Sekali's preference for free-choice was overridden by a side preference, and therefore, that her preference for free-choice was not particularly robust.

Experiment 2: Varied Choices, Varied Outcomes

Sekali demonstrated some inconsistency in her preference for free- or forced- choice in Experiment 1. The same type of behavior was observed for both Sekali and Ramai in Ritvo and MacDonald's (2020) investigation of free-choice. Based on the hypothesis that the paradigm tested in Experiment 1 may still not have provided enough variety to be interpreted as a 'free-choice' by orangutans, the purpose of Experiment 2 was to determine if increasing fidelity even further by varying both the choice options and choice outcomes would elicit stronger, more consistent preference behavior, particularly for Sekali.

Method

Subjects. The same four subjects participated in Experiment 2.

Apparatus and stimuli. Apparatus and stimuli were identical to that employed in Experiment 1, with the exception that in addition to the image of the purple sewing button, stimuli consisted of photographs of a slice of tofu, a slice of carrot, and a slice of celery. As in Experiment 1, all stimuli were approximately the same size. When subjects correctly completed a trial by selecting one of the three food images, they received a slice of the food pictured as a reward. If they incorrectly completed the trial by selecting the button on the other hand, they received no reward.

Design. The study design was identical to Experiment 1 with the exception that as a means of further increasing the fidelity of the choice paradigm, subjects were offered a variety of both choice options and outcomes. In Experiment 2, choice options (i.e., reward keys) consisted of size-matched images of three distinct food types, while neutral keys continued to be represented by an image of a purple sewing button. The food types selected comprised a three-item food preference hierarchy:

(1) Tofu – the most preferred food type;

- (2) Carrot – a food type preferred more than celery, but less than tofu; and
- (3) Celery – the least preferred food type.

To facilitate diversity of choice outcomes, subjects received a slice of the type of food they selected as a reward for a correct trial response. As in Experiment 1, selection of the neutral button key was considered an incorrect response and resulted in no reward. To ensure that subjects did not select the free-choice terminal link only as a means of avoiding being forced to select a food type they disliked in the forced-choice terminal link, in addition to the three neutral button keys, the forced-choice terminal link only offered the mostly highly preferred food, tofu (see Figure 2 for visual example of a trial). In other words, when subjects selected the forced-choice terminal link, they were presented with a forced-choice of tofu, rather than a choice of tofu, carrot, or celery available in the free-choice terminal link (see Figure 5 for visual example of a trial).

Preliminary training and testing. Both preliminary training and testing procedures were identical to Experiment 1.

Results and Discussion

Free-choice left, forced choice-right (free-left 2). Relative choice percentages from sessions in which the free-choice initial link key was positioned on the left side of the display and the forced-choice initial link key was positioned on the right side of the display are provided in Figure 6. Budi, Ramai, and Sekali demonstrated a preference for free-choice. Sekali did so immediately, meeting criterion in sessions 2-5. Ramai also consistently selected free-choice more often than forced-choice in every session, and met criterion in sessions 6, 12, 14 and 15. Although Budi was slightly less consistent in his choices than Sekali and Ramai before he met criterion, he also selected free-choice in the majority of testing sessions. Once he met criterion

for free-choice in session 8 his selections became consistent, meeting criterion in sessions 9 and 11-12. Unlike the other subjects, Jingga did not demonstrate a preference for either free- or forced-choice, even after 32 sessions of testing, four times the number of the other participants. Although Jingga selected the forced-choice terminal link more often than free-choice terminal link in three quarters of the testing sessions, this was most often only to a minor degree.

Free-choice right, forced-choice left condition (free-right 2). As a control condition, the positions of the free- and forced- choice initial link keys were reversed. Relative choice percentages from the free-right condition are provided in Figure 7. All subjects demonstrated a preference for free-choice, meeting criterion by selecting the free-choice terminal link in at least 80% of trials in four test sessions. Jingga and Sekali showed the most immediate preference for the free-choice initial link key, meeting criterion in sessions 6, 13, 22 and 24; and 9-10 and 14-15 respectively. Budi and Ramai took longer to demonstrate a definitive preference for either terminal link. This was especially true of Ramai, who briefly met the preference criterion for forced-choice in session 7 and 19, and then demonstrated little preference for either terminal link from sessions 20 to 48, before meeting criterion in sessions 49, 52, 58 and 61. Budi met criterion for free-choice in sessions 27, 37, 39 and 41 and showed more consistency in his choices than Ramai, choosing free-choice 75% of the time or more in sessions 31, 36, 38 and 40.

Free-choice top, forced-choice bottom condition (free-top 2). Jingga's preferences were inconsistent from the free-left to the free-right condition. As a means of determining if Jingga would continue selecting free-choice when left-right initial link positions were controlled for, she was tested in a second control condition. In the free-top condition initial link keys were changed from a horizontal to a vertical orientation in which the free-choice initial link key was located at the top of the display and forced-choice at the bottom.

Jingga's relative choice percentages from free-top sessions are provided in Figure 8. As observed of other subjects that exhibited similar behavior in Ritvo and MacDonald (2020) and Experiment 1, once horizontal side preferences were controlled for, Jingga showed an immediate and consistent preference for free-choice. She met the preference criterion for free-choice immediately in session 1 and was consistent in that preference, meeting criterion in sessions 2-4 as well.

Post-Hoc Analysis

Both Jingga and Ramai exhibited periods of indifference in Experiment 2 that were not observed in Experiment 1 or in a previous investigation by Ritvo and MacDonald (2020). In the Free-Left 2 condition, Jingga never met the preference criterion for either free- or forced- choice in 32 test sessions. In the Free-Right 2 condition, Ramai briefly showed a preference for forced-choice in sessions 7 and 19, then failed to meet criterion for either free- or forced- choice for 29 sessions, before demonstrating a preference for free-choice in sessions 49, 52, 58 and 61. During these periods of indifference, the experimenter observed that both subjects selected tofu almost exclusively. This was true even when they had selected the free-choice terminal link which provided a choice of two other food types. This behavior differed from other subjects who selected other, lower valued foods in the free-choice terminal link in addition to tofu. The experimenter also observed that as Jingga began selecting free-choice more consistently in the Free-Right 2 and Free-Top 2 conditions, and Ramai began selecting free-choice more consistently in later Free-Right 2 condition trials, they both also began selecting carrot and celery more often. To assess if there was a negative relationship between tofu selection and preference for free-choice, post hoc one-tailed Pearson product-moment correlations were calculated per subject. The results provided in Table 1 indicate that as suspected, the frequency of tofu

selections and the frequency of free-choice selections were significantly negatively correlated. For all subjects, decreases in selection of the most highly preferred food, tofu, were strongly associated with increases in selection of free-choice.

General Discussion

In a previous investigation of orangutans' preference for free- or forced- choice, Ritvo and MacDonald (2020) found that although all subjects indicated a preference for free-choice in the first test condition (free-left), in two control conditions (free-right, and free-top) their preferences varied, suggesting a weaker preference for free-choice than in the other nonhuman species previously tested. These results differed from Catania and Sagvolden's (1980) findings in which the majority of pigeons tested with the same choice paradigm consistently shifted initial link key preference with corresponding shifts of the free-choice initial link key from one side of a display to the other. Ritvo and MacDonald (2020) speculated that their choice paradigm, modeled after Catania and Sagvolden (1980), may not have provided enough variety to be interpreted by orangutans as a 'free-choice' and that this could have accounted for observed weaker free-choice preferences. In the choice paradigm employed by both Ritvo and MacDonald (2020) and Catania and Sagvolden (1980), both the free-choice options (i.e., the reward keys) and the outcomes (i.e., the food reward) did not vary. The present study assessed if increasing the fidelity of the choice paradigm by providing more variety in choice options or outcomes would elicit stronger, more consistent free-choice preferences in orangutans. These changes were undertaken in a stepwise manner: In the first experiment, free-choice options were varied while holding choices outcomes constant. In the second experiment, both the free-choice options and outcomes were varied.

Results of Experiment 1 indicated that all subjects initially demonstrated a preference for free-choice in the first condition (free-left 1). In the second condition (free-right 1), Ramai, Budi, and Jingga maintained a preference for free-choice, but Sekali exhibited a preference for forced-choice. Consequently, Sekali was tested in a second, vertically orientated control condition (free-top 1) in which she quickly and consistently demonstrated a preference for free-choice, suggesting that a side bias that had developed through the selection of the free-choice initial link key in the first (free-left 1) condition, conflicted with her preference for free-choice in the second (free-right 1) condition (see Table 2 for summary of preference results per subject). Thus, in Experiment 1, given that Sekali selected free choice in two of three conditions, it is reasonable to conclude that she preferred free-choice but that this preference was outweighed by a learned side bias.

In Experiment 1, three quarters of subjects maintained their preference for free-choice from the first (free-left 1) condition to the second (free-right 1) condition, while a single subject displayed a preference for free-choice in both the first (free-left 1) and third (free-top 1) conditions, but not in the second (free-right 1) condition. Thus, increasing the fidelity of the choice paradigm by varying choice options while holding outcomes constant, resulted in a larger majority of subjects maintaining their preference for free-choice as the location of the free-choice initial link changed locations than in Ritvo and MacDonald (2020). On an individual level, Ramai maintained a consistent preference for free-choice across conditions in Experiment 1, which was not the case in Ritvo and MacDonald (2020).

To determine if enhancing the choice paradigm fidelity further would elicit even stronger, more consistent free-choice preferences, Experiment 2 varied both the choice options and outcomes in the free-choice alternative. With this choice paradigm, Ramai, Sekali, and Budi

maintained their preference for free-choice from the first (free-left 2) condition to the second (free-right 2) control condition. Jingga, however, exhibited a response not previously observed. While she did not demonstrate a preference for either free- or forced-choice in the first (free-left 2) condition, she preferred free-choice in the two latter control conditions (free-left 2 and free-top 2) (see Table 2 for summary of preference results per subject).

Given Jingga's unexpected behaviour in the free-right 2 condition, it is difficult to infer that varying both the choice options and outcomes in Experiment 2 resulted in stronger preferences than those observed in Experiment 1. In both experiments three-quarters of subjects exhibited consistent preferences for free-choice across conditions, and a single subject did not. Sekali exhibited more consistent preferences in Experiment 2 than in Experiment 1 by maintaining her preference for free-choice across conditions, but for Jingga the opposite was true. Jingga maintained her preference for free-choice across conditions in Experiment 1, but not in Experiment 2. Because none of the subjects in Experiment 2 demonstrated a preference for forced-choice, one could argue that in part, it resulted in stronger, more consistent free-choice preferences than in Experiment 1. However, if this is true, it is a marginal effect.

The paradigm in Experiment 2 elicited behavior not observed in either Experiment 1 or in a prior investigation by Ritvo and MacDonald (2020). In the first (free-left 2) condition, Jingga was indifferent to the free- and forced- choice terminal links. Similarly, although Ramai ultimately reached criterion for free-choice in the free-right 2 condition, before doing so she also exhibited a substantial period of responding at near chance levels for both initial link keys. Given that both Jingga and Ramai had demonstrated a preference for free-choice in the free-left 1 and free-right 1 conditions in Experiment 1, conflict arising from a side preference was not a likely explanation for this behavior. Intriguingly however, the experimenter observed that both subjects

selected the most highly preferred food, tofu, almost exclusively during ‘indifferent’ test sessions. This was true even when they had selected the free-choice terminal link which provided a choice of two additional food types (i.e., tofu, carrot, or celery). Conversely, in test sessions when Jingga and Ramai exhibited preference for free-choice, they also selected carrot and celery more often. Post hoc analyses motivated by these observations revealed that the frequency of tofu selections and the frequency of free-choice selections were significantly negatively correlated for all subjects. Decreases in selection of tofu, the most preferred food, were associated with increases in selection of free-choice. This finding suggests that subjects were more likely to select free-choice when they were exploiting the variety of options and outcomes afforded by that alternative.

This behavior pattern may explain why Ramai and Jingga exhibited periods of indifference when the other subjects did not. Both Ramai and Jingga appeared to prefer tofu more than the other subjects. This was evidenced by (a) by zookeepers’ anecdotal observations of typical feeding behaviours, and (b) periods in which both subjects exclusively selected tofu, ignoring other food types (a behavior not observed of Sekali or Budi). During periods of exclusive tofu selection Ramai and Jingga likely did not demonstrate preference for one terminal link over the other because both offered *equal access* to tofu. In other words, when they were not taking advantage of the variety of outcomes afforded by the free-choice link, they were not motivated to select that alternative. Likewise, when they started to show interest in the other food types available in the free-choice link, they also began to demonstrate a preference for that alternative. These results suggest that at least to some degree, some orangutans may only prefer “free-choice” when they are motivated to take advantage of the options afforded by it. If, on the other hand, they are exclusively interested in an outcome that is equally accessible via both the

free- and forced- choice alternatives, they may not necessarily prefer a ‘free-choice’.

Consequently, this could indicate that these individuals do not prefer free-choice in and of itself. Rather, they prefer a free-choice when the outcomes afforded by it are demonstrably beneficial to them.

These results differ from other investigations of choice that have found that humans (Bown et al., 2003; Suzuki, 1997), monkeys (Suzuki, 1999), pigeons (Catania, 1975; Catania & Sagvolden, 1980), and rats (Voss & Homzie, 1970) reliably select choice over non-choice even when outcomes are equated. The tendency of these species to select an option that requires a greater expenditure of energy when there is no tangible benefit to doing so, suggests that such behavior is rewarding in and of itself (Leotti et al., 2010). The results of Experiment 2, specifically the behavior of Jingga and Ramai, suggests that this is not necessarily the case for orangutans. Rather, Ramai’s and Jingga’s preferences for the free-choice alternative were at least partially dependent on the opportunities afforded by selecting that route. Given the small sample size in this series of investigations, and the fact that half of the subjects did not exhibit indifference in any condition, it’s difficult to determine if this behavior is specific to individuals, or generalizable to all orangutans. It would be ideal to re-test this paradigm using a food hierarchy organized on an interval scale of preference that is equally favored across subjects. However, titrating food preferences to the degree required and matching those preferences across subjects is challenging, if possible at all.

The results of Experiment 2 do however share some similarities with those of Catania and Sagvolden’s (1980) investigation of pigeons’, which used a similar paradigm. Catania and Sagvolden (1980) reported that three of four subjects, consistently changed initial link key preference as a free-choice initial link key shifted from one side of the display to the other. This

was similar behavior to Ramai, Sekali, and Budi, who changed initial link key preferences from left to right from the first to the second condition. However, Catania and Sagvolden's (1980) also reported that a single pigeon only shifted preference for the free-choice initial link key in the last two conditions tested. Likewise, Jingga only exhibited preference for the free-choice initial link key in the last two conditions tested.

Moreover, similar to Cerutti and Catania's (1997) findings, the results of Experiment 2 suggest that orangutans' preference for free choice is not reducible to larger key area or the ease of selecting a reward key in the free-choice terminal link. Orangutans' preferences for free-choice in Ritvo and MacDonald (2020) could in theory have been attributed to (a) the larger key area provided by multiple reinforcement keys in the free-choice terminal link as opposed to a single key in the forced-choice terminal link, or (b) the additional effort required to locate and select a single reward key in the forced-choice terminal link as opposed to the comparative ease of selecting any one of three reward keys in the free-choice terminal link. The latter limitation is also applicable to Experiment 1. Because the free-choice terminal link reward keys in Experiment 2 were each associated with a distinct type of food, subjects were required to select a single reward key to access desired food type. In this way, the free-choice terminal link did not provide more key surface area than the forced-choice alternative which also required selection of a single reward key. Likewise, because the free-choice terminal link provided a choice of three foods, and the forced-choice terminal link provided only a single food option, the free-choice alternative did not provide a more "effortless" selection process. Rather, the free-choice terminal link required consideration and selection of a single food type among three options, a process that requires more effort and energy than locating and selecting the only food type available in

the forced-choice terminal link. Thus, orangutans' preference for free-choice in Experiment 2 cannot be reduced to preference for larger key area or ease of selection.

As discussed in Ritvo and MacDonald (2020), it is important to note that the present findings were likely affected by subjects' prior experiences with environmental control. Environmental control, achieved through decision making, reinforces individual expectations of our ability to succeed (Leotti et al., 2010). The more experience with exercising control by making choices, the stronger one's personal beliefs in their ability to achieve desired outcomes and their motivation to do so. Conversely, lack of experiencing exercising choice can challenge these beliefs (Blackburn & Owens, 2015; Deci, 1981; Devins et al., 1982; Kwasky & Groh, 2014; Leotti et al., 2010; Maddux & Meier, 1995; Ryan & Deci, 2000; Seligman, 1972; Shnek et al., 1997). Thus, prior experiences in applying environmental control can strengthen or weaken tendencies to exercise choice. Given that this series of investigations tested captive orangutans, it's possible that living in captivity where free-choice is unavoidably limited to some extent, may have affected their tendencies to exercise free-choice.

Cumulatively, the results of these two experiments conjunction with those of Ritvo and MacDonald (2020) suggests a preference for free-choice over forced-choice in Sumatran orangutans, but one that can (a) be overwhelmed by competing factors (i.e., a learned side preference), and (b) depend on the advantage afforded by it (i.e., access to valued food types). The latter result also suggests individual differences in the strength and quality of free-choice preferences for this species. The present findings also indicate that for orangutans, observed preferences for free-choice can be affected by the fidelity of the choice paradigm. When the results of prior research by Ritvo and MacDonald (2020), and Experiment 1 and Experiment 2 are compared, at least in part, free-choice preferences became stronger and more consistent as

the fidelity of the choice paradigm was strengthened. We argue that by providing a more realistic and tangible “free-choice” alternative by varying choice options or outcomes, more subjects interpreted the free-choice terminal link as a true ‘free-choice’. It is difficult to say why this would not also be the case for pigeons (Catania & Sagvolden, 1980), or monkeys (Suzuki, 1999) that have reliably demonstrated preference for free-choice over forced-choice when tested with paradigms with no variety in choice options or outcomes. It is possible that this interspecies difference reflects a more complex understanding of what constitutes a “free-choice” among orangutans, when compared to pigeons and monkeys.

The results of present study may also have wider implications for the study of preference for choice in nonhuman animals. Previous investigations of nonhuman species’ choice preferences have typically found that the species under investigation either prefers more choice or does not. Our current results suggest that a species’ preference for choice may be more accurately conceptualized along a spectrum and that the motivation to exercise free-choice can vary across disparate experimental contexts. When we consider nonhuman animals’ preferences for choice this way, the question becomes in what contexts do subjects prefer choice, and why?

References

- Acer LCD Monitor (Model G18HV b)*. (2010). [LCD Monitor]. Acer, Inc.
- Adams, L., Wilkinson, F. E., & MacDonald, S. E. (2016). Limits of spatial vision in Sumatran orangutans (*Pongo abelli*). *Animal Behavior and Cognition*.
- Blackburn, L., & Owens, G. P. (2015). The effect of self efficacy and meaning in life on posttraumatic stress disorder and depression severity among veterans: Self-efficacy and meaning. *Journal of Clinical Psychology, 71*(3), 219–228.
<https://doi.org/10.1002/jclp.22133>
- Bloomsmith, M. A., Ross, K. C., & Baker, K. C. (2000). Control over computer-assisted enrichment for socially housed chimpanzees. *American Journal of Primatology, 51*(5), 45.
- Bown, N. J., Read, D., & Summers, B. (2003). The lure of choice. *Journal of Behavioral Decision Making, 16*(4), 297–308. <https://doi.org/10.1002/bdm.447>
- Catania, A. C. (1975). Freedom and knowledge: An experimental analysis of preference in pigeons. *Journal of the Experimental Analysis of Behavior, 24*(1), 89–106.
<https://doi.org/10.1901/jeab.1975.24-89>
- Catania, A. C., & Sagvolden, T. (1980). Preference for free choice over forced choice in pigeons. *Journal of the Experimental Analysis of Behavior, 34*(1), 77–86.
<https://doi.org/10.1901/jeab.1980.34-77>
- Cerutti, D., & Catania, A. C. (1997). Pigeons' preference for free choice: Number of keys versus key area. *Journal of the Experimental Analysis of Behavior, 68*(3), 349–356.
<https://doi.org/10.1901/jeab.1997.68-349>
- Deci, E. L. (1981). *The psychology of self-determination*. Health.

- Devins, G. M., Binik, Y. M., Gorman, P., Dattel, M., McCloskey, B., Oscar, G., & Briggs, J. (1982). Perceived self-efficacy, outcome expectancies, and negative mood states in end-stage renal disease. *Journal of Abnormal Psychology, 91*(4), 241–244.
<https://doi.org/10.1037/0021-843X.91.4.241>
- Kurtycz, L. M., Wagner, K. E., & Ross, S. R. (2014). The choice to access outdoor areas affects the behavior of great apes. *Journal of Applied Animal Welfare Science, 17*(3), 185–197.
<https://doi.org/10.1080/10888705.2014.896213>
- Kwasky, A. N., & Groh, C. J. (2014). Vitamin D, Depression and coping self-efficacy in young women: Longitudinal study. *Archives of Psychiatric Nursing, 28*(6), 362–367.
<https://doi.org/10.1016/j.apnu.2014.08.010>
- Leotti, L. A., Iyengar, S. S., & Ochsner, K. N. (2010). Born to choose: The origins and value of the need for control. *Trends in Cognitive Sciences, 14*(10), 457–463.
<https://doi.org/10.1016/j.tics.2010.08.001>
- Lonsdorf, E., Ross, S. R., Matsuzawa, T., & Goodall, J. (Eds.). (2010). *The mind of the chimpanzee: Ecological and experimental perspectives*. University of Chicago Press.
- Maddux, J. E., & Meier, L. J. (1995). Self-efficacy and depression. In J. E. Maddux (Ed.), *Self-Efficacy, Adaptation, and Adjustment* (pp. 143–169). Springer US.
https://doi.org/10.1007/978-1-4419-6868-5_5
- Magic Touch Add-On Touchscreen*. (2016). [Touchscreen]. Keytec, Inc.
<http://www.magictouch.com/addon-1.html>
- Morimura, N. (2003). A note on enrichment for spontaneous tool use by chimpanzees (*Pan troglodytes*). *Applied Animal Behaviour Science, 82*(3), 241–247.
[https://doi.org/10.1016/S0168-1591\(03\)00058-3](https://doi.org/10.1016/S0168-1591(03)00058-3)

- Perdue, B. M., Evans, T. A., Washburn, D. A., Rumbaugh, D. M., & Beran, M. J. (2014). Do monkeys choose to choose? *Learning & Behavior*, *42*(2), 164–175.
<https://doi.org/10.3758/s13420-014-0135-0>
- Ritvo, S. E., & MacDonald, S. E. (2016). Music as enrichment for Sumatran orangutans (*Pongo abelii*). *Journal of Zoo and Aquarium Research*, *3*. <https://doi.org/10.19227/jzar.v4i3.231>
- Ritvo, S. E., & MacDonald, S. E. (2020). Preference for free or forced choice in Sumatran orangutans (*Pongo abelii*). *Journal of the Experimental Analysis of Behavior*, *113*(2), 419–434. <https://doi.org/10.1002/jeab.584>
- Ryan, R. M., & Deci, E. L. (2000). Self-determination theory and the facilitation of intrinsic motivation, social development, and well-being. *American Psychologist*, *55*(1), 68–78.
<https://doi.org/10.1037/0003-066X.55.1.68>
- Seligman, M. E. P. (1972). Learned helplessness. *Annual Review of Medicine*, *23*, 407–412.
- Shnek, Z. M., Foley, F. W., LaRocca, N. G., Gordon, W. A., DeLuca, J., Schwartzman, H. G., Halper, J., Lennox, S., & Irvine, J. (1997). Helplessness, self-efficacy, cognitive distortions, and depression in multiple sclerosis and spinal cord injury. *Annals of Behavioral Medicine*, *19*(3), 287–294. <https://doi.org/10.1007/BF02892293>
- Suzuki, S. (1997). Effects of number of alternatives on choice in humans. *Behavioural Processes*, *39*(2), 205–214. [https://doi.org/10.1016/S0376-6357\(96\)00049-6](https://doi.org/10.1016/S0376-6357(96)00049-6)
- Suzuki, S. (1999). Selection of forced- and free-choice by monkeys (*Macaca Fascicularis*). *Perceptual and Motor Skills*, *88*(1), 242–250. <https://doi.org/10.2466/pms.1999.88.1.242>
- Voss, S. C., & Homzie, M. J. (1970). Choice as a value. *Psychological Reports*, *26*(3), 912–914.
<https://doi.org/10.2466/pr0.1970.26.3.912>

Tables

Table 3.1

Experiment 2: Frequency of Tofu Selections x Frequency of Free-Choice Selections Correlations Per Subject

Subject	<i>n</i>	<i>r</i>
Ramai	76	-.615*
Sekali	20	-.771*
Budi	53	-.752*
Jingga	60	-.606*

* $p < .01$ (one-tailed)

Table 3.2*Free- vs. Forced- Choice Preferences Per Subject*

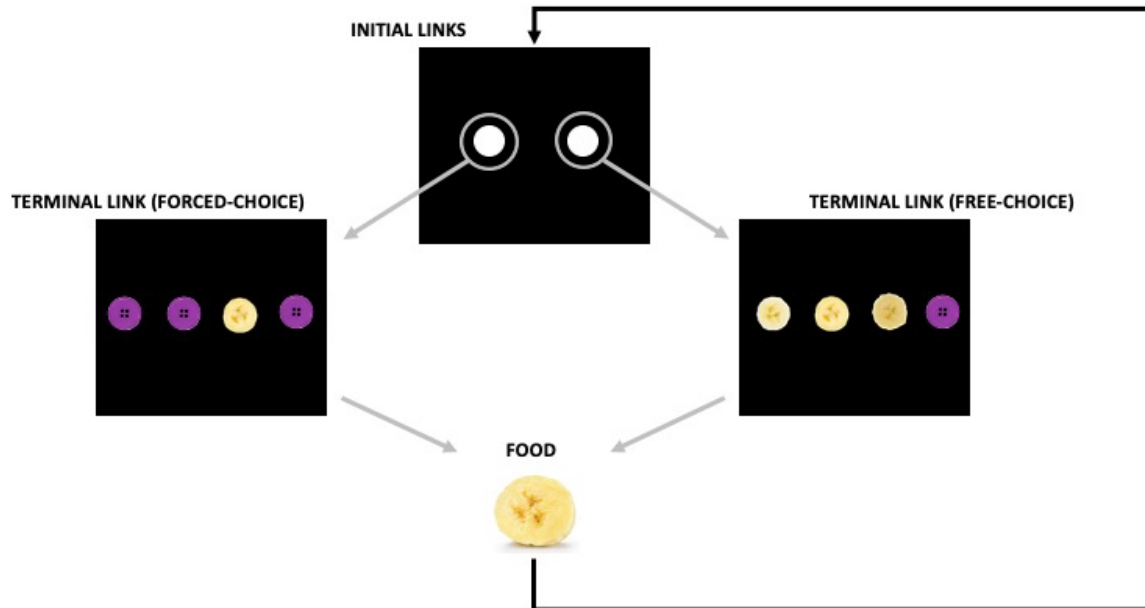
Experiment 1			
	Free-Left 1	Free-Right 1	Free-Top 1
Ramai	Free Choice	Free Choice	Not tested
Sekali	Free Choice	Forced Choice	Free Choice
Budi	Free Choice	Free Choice	Not tested
Jingga	Free Choice	Free Choice	Not tested
Experiment 2			
	Free-Left 2	Free-Right 2	Free-Top 2
Ramai	Free Choice	Free Choice	Not tested
Sekali	Free Choice	Free Choice	Not tested
Budi	Free Choice	Free Choice	Not tested
Jingga	No preference	Free Choice	Free Choice

Note: Cells are color-coded to aid in data visualization

Figures

Figure 3.1

Example of a Test trial in the Free-Right Condition of Experiment 1

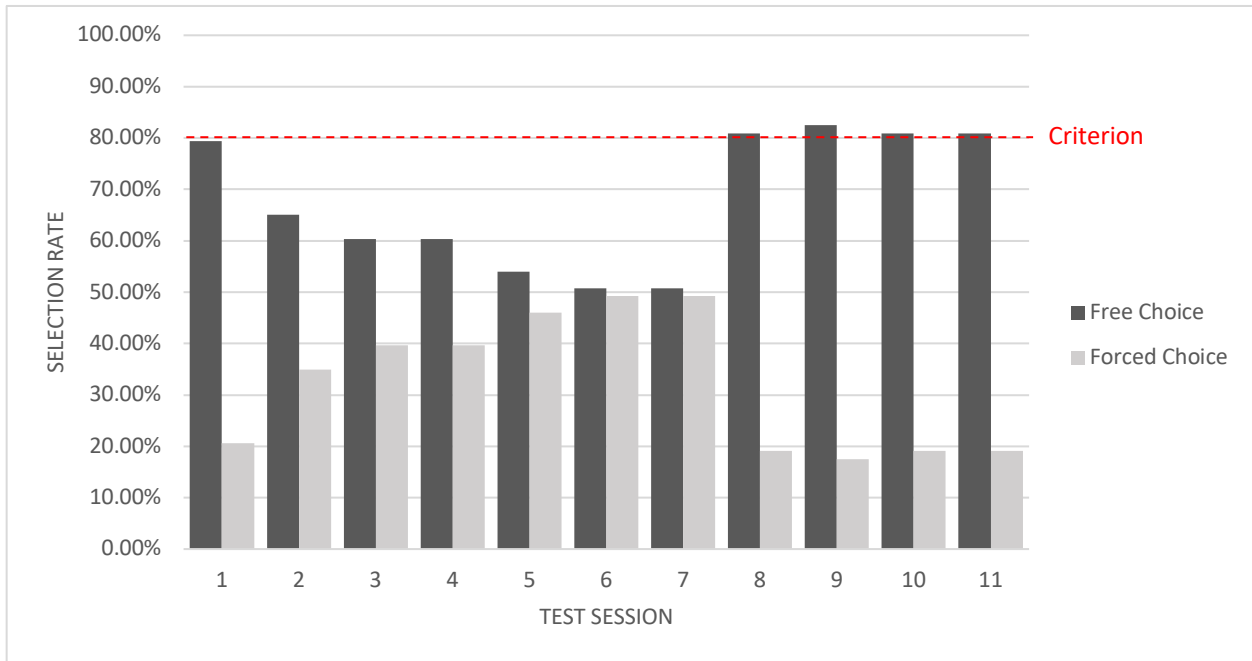


Note. In the initial links (top square), the free-choice terminal link is accessed via selection of the right white initial link key, and the forced-choice terminal link is accessed via selection of the left white initial link key. In the forced-choice terminal link (left square), subjects must select the only banana key available amongst the three button keys to receive a reward. In the free-choice terminal link (right square), subjects may select one of any of the three banana keys displayed to receive a reward. Selection of a banana key in either terminal link resulted an auditory bridge, followed by a slice of banana and initiation of a new trial. Selection of a button initiated a new trial, with no reward.

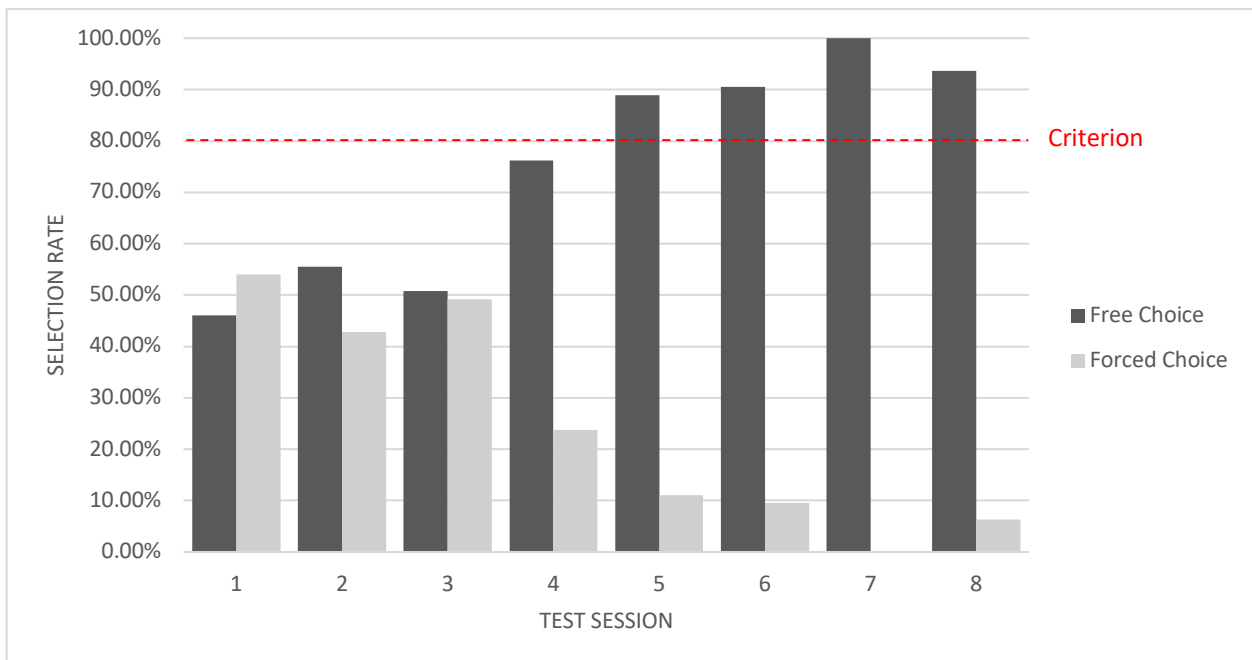
Figure 3.2a, 3.2b, 3.2c and 3.2d

Frequency of Free- and Forced- Choice Initial Link Key Selections

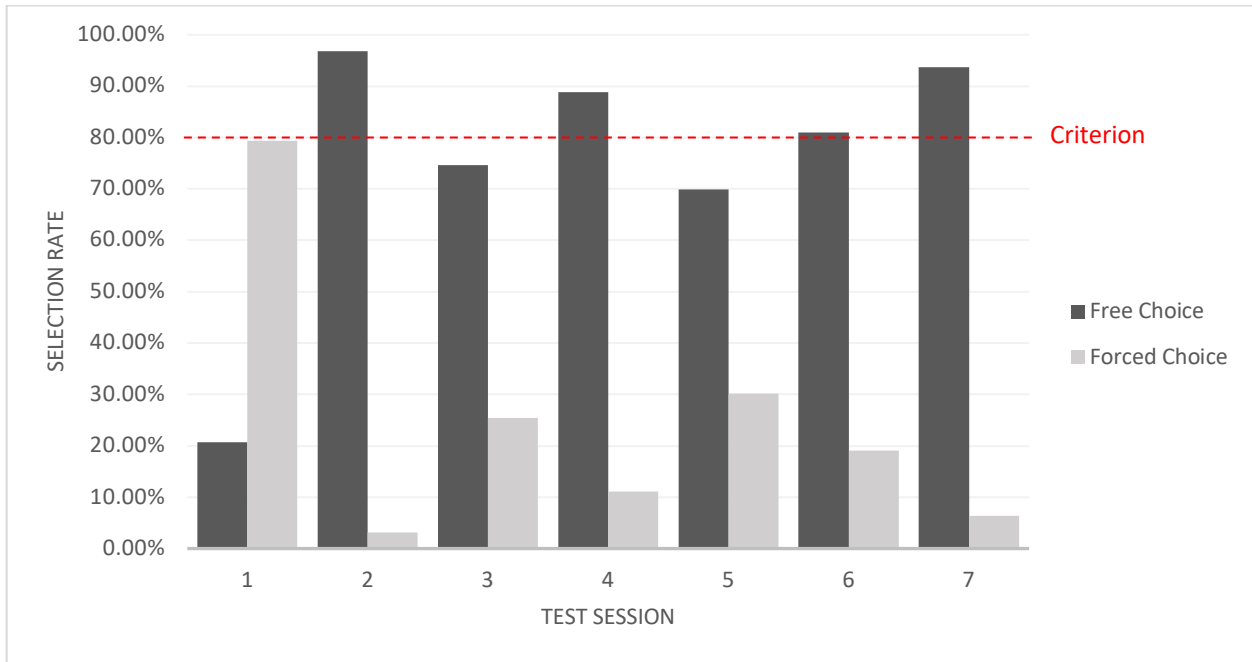
a) Ramai



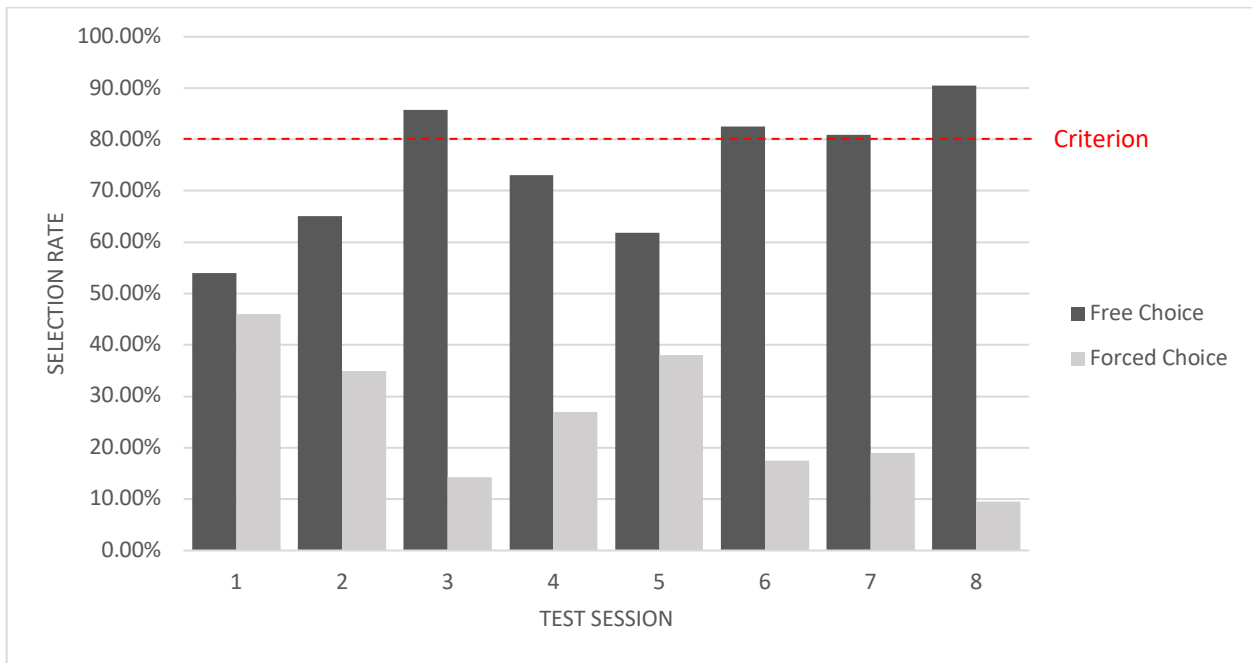
b) Sekali



c) Budi



d) Jingga

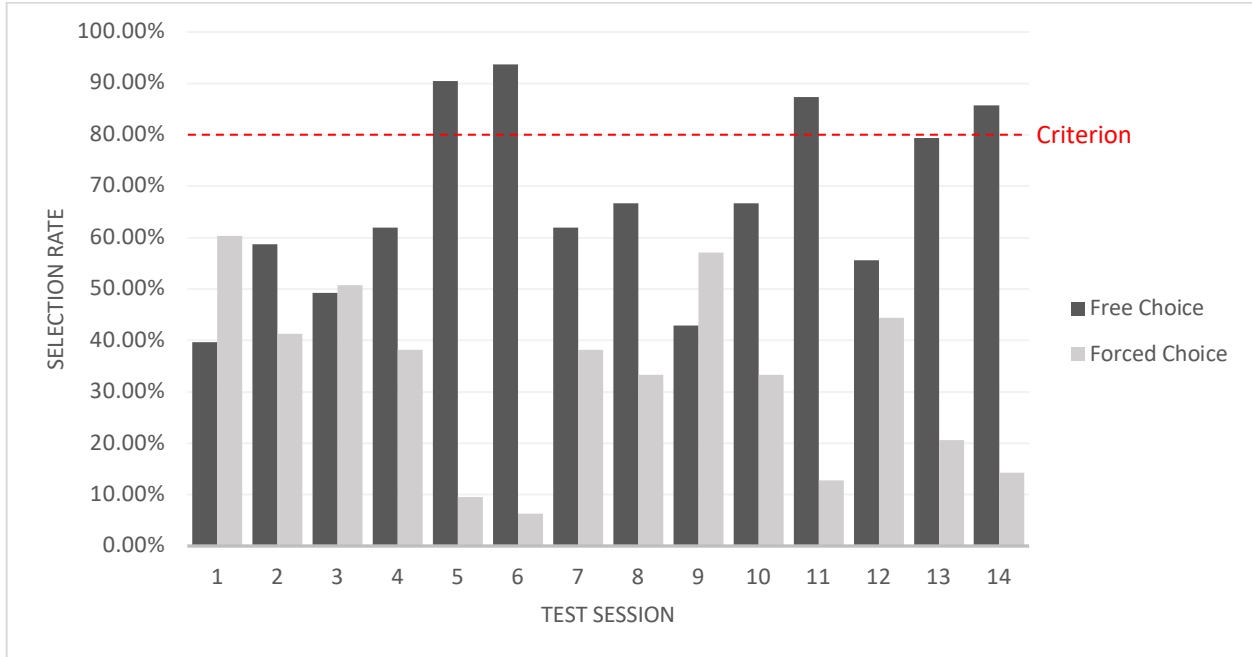


Note. Based on 64-trials per session, in comparison to preference criterion for each orangutan, in the Free-Left condition of Experiment 1.

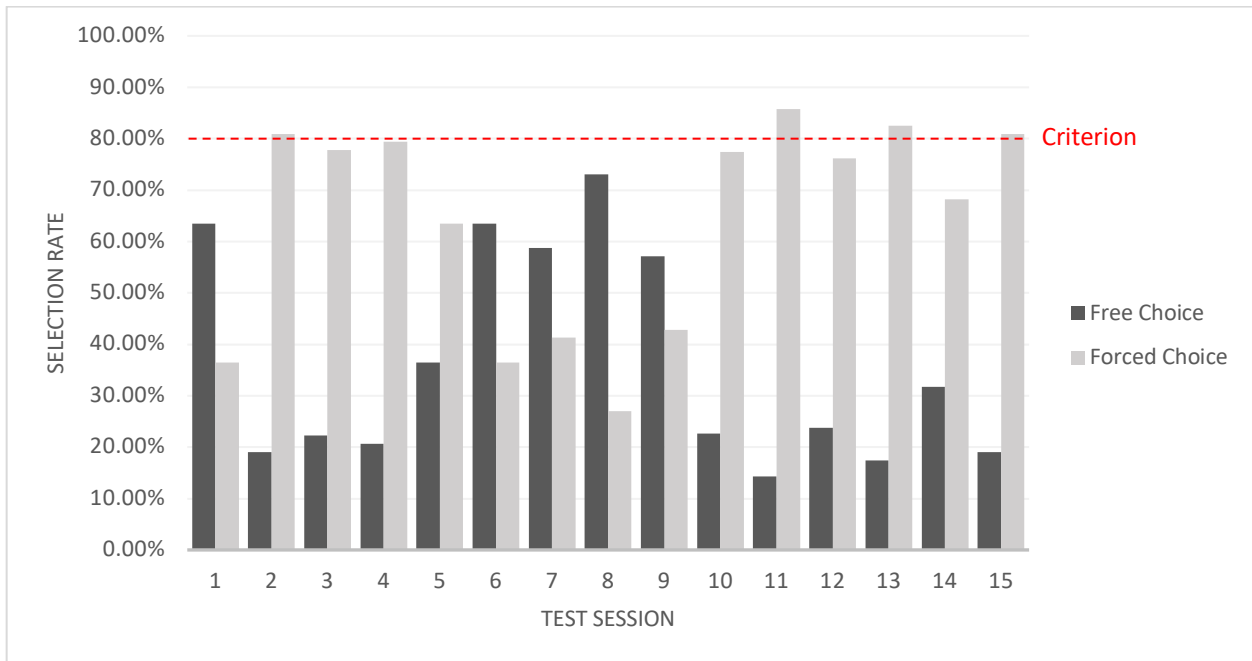
Figure 3.3a, 3.3b, 3.3c and 3.3d

Frequency of Free- and Forced- Choice Initial Link Key Selections

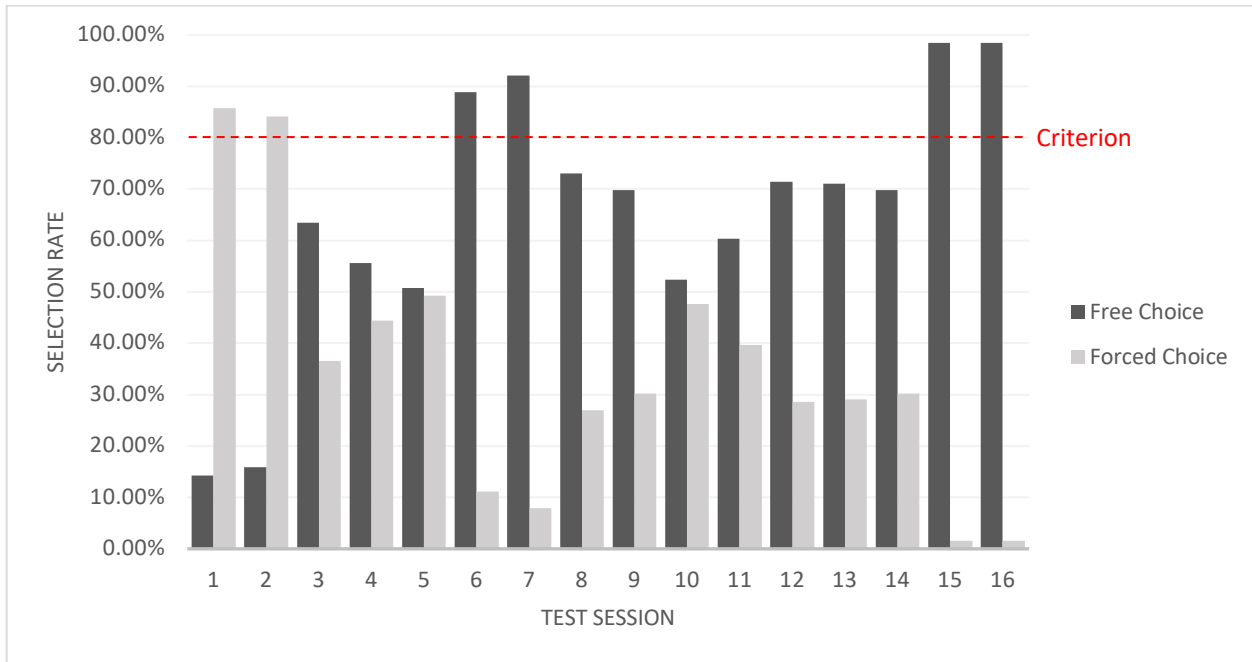
a) Ramai



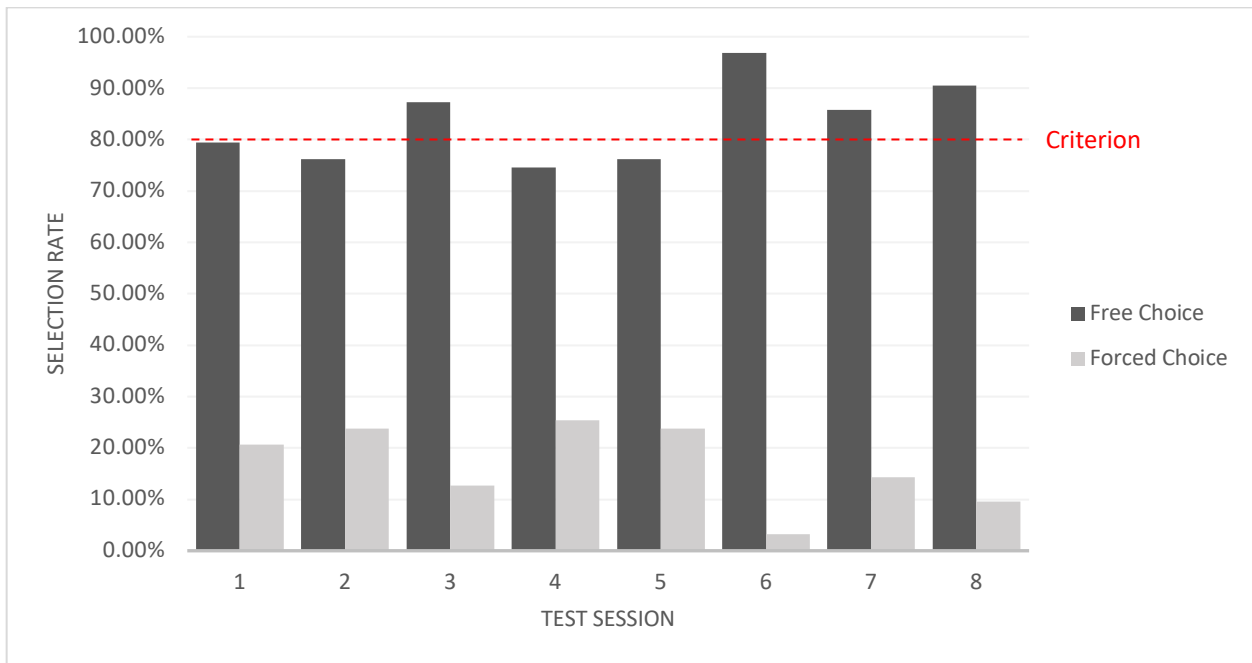
b) Sekali



c) Budi



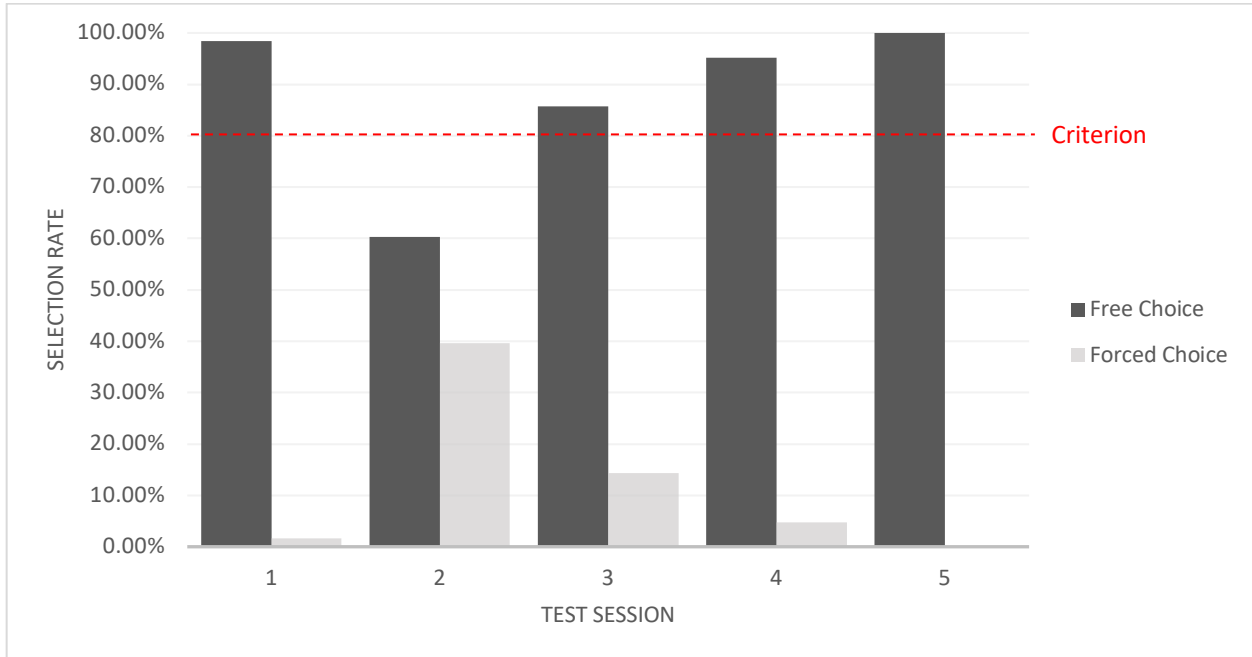
d) Jingga



Note. Based on 64-trials per session, in comparison to preference criterion for each orangutan, in the Free-Right condition of Experiment 1.

Figure 3.4

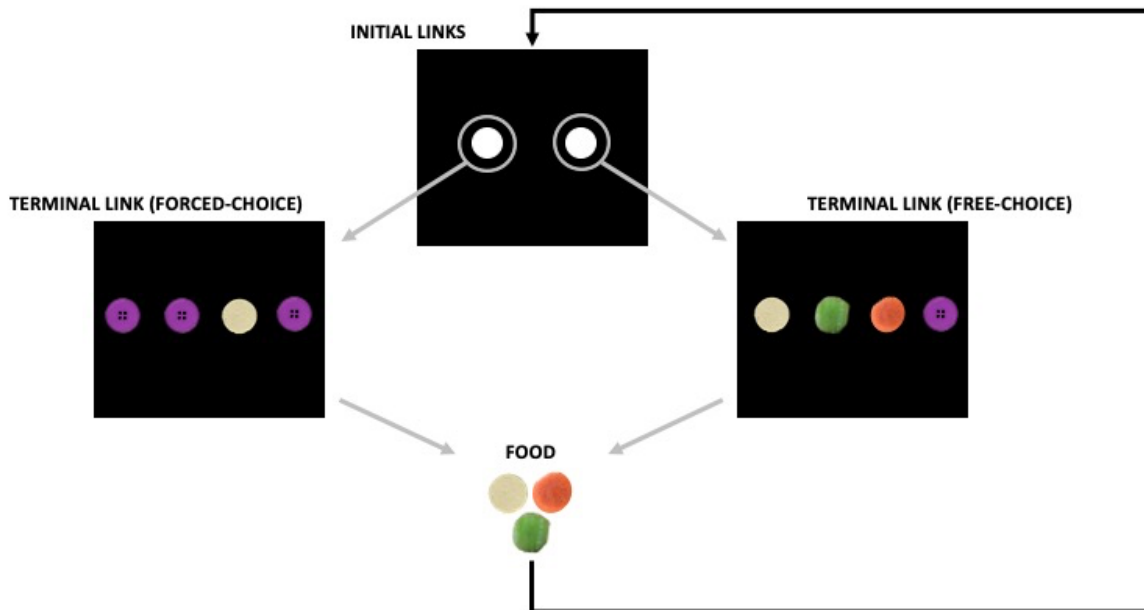
Frequency of Free- and Forced- Choice Initial Link Key Selections



Note. Based on 64-trials per session, in comparison to preference criterion for Sekali in the Free-Top condition of Experiment 1.

Figure 3.5

Example of a Test Trial in the Free-Right Condition of Experiment 2

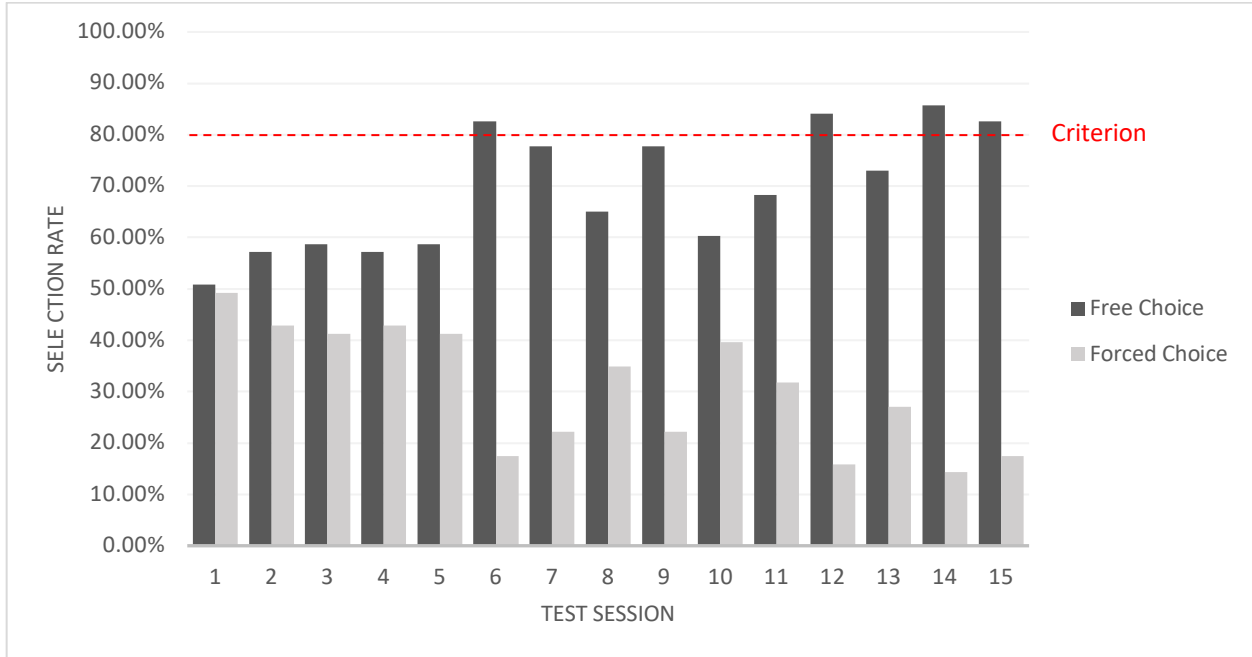


Note. In the initial links (top square), the free-choice terminal link is accessed via selection of the right white initial link key, and the forced-choice terminal link is accessed via selection of the left white initial link key. In the forced-choice terminal link (left square), subjects must select the tofu key amongst three button keys to receive a reward. In the free-choice terminal link (right square), subjects may select one of any of the three food types displayed to receive a reward. Selection of a food key in either terminal link resulted an auditory bridge, followed by a slice of the food type selected and initiation of a new trial. Selection of a button initiated a new trial, with no reward.

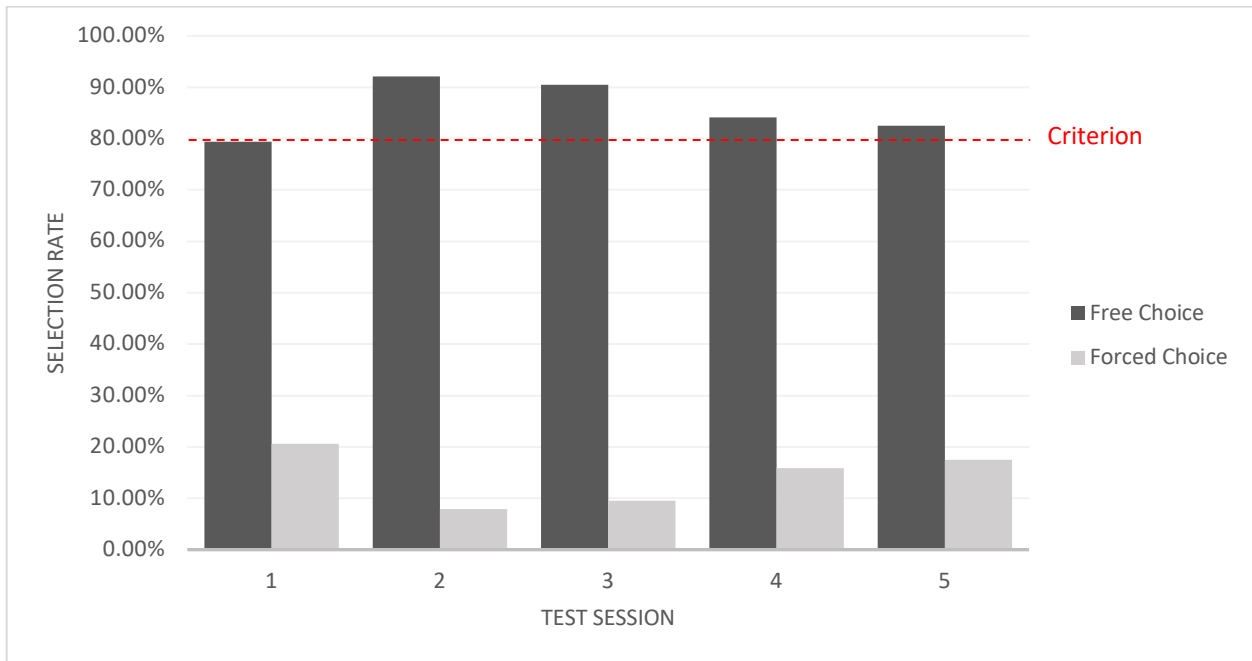
Figure 3.6a, 3.6b, 3.6c and 3.6d

Frequency of Free- and Forced- Choice Initial Link Key Selections

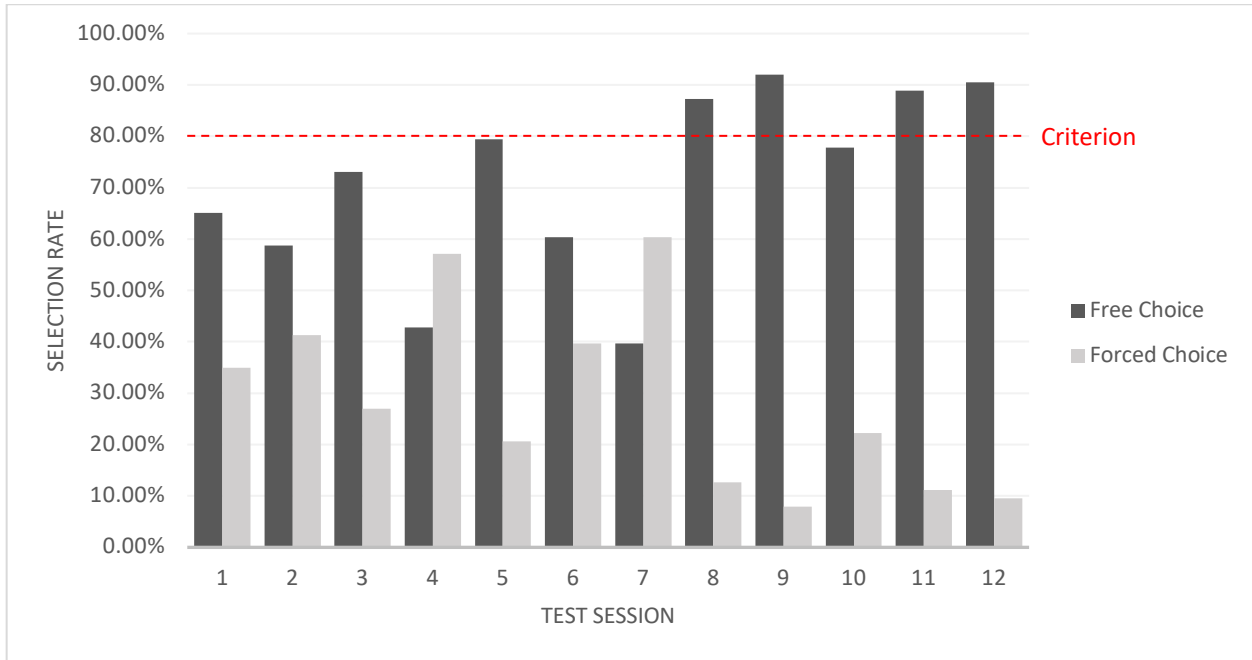
a) Ramai



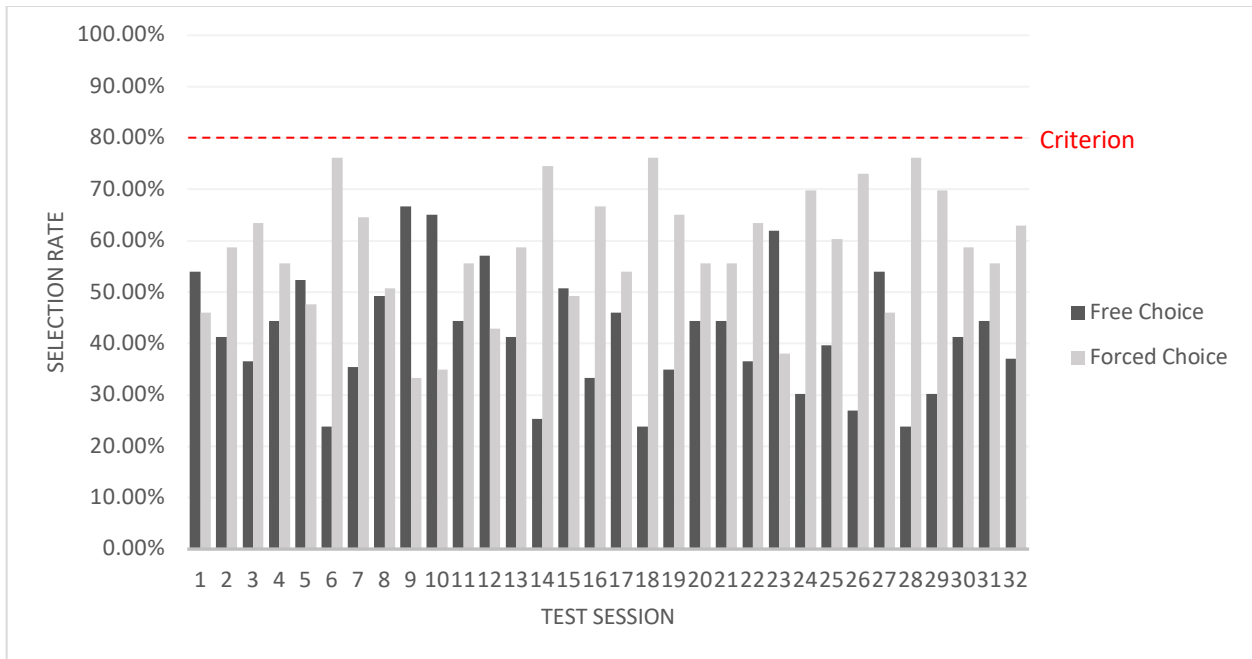
b) Sekali



c) Budi



d) Jingga

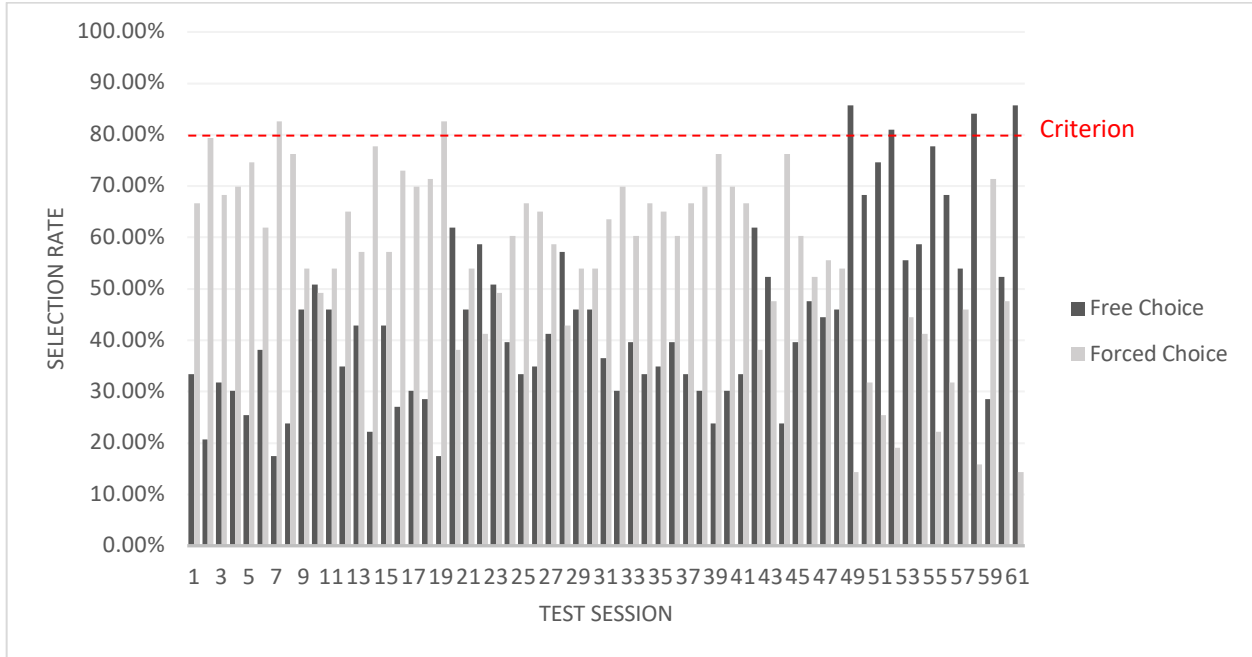


Note. Based on 64-trials per session, in comparison to preference criterion for each orangutan, in the Free-Left condition of Experiment 2.

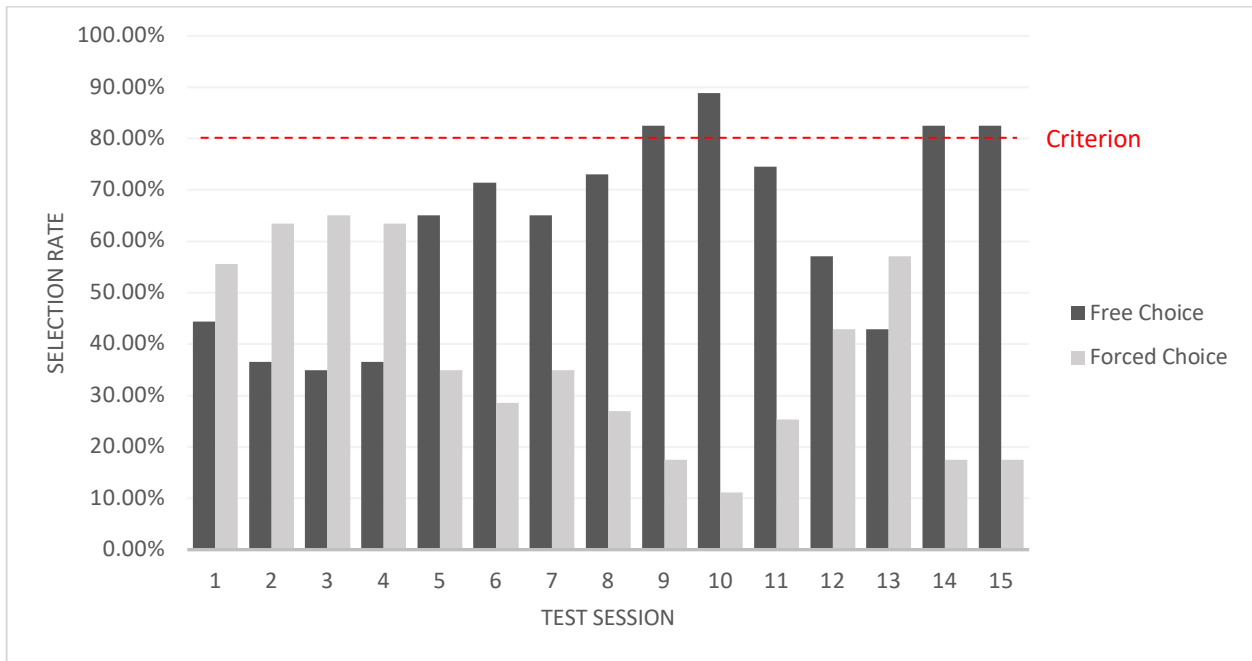
Figure 3.7a, 3.7b, 3.7c and 3.7d

Frequency of Free- and Forced- Choice Initial Link Key Selections

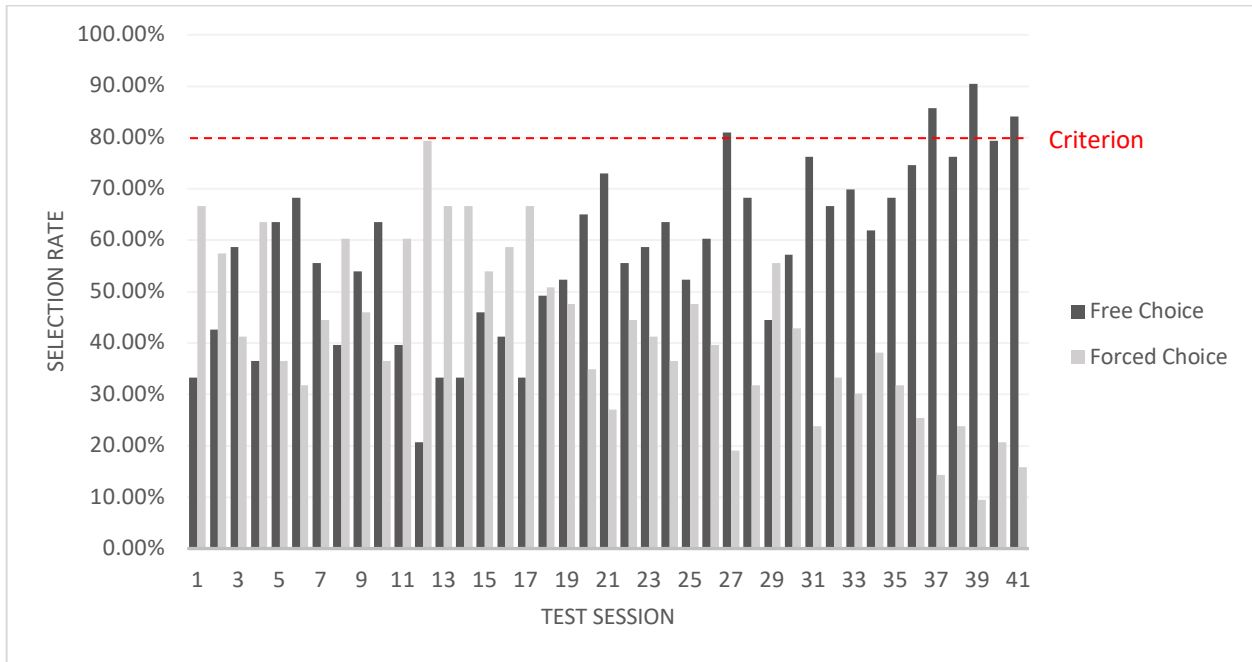
a) *Ramai*



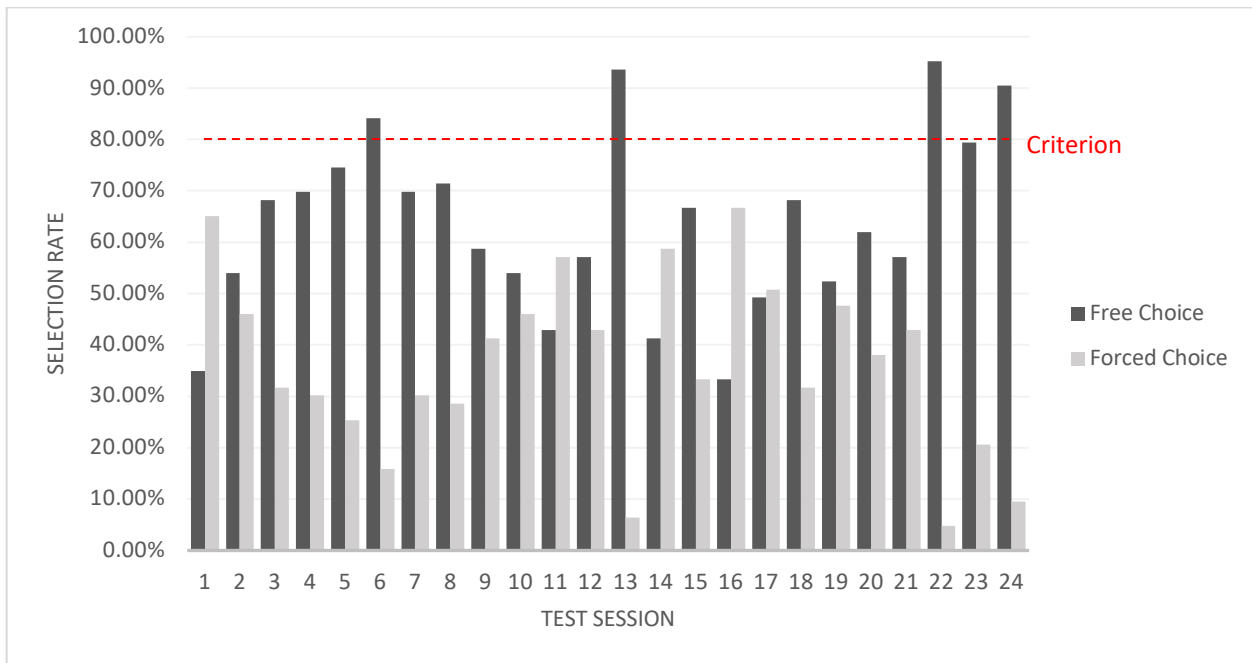
b) *Sekali*



c) Budi



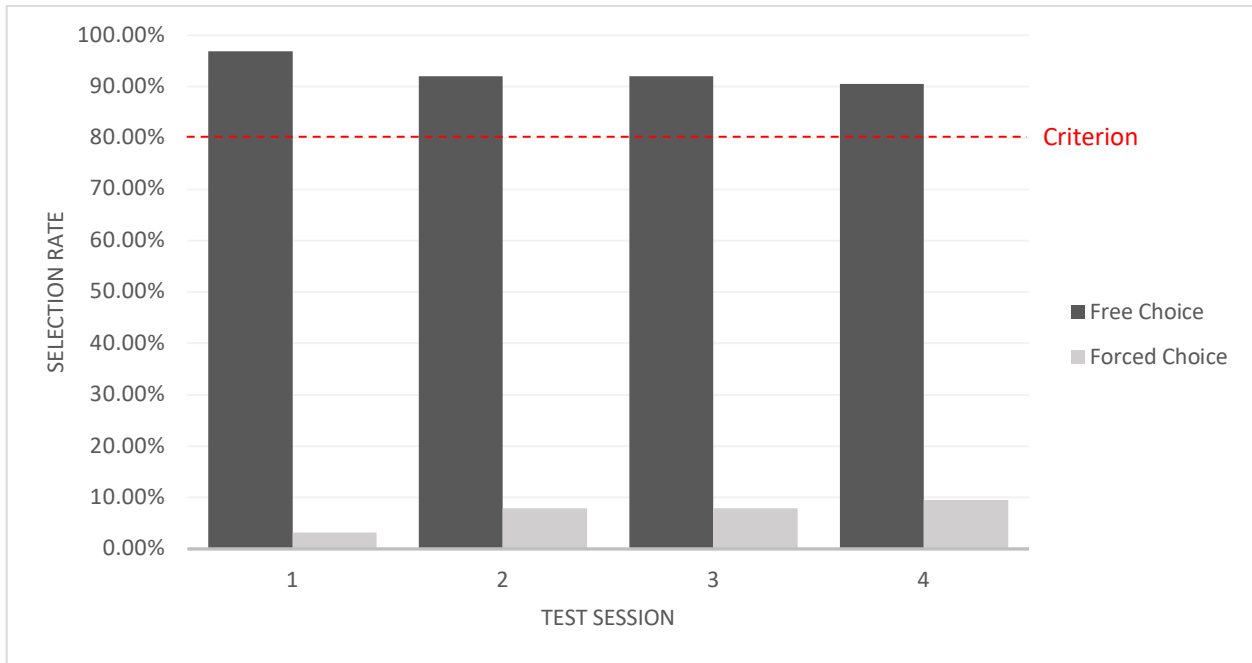
d) Jingga



Note. Based on 64-trials per session, in comparison to preference criterion for each orangutan, in the Free-Right condition of Experiment 2.

Figure 3.8

Frequency of Free- and Forced- Choice Initial Link Key Selections



Note. Based on 64-trials per session in comparison to preference criterion for Jingga in the Free-Top condition of Experiment 2.

CHAPTER 5: GENERAL DISCUSSION AND CONCLUSIONS

Human and animal research suggests that provision of choice through ACI is a promising means of captive orangutan enrichment. However, in the development of choice-providing ACI enrichment systems, we cannot assume that choice preferences observed in other primate species apply to orangutans. Doing so could result in systems that are unsuitable for users with potentially negative impacts on their welfare. Given that preference for choice has not previously been investigated in orangutans, the first step in UCD of choice providing systems is to determine if orangutans prefer choice to no choice. Furthermore, because digital choice options will likely be represented by application icons, it is important to establish whether orangutans can effectively identify 2-D pictures. Accordingly, this dissertation examined orangutan (a) preferences for computer touchscreen-provided free-choice, and (b) abilities to recognize pictorial content. In addition to advancing the development of choice-facilitating ACI systems, investigation of these factors is important for expanding our understanding of orangutan cognition. The sections that follow discuss findings in relation to these research purposes.

Preference for Touchscreen-Provided Choice

Orangutans' preference for touchscreen-delivered free-choice over forced-choice was examined using several choice paradigms. Additionally, to investigate how the fidelity of the choice-paradigms affected the strength of exhibited choice preferences, the amount of variety in choice options and choice outcomes varied per experiment.

First, in Chapter 2, in an attempt to evaluate if orangutans are intrinsically and independently motivated by preference for free-choice in and of itself, three orangutans' preferences for a free-choice alternative in which both the choice options and outcomes did not vary were examined. Because selection of any of the identical choice options (i.e., reward keys)

resulted in the same outcome (i.e., the same type and quantity of food), the choice offered to subjects with this paradigm was partly illusory. Given that in this context, subjects had nothing materially to gain from selecting the free-choice terminal over the forced-choice terminal, preference for the former indicated an intrinsic preference for choice itself (i.e., preference for choice that is independent of prospective rewards for making one choice vs. another). Although all three subjects initially exhibited a preference for free-choice in the first condition, their preferences varied in two control conditions. Two subjects displayed a preference for forced-choice in the second condition (i.e., control condition 1) and free-choice in the third condition (i.e., control condition 2), and a single subject maintained a preference for free-choice in the second condition but preferred forced-choice in the third condition. For two subjects, it appears that a side bias, learned in the first condition, confounded results in the second condition. This explanation was confirmed by results of the third condition in which both subjects continued to exhibit a preference for free-choice when left-right side biases were controlled. For the other subject, unexpected forced-choice selections in the third condition following consistent preference for free-choice in the first and second conditions could be explained by boredom (i.e., the subject began selecting the forced choice terminal because of the challenge and novelty it offered) or by the phenomena of ‘hypothesis testing’ in which subjects test alternative solutions to a task to determine if their hypothesis about the solution is correct. In either case, these results suggest, at minimum, a weak preference for free choice for this subject. Cumulatively, given that all the orangutans tested in this experiment demonstrated a preference for the free-choice terminal in the first naïve condition, results suggest an inclination towards free-choice when choice options and outcomes are equated that is vulnerable to influence by competing factors. Given that both pigeons (Catania, 1975; Catania & Sagvolden, 1980) and monkeys (Suzuki,

1999) have demonstrated stronger and more consistent preferences for free-choice in nearly identical conditions, it was possible that a choice paradigm in which the choice options and outcomes were identical may not have provided enough variety to be interpreted as a true ‘free choice’ by a cognitively complex species like orangutans.

In the two experiments described in Chapter 4, this hypothesis was tested by assessing whether increasing the fidelity (i.e., verisimilitude) of the choice paradigm in a stepwise manner, by providing more variety of choice options or outcomes, elicited stronger and more consistent choice preferences. In Experiment 1, a variety of choice options were provided while holding outcomes constant. In Experiment 2, both the choice options and outcomes varied. Results of Experiment 1 indicated that, as predicted, three of four subjects demonstrated stronger and more consistent preferences for free-choice than those observed in Chapter 2. However, a single subject, Sekali, exhibited the same behavior previously observed. Likely as a result of a learned side-bias, Sekali demonstrated inconsistent preferences by selecting free-choice in the first and third conditions (i.e., control condition 2), and forced-choice in the second condition (i.e., control condition 1). Thus, results of Experiment 1 of Chapter 4 suggested that increasing the fidelity of the choice paradigm resulted in stronger, more consistent preferences for free-choice in three subjects, but had no effect for one subject.

When the fidelity of the choice paradigm was increased a step further in Experiment 2, by varying both the choice options *and* outcomes, three subjects (including Sekali) demonstrated strong and consistent preference for free-choice. However, a single subject exhibited a response not previously observed in prior experiments. Jingga exhibited no preference in the first condition, but preferred free-choice in the two latter control conditions. Thus, in both Experiment 1 and 2, three-quarters of subjects exhibited consistent preferences for free-choice across

conditions, and a single subject did not. However, because none of the subjects in Experiment 2 demonstrated a preference for forced-choice (as was the case in Experiment 1), it is arguable that Experiment 2 resulted in stronger, more consistent free-choice preferences than Experiment 1.

Additional data analyses indicated that Jingga was not the only subject to exhibit a notable degree of indifference in Experiment 2. In the second condition, Ramai also initially selected free- and forced- choice with equal frequency. Additionally, during indifferent test sessions, both subjects selected *tofu*, the most highly preferred food almost exclusively (i.e., even after selecting the free-choice terminal that offered two additional food types). Conversely, when Jingga and Ramai began selecting the free-choice terminal in later test sessions, they also began selecting the other food types (i.e., carrot and celery) more often. Post hoc analyses based on these observations revealed that, for all four subjects, selection frequency of the most preferred food type (*tofu*) and selection frequency of free-choice were significantly negatively correlated. Given that *tofu* was the only food type available in both the free- and forced- choice terminals, this finding suggests that subjects were more likely to select free-choice when exploiting the variety of options and outcomes afforded by that alternative (i.e., food types other than *tofu*). Moreover, this behavior pattern, combined with the observation that Ramai and Jingga preferred *tofu* more than other subjects did, may explain why they exhibited periods of indifference when others did not. That is, Ramai and Jingga did not demonstrate a preference for either terminal link because they were exclusively interested in *tofu* and both terminals provided *equal access* to this food type (i.e., both offered a single *tofu* key). When they were uninterested in exploiting the other food-type options available exclusively in the free-choice link, the free- and forced- choice terminals were equally attractive.

Taken together, several conclusions can be drawn about orangutans' preference for touchscreen-provided choice. First, based on the findings of Chapter 2 and Chapter 4, orangutans demonstrated a general preference for free-choice over forced-choice. In all three of the experiments described in these chapters, subjects exhibited a clear preference for free-choice over forced-choice in the majority of conditions tested. Furthermore, as demonstrated in Chapter 4, Experiment 2, this preference was not reducible to larger key area or to the ease of selecting a reward key in the free-choice terminal link. However, instances of inconsistent choice preferences from one condition to the next in all three experiments indicated that orangutans' preference for choice can be influenced by competing factors, including learned side preferences, boredom, hypothesis testing, or food favoritism.

Additionally, the results of Experiment 2 of Chapter 4, indicate that some orangutans only prefer free-choice when they are motivated to take advantage of the options afforded by it. If, on the other hand, they are exclusively interested in an outcome equally accessible via free- and forced-choice alternatives, they do not necessarily prefer the free-choice. In turn, this finding implies that these individuals do not exclusively value free-choice in and of itself, but rather, their valuation depends on whether choice provides access to desired outcomes. This interpretation of the results is supported by the negative correlation between the selection frequency of tofu and the selection frequency of free-choice revealed in Experiment 2 of Chapter 4. Subjects were more likely to select free-choice when taking advantage of the variety of outcomes it afforded. Likewise, the finding that subjects' free-choice preferences were the least consistent and most vulnerable to interference in Chapter 2 when both choice options and outcomes did not vary (i.e., the choice was partly illusory) lends additional support to this interpretation. However, even in that unvaried choice-context, all subjects exhibited preference

for free-choice in the first condition. In this way, the orangutans tested exhibited some evidence of preference for choice in and of itself.

In any case, these findings differ from previous investigations of choice that have found that humans (Bown et al., 2003; Suzuki, 1997), monkeys (Suzuki, 1999), pigeons (Catania, 1975; Catania & Sagvolden, 1980), and rats (Voss & Homzie, 1970) reliably select choice over non-choice even when outcomes are do not vary. To select an option that requires a greater expenditure of energy with no tangible benefit in doing so suggests that such behavior is intrinsically rewarding (Leotti et al., 2010). Of particular interest is Catania and Sagvolden (1980)'s investigation of pigeons and Suzuki (1999)'s investigation of monkeys; both studies reported that these species reliably demonstrate preference for free-choice over forced-choice when tested with nearly identical paradigms to that of Chapter 2 that afford no variety in choice options or outcomes. Discrepant findings between these species and orangutans may, in part, reflect a more complex understanding of what constitutes a free-choice among orangutans when compared to pigeons and monkeys. This hypothesis is partially supported by the observation that when the results of the three experiments described in Chapter 2 and Chapter 4 are compared, at least in part, free-choice preferences became stronger and more consistent as the fidelity of the choice paradigms were improved. Additionally, the results of Chapter 4, Experiment 2 are the most similar to Catania and Sagvolden's (1980) investigation of pigeons in which three of four subjects consistently demonstrated preference for free-choice in every condition and a single pigeon only did so in the last two conditions tested. Similarly, Ramai, Sekali, and Budi consistently exhibited preferences for free-choice in every condition of Chapter 4, Experiment 2, but Jingga only did so in the last two conditions tested. It appears that by providing a more realistic and tangible free-choice alternative by providing a variety of choice options or outcomes

(i.e., one that is more similar to choices found in the natural environment), more orangutans interpreted the free-choice terminal link in Chapter 4, Experiment 2 as a true free-choice than in the previous choice paradigms tested in Chapter 2 and Experiment 2 of Chapter 4.

Picture Recognition

During training for the experiment described in Chapter 2, subjects demonstrated difficulty learning associations between colored computer application icons and food rewards. After approximately 12 months of practice, two of five orangutans recruited for the study failed to learn to select the reward colored button over a neutral colored button displayed on a touchscreen. To determine if this observation was the result of difficulty identifying touchscreen displayed pictures or pictures in general, Chapter 3 explored whether orangutans can spontaneously recognize the content of novel pictorial stimuli in digital or printed mediums. Specifically, a series of three experiments tested whether subjects demonstrated the same hierarchical preferences for real food types and pictures of the same food types in digital mediums (Experiments 1 and 3) versus printed mediums (Experiments 2 and 3). Additionally, experimental conditions varied based on the how food was pictured (i.e., food slices vs. whole food), the picture background, the type of digital displays, the dimensions of printed displays, and the number of displays pictures were presented on.

Collectively, orangutans of varying ages performed surprisingly poorly in all the formats tested. However, they were successful in recognizing food picture content in some formats and were slightly more proficient in print mediums than in digital ones. This result was especially notable for one of the youngest subjects who excelled at recognizing printed image content, suggesting that the capacity to recognize picture content varies across individuals and does not necessarily improve with age.

Specifically, subjects were able to recognize printed food images in the following formats. First, subjects recognized picture content when food was pictured as slices, in separate print cutouts that did not include a background, presented resting on the wooden platform previously used for real food trials (i.e., conditions 2-D and 3-F). This result is perhaps not surprising because, with the exception of the two dimensional quality of the pictures, these conditions most closely emulated the sight of real food slices resting on the platform. Additionally, presenting food pictures on the same platform used for real food presentation may have acted as a memory cue to the real food scenario. However, because subjects did not recognize food slice images in other conditions in which food was pictured resting on the same platform (i.e., conditions 1-D, 2-C, and 3-G), the platform could not have been the only contributing factor. Alternatively, success in recognizing the picture content in these conditions (i.e., conditions 2-D and 3-F) may indicate that orangutans have difficulty interpreting a single display as including two distinct objects. However, subjects did not recognize picture content when food images were presented on separate digital displays. In this case, subjects may have found it more difficult to identify digital images of food than printed ones.

Secondly, subjects also were able to recognize printed images of whole foods pictured on a black background in a single display (i.e., Conditions 2-B and 3-E). This result may be attributable to the fact that whole food pictures provide more visual cues about content than food slice images. However, the same effect was not found for digital images, as subjects did not recognize whole foods when pictured on a desktop computer monitor (i.e., Conditions 1-B and 3-B).

Finally, subjects were able to recognize image content in a digital condition in which food slice images, pictured against a black background, were presented on a desktop computer

monitor. The black background in this condition may have helped subjects focus attention on image cues used to recognize pictured objects. Furthermore, apart from demonstrating that subjects could spontaneously recognize the content of food images in at least one digital format, this finding indicates that subjects did not require a single display per food item, a picture of the whole food, or the wooden platform used for real food presentation to recognize food image content.

Additionally, consistent with human studies that suggest that experience is important in learning to comprehend a picture's content, present results indicate that in certain formats (i.e., mirror conditions 1-A/3-A; and 1-E/3-G), experience with the experimental paradigm and the pairing of food pictures with corresponding food types improved picture identification. This finding indicates that orangutans are capable of learning associations between a picture and an outcome with relatively little practice (i.e., ~60 trials).

Implications for Choice-Providing Orangutan ACI

Environmental enrichment is important for managing and preserving captive orangutans, a critically endangered species facing extinction. Given their semi-solitary lifestyles and the limited space available in captive facilities, captive orangutans can spend long hours off exhibit in small holding areas with reduced environmental stimuli. Based on research with humans and select monkey species, choice-facilitating ACI systems are a promising means of improving captive orangutans' mental and physical welfare via apparatuses with small physical footprints. However, an important step in development of such systems is investigation of their theoretical and practical appropriateness for this species. The findings described previously have important implications in this regard.

First, the results of the experiments described in Chapters 2 and 4 suggest that orangutans generally prefer computer-provided free-choice over forced-choice. These findings support the proposition that choice-facilitating ACI may be a useful means of environmental enrichment for captive orangutans. Moreover, results suggest that for an intelligent species like orangutans, the fidelity of choice paradigms delivered by ACI applications is important for ensuring a meaningful interpretation of choices provided and, consequently, an effective enrichment intervention. More specifically, ACI applications that provide a variety of choice options or outcomes are more likely to be interpreted as a true free-choice and, therefore, are more likely to yield stronger effects for orangutans. As discussed in Chapter 2, because zoos and other captive primate facilities put a great deal of time and consideration into animal care plans, changes to established routines and protocols can be difficult to acquire approval for and disruptive to operations. Thus, an enrichment system that does not affect orangutans' diets, environments, or schedules is preferential. For these logistical reasons, given that the experimental choice paradigms that provided (a) varied choice options and unvaried outcomes or (b) varied choice options *and* varied outcomes resulted in a similar degree of preference for free-choice, ACI systems that provide a variety of choice options but do not affect outcome may be favorable over those that produce a variety of outcomes.

Second, findings from Chapter 3 provide guidance regarding how choice may be most effectively presented and communicated to orangutan users. Results indicated that orangutans were only able to recognize picture content in one digital format – when images of familiar objects, pictured against a black background, were presented on a desktop touchscreen computer monitor. This finding suggests that in the design of choice-providing ACI systems, it is advantageous to use application icons represented by images of objects that orangutan users are

familiar with to communicate choice options, and in so doing, convey the system's purpose. Moreover, presenting application icons against a black background may help to focus orangutan users' attention on pictures and the image cues therein that facilitate content recognition. It is also important to note that results from the print conditions of the experiment described in Chapter 4 suggest that presenting images of *whole* objects, in *familiar* visual settings, on *separate* displays may additionally support image recognition. However, because orangutans did not recognize digitally displayed picture content in these formats, this recommendation should be considered provisional. Finally, orangutans' surprisingly poor performance in all the formats tested suggests that training with both ACI application paradigms and pictorial stimuli is important in ensuring that orangutan users comprehend the purpose of the system and its components. Confirmation of users' comprehension in this regard is imperative to ensure the effective use and welfare benefits of prospective ACI systems. The observation that, in select formats, subjects learned associations between images that were not initially recognized (i.e., images of food types) and outcomes (i.e., receipt of associated food types) in approximately 60 trials suggests that even moderate amounts of training will likely be efficacious.

The Task Ahead

With respect to orangutans' preference for choice, given the small sample size in this series of investigations, it's difficult to determine whether the strength and quality of individual preferences for free-choice observed are specific to the study sample or generalizable to the species. Thus, it will be revealing to test the three choice paradigms employed in these investigations with other orangutans and other great ape species. It would be particularly interesting to test the choice paradigm employed in Chapter 4, Experiment 2 using a food hierarchy organized on an interval scale of preference common across all subjects. If, in this

context, some subjects exhibited consistent preferences and some exhibited similar behavior to Ramai and Jingga, there would be further indication of a lack of intrinsic preference for free-choice in some species members and individual variance in the valuation of choice. However, titrating food preferences to the degree required and matching those preferences across subjects is challenging.

Additionally, given subjects' difficulty recognizing picture content, especially digitally presented pictures, it is possible that presenting choices digitally, affected orangutans' choice preferences. Therefore, it will be worthwhile to re-test the choice paradigms employed here in the physical realm. For example, it would be informative to examine if orangutans' preferences for choices that do not affect outcomes are stronger and more consistent when orangutans are presented with a free-choice of four food items of the same type (e.g., four banana slices) versus a forced-choice of a single food item and three identical unrewarding objects (e.g., one banana slice and three identical stones).

Furthermore, the orangutans tested in these investigations were born and raised in a captive zoo setting. Living in an environment where free-choice is limited may have resulted in a conditioning effect that reduced these orangutans' tendencies to exercise free-choice. Pigeons (Catania, 1975; Catania & Sagvolden, 1980) and rats (Voss & Homzie, 1970), with shorter life spans and therefore lesser durations of prior conditioning, may be more likely to behave in ways more consistent with preference for choice than great apes exposed to several years of conditioning that weakened choice-oriented tendencies. Likewise, the monkeys tested in Suzuki (1999) ranged in age from 5 to 6 years old, and therefore could be expected to behave more consistently regarding choice than the orangutans tested, who ranged in age from 11 to 33 years. In other words, given the duration of time they have lived in captivity with limited environmental

control compared to that found in the wild, test subjects may have been suffering from some degree of learned helplessness resulting in less coherent and consistent free-choice behavior. If that is the case, it would also explain why Budi, one of the youngest participants, exhibited stronger and more consistent preference for free-choice across all three experiments described in Chapters 2 and 4. Because Budi had been living in a captive environment for less time than Ramai and Sekali, he was less likely to develop learned helplessness. To test this hypothesis, future studies of great ape preference for free-choice could take prior free-choice conditioning into account by testing samples of subjects from a variety of environmental backgrounds. In the same vein, it would be interesting to observe if other species of great apes of varying ages, including human children, respond to this paradigm in a similar way to the sample of orangutans tested here.

Second, the results of Chapters 2 and 4 suggest that future investigations of animal choice preferences may benefit from conceptualizing preference for free-choice along a spectrum rather than a dichotomy (i.e., present or not present) as has been the case in the past (Catania, 1975; Catania & Sagvolden, 1980; Suzuki, 1999; Voss & Homzie, 1970). Trait theorists have conceptualized human characteristics in this way, defining a single trait as comprising a continuum bounded by two extremes (e.g., introversion – extroversion) (Fleeson, 2001; Goldberg, 1993). It is believed that an individual may fall along any point in a trait's continuum and where that individual falls influences how they behave in various contexts. In the same way, animals' motivation to exercise free-choice likely varies between individuals and across disparate experimental contexts, as was the case for the orangutans' in this series of investigations. Reconceptualizing animal preferences for choice in this way inspires new questions and avenues of inquiry such as: In what contexts does a species prefer choice? What

motivates expression of choice preference? Which factors are the most and least influential in these contexts? And why?

Third, with respect to orangutans' capacity to recognize picture content, given the small sample size in these investigations, replication studies will be required to determine if findings generalize to other orangutans and other species of great ape. Moreover, the lack of competency in recognizing image content in this sample of orangutans warrants further investigation, particularly in digital mediums. Given the importance of experience in interpreting picture content and subjects' more extensive experience with digital images than printed images, it is surprising subjects were less successful at recognizing digital image content. Phylogenetic psychophysical studies indicate that the development of primate visual systems likely plateaued in catarrhine monkeys, which are trichromatic and have the same wavelength sensitivities and similar flicker sensitivity and visual acuities as humans (De Valois & De Valois, 1988; Jacobs & Deagan, 1999). Therefore, all primates who evolved thereafter are likely to physically process pictures the same way humans do. For this reason, differences in humans' and orangutans' capacities to recognize pictures are more likely attributable to cognitive factors than psychophysical ones. To identify a picture's content, one must cognitively overcome the perceptual differences between pictures and objects (i.e., size, colour, stereoscopic, and motion parallax cues) (Bovet & Vauclair, 2000; Fagot & Parron, 2010). Consequently, even species with identical visual systems may process pictures differently based on their proficiency at solving referential cognitive problems (Fagot & Parron, 2010).

Fourth, there is evidence that interest in pictures can influence picture recognition and that such interest can be facilitated by pictorial stimuli that are derived from an animal's social environment (Bovet & Vauclair, 2000; Humphrey, 1974). For example, several species have

been observed to adaptively respond to pictures of conspecifics more easily than pictures of other categories of stimuli (Bovet & Vauclair, 2000). Thus, in future investigations, it will be important to examine if orangutans demonstrate superior picture recognition when stimuli consist of socially derived images rather than food. Additionally, another factor not examined in this series of investigations is picture complexity. Simple pictures of geometric shapes or object profiles might be more recognizable than complex photographs (Bovet & Vauclair, 2000). Orangutans' aptitude with these types of pictures could provide insight into how orangutans process pictures.

Fifth, in considering the implications of the findings of this dissertation for the development of ACI technology, it is important that they are not interpreted or applied out of context. For example, orangutans' preferences for free-choice could be misinterpreted to imply that for captive members of this species, the more choice, the better. Yet, research with humans indicates that too many choices can negatively impact emotion, motivation, and satisfaction (Iyengar & Lepper, 2000). The research described herein explored the effects of a maximum of three choice options. Therefore, the observed choice preferences and related implications can only be presumed to apply to circumstances with relatively few choices. Further species-specific research will be required to determine how orangutans and other great ape species respond to more extensive choice options.

Finally, it is important to acknowledge that a preference for free- over forced- choice does not necessitate that it is either liked or beneficial. Dichotomous choices are comparative and therefore can reflect selections based on either 'liking' or 'less aversion'. In other words, subjects may select one option over another because they *like* that option *more* than the alternative, or because they *dislike* that option *less* than the alternative. However, Lamont (2005)

has suggested that participant-controlled procedures in which subjects control the duration or the types of stimulus during testing facilitate greater confidence in the interpretation of observed preferences as being motivated by 'liking'. Thus, given that in the experiments herein subjects controlled both exposure to free-choice as well as the duration of exposure through voluntary participation in test sessions and selections of the free- or forced- choice terminals during test sessions, we can be reasonably confident that observed preferences reflect a desire for free-choice. However, even if orangutans desire free-choice, that does not necessarily entail that it is beneficial. What we desire is not always mentally or physically advantageous. Consider the effects of recreational drug use, the consumption of high fat foods, or extreme dieting. Partaking in desired substances and activities can negatively affect wellbeing. Although research on the positive effects of free-choice on human welfare indicates that choice is likely to be beneficial for orangutans, we cannot assume that is the case. For this reason, user experience assessments that directly measure both short and long term behavioural and physiological effects of choice-facilitating ACI prototypes will be critical in confirming that they are an effective means of beneficial enrichment for orangutans.

References

- Bovet, D., & Vauclair, J. (2000). Picture recognition in animals and humans. *Behavioural Brain Research, 109*(2), 143–165. [https://doi.org/10.1016/S0166-4328\(00\)00146-7](https://doi.org/10.1016/S0166-4328(00)00146-7)
- Bown, N. J., Read, D., & Summers, B. (2003). The lure of choice. *Journal of Behavioral Decision Making, 16*(4), 297–308. <https://doi.org/10.1002/bdm.447>
- Catania, A. C. (1975). Freedom and knowledge: An experimental analysis of preference in pigeons. *Journal of the Experimental Analysis of Behavior, 24*(1), 89–106. <https://doi.org/10.1901/jeab.1975.24-89>
- Catania, A. C., & Sagvolden, T. (1980). Preference for free choice over forced choice in pigeons. *Journal of the Experimental Analysis of Behavior, 34*(1), 77–86. <https://doi.org/10.1901/jeab.1980.34-77>
- De Valois, R., & De Valois, K. (1988). *Spatial Vision*. New York: Oxford University Press.
- Evans, C. S., & Marler, P. (1991). On the use of video images as social stimuli in birds: Audience effects on alarm calling. *Animal Behaviour, 41*(1), 17–26. [https://doi.org/10.1016/S0003-3472\(05\)80499-3](https://doi.org/10.1016/S0003-3472(05)80499-3)
- Fagot, J., & Parron, C. (2010). Picture perception in birds: Perspective from primatologists. *Comparative Cognition & Behavior, 5*, 132–135. <https://doi.org/doi:10.3819/ccbr.2010.50007>
- Fleeson, W. (2001). Toward a structure- and process-integrated view of personality: Traits as density distributions of states. *Journal of Personality and Social Psychology, 80*(6), 1011–1027. <https://doi.org/10.1037/0022-3514.80.6.1011>
- Goldberg, L. R. (1993). The structure of phenotypic personality traits. *American Psychologist, 48*(1), 26–34. <https://doi.org/10.1037/0003-066X.48.1.26>

- Humphrey, N. K. (1974). Species and Individuals in the Perceptual World of Monkeys. *Perception*, 3(1), 105–114. <https://doi.org/10.1068/p030105>
- Iyengar, S. S., & Lepper, M. R. (2000). When choice is demotivating: Can one desire too much of a good thing? *Journal of Personality and Social Psychology*, 79(6), 995–1006. <https://doi.org/10.1037/0022-3514.79.6.995>
- Jacobs, G. H., & Deagan, J. F. (1999). Uniformity of colour vision in Old World monkeys. *Proceedings of the Royal Society: Biological Sciences*, 266, 2023–2028. <https://doi.org/10.1098/rspb.1999.0881>
- Lamont, A. M. (2005). What do monkeys' music choices mean? *Trends in Cognitive Sciences*, 9(8), 359–361. <https://doi.org/10.1016/j.tics.2005.06.014>
- Leotti, L. A., Iyengar, S. S., & Ochsner, K. N. (2010). Born to choose: The origins and value of the need for control. *Trends in Cognitive Sciences*, 14(10), 457–463. <https://doi.org/10.1016/j.tics.2010.08.001>
- Suzuki, S. (1997). Effects of number of alternatives on choice in humans. *Behavioural Processes*, 39(2), 205–214. [https://doi.org/10.1016/S0376-6357\(96\)00049-6](https://doi.org/10.1016/S0376-6357(96)00049-6)
- Suzuki, S. (1999). Selection of Forced- and Free-Choice by Monkeys (*Macaca Fascicularis*). *Perceptual and Motor Skills*, 88(1), 242–250. <https://doi.org/10.2466/pms.1999.88.1.242>
- Voss, S. C., & Homzie, M. J. (1970). Choice as a Value. *Psychological Reports*, 26(3), 912–914. <https://doi.org/10.2466/pr0.1970.26.3.912>