Summer 8-2016

An Assessment of Number Representation in the Small-Eared Bushbaby (Otolemur garnettii)

Tiffany Aycia Woodard Baker
University of Southern Mississippi

AN ASSESSMENT OF NUMBER REPRESENTATION IN THE SMALL-EARED BUSHBABY (*OTOLEMUR GARNETTII*)

by

Tiffany Alycia Woodard Baker

A Thesis
Submitted to the Graduate School
and the Department of Psychology
at The University of Southern Mississippi
in Partial Fulfillment of the Requirements
for the Degree of Master of Science

Approved:

_____
Dr. Tammy Greer, Committee Chair
Associate Professor, Psychology

_____
Dr. Alen Hajnal, Committee Member
Associate Professor, Psychology

_____
Dr. B. Katherine Smith, Committee Member
Assistant Professor, Anthropology and Sociology

_____
Dr. Karen S. Coats
Dean of the Graduate School

August 2016

Published by the Graduate School

ABSTRACT

AN ASSESSMENT OF NUMBER REPRESENTATION IN THE SMALL-EARED BUSHBABY (*OTOLEMUR GARNETTII*)

by Tiffany Alycia Woodard Baker

August 2016

In an effort to explain the underlying mechanisms of number representation, both the object-file and the approximate number system have been proposed. Despite the recognition in animals, both nonhuman and human, it remains unclear how numbers are represented cognitively or what system is employed. Furthermore, primate numerosity research has been almost exclusively conducted within haplorhine species (monkeys and apes). Within the strepsirhines (lemurs, lorises, and galagos), it has only been investigated in 15 diurnal and cathermal Malagasy primate species. No study to date has looked at this ability in either African strepsirhines or nocturnal primates. To examine the extent of numerical representation among the strepsirhines, the current study examined a nocturnal African primate, Garnett's Greater Bushbaby (*Otolemur garnettii*). Using a modified search task developed by Lewis, Jaffe, and Brannon (2005), bushbabies searched for raisins in an opaque pail across 10 paired trials. Each pair consisted of one "honest" presentation (number observed = number retrievable) and one "deceitful" presentation (number observed > number retrievable), with trial conditions consisting of 1 vs. 2, 2 vs. 3, and 3 vs. 4. False bottoms in the pails allowed for "deceitful" presentations. A 5 (1:1, 2:4. 4:8, 2:3, 3:4) X 2 (honest vs deceitful) fully repeated measures analysis of variance examined the within-subject effects of trial type and ratio

of raisins revealing longer search times on deceitful versus honest trials only with ratios of 1:2 and 2:4.

ACKNOWLEDGMENTS

First and foremost, I would like to extend my deepest gratitude to Dr. Tammy Greer whose wisdom, generosity, and intelligence made the completion of this project possible. I would also like to thank Dr. Alen Hajnal for his inspiration and guidance as well as Dr. Katie Smith for her support and invaluable feedback throughout the course of this study. In addition, I would like to acknowledge Jen Christopher whose continued support, both as a lab mate and a friend, provided a firm ground for me to persevere. Thank you.

DEDICATION

It is with great pleasure that I dedicate this thesis to Kylie Baker. She perhaps sacrificed the most for the completion of this project. Indeed, she has the same hours invested in this work as me. I will forever be grateful. Moreover, I would like to dedicate this project to Dr. Sheree Watson. It is because of her that I was given the opportunity to begin. It is only fitting that she shares in the end product. Thank you.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF ILLUSTRATIONS

CHAPTER I – INTRODUCTION

Numerosity Defined

The concept of numerosity has been defined several different ways but can be generally conceptualized as the "numerical attributes of the world" (Merritt, MacLean, Crawford, & Brannon, 2011), number cognition (Uller, Jaeger, Guidry, & Martin, 2003), or thinking about and reasoning with numbers (Coolidge & Overmann, 2012). Research has focused on developing two domains of numerosity: uncovering the underlying mechanisms of numerosity representation and expanding the first domain to the computations that can be performed using them (Feigenson, Carey, & Hauser, 2002). The current study focuses on the former.

Theoretical and Applied Mathematics

In their most complicated uses, numbers are studied for their own attributes, applied to explain natural phenomena, and used to solve real world problems. These uses were illustrated as early as the 26th century BC through the geometrical principles involved in the building and infrastructure of the Egyptian pyramids (Wier, 1996). But number is also inherent in our environment. Several theorists have attempted to explain the mathematical equations behind different relationships that are embedded in the world. For example, The Vitruvian Man, drawn by Leonardo da Vinci around 1487, illustrated particular ratios of the human body (e.g., height to arm span is 1:1; height to hand span is 10:1), with ratios conceptualized from the architectural ideas of Vitruvius (Le Floch-Prigent, 2008; Reeder, 2007). Moreover, there are numerical relationships between musical notes with every 8th note beginning a new octave, an interval between one musical pitch and another with half or double its frequency depending on whether the

pitch is higher or lower (Krumhansl, 1995). Because number has been so easily manipulated by humans to successfully solve problems as well as naturally explains phenomena embedded in our environment, it should be no surprise that basic forms of number, or numerosity, exists throughout the animal kingdom (Brannon, 2006; Coolidge & Overmann, 2012; Dehaene, 1997; Vallortigara, 2015).

Evolutionary Advantage

In the most basic form, numerosity includes processes such as more versus less and counting operations. These rudimentary elements of numerosity are thought to be the precursors to human mathematical ability (Vallortigara, 2015). The animal and its niche provide an opportunity to examine how pervasive numerosity is among animals by isolating natural behaviors in which numerosity occurs. For example, animals must discriminate between locations in which food resources are abundant or scarce (Emmerton, 2001), or when predators that are nearby may be fewer or outnumber the group (Hauser, 2001). We see this use of numerosity in lions as they listen to the number of roars from distant male competitors in order to make decisions about fighting or fleeing (Hauser, 2001, p. 46-48). Birds discriminate between the number of flock members currently engaged in surveillance for predators rather than food gathering activities to decide upon their own behaviors (Emmerton, 2001). Mothers must keep track of the number of infants they have as well as divide resources among them. For all of these niche specific tasks, a rudimentary understanding of numerosity, which occurs naturally and spontaneously, is required (Beran, Smith, Redford, & Washburn, 2006). It is because these forms of numerosity provide an evolutionary advantage that we expect numerosity to be present at some level in nonhuman animals (Hauser, MacNeilage, &

Ware, 1996). In fact, numerosity is so fundamental that it has been well documented in species ranging from salamanders (Uller et al., 2003) to preverbal human infants (Feigenson et al., 2002; Feigenson & Carey, 2003). Despite the recognition of this capacity in animals, both nonhuman and human, it is not clear how numerosity is represented cognitively. The object-file system and the approximate number system have both been proposed in an effort to explain the underlying mechanisms for the representation of number.

Theories of Numerosity

The object-file system posits that "individual objects are represented only implicitly" (Feigenson et al., 2002). Each object equates to one open file and is then placed into one of two models. Theoretically a one-to-one mapping between each object and its corresponding file is maintained within its appropriate model. This strenuous nature of the object-file system results in a limitation to the number of files that can be open at a particular time. Typically, four is the maximum number of files that can be open simultaneously in a given model and held parallel in short term memory (Uller et al., 2003). Therefore, discrimination is not a function of the size of the discrepancy between quantities but rather contingent on a set-size limitation. This limitation is the distinguishing characteristic of the object-file system. During a food-choice task, for example, naïve semi-free ranging rhesus monkeys *(Macaca mulatta*) approached boxes holding two numerosities of apple slices differing in comparisons of 1 versus 2, 3 versus 4, 3 versus 5, 4 versus 8, and 3 versus 8. Monkeys preferred boxes with more slices, provided the total number of slices in the boxes was less than four. As interpreted by the authors, the pattern of results supports the object-file system because of the apparent set-

size limitation of four (Hauser, Carey, & Hauser, 2000). It is important to note that the object-file system has not been extensively researched in nonhuman animals (Jones & Brannon, 2012). However, studies on reaction time to numerical presentation in both human and nonhuman animals have shown faster and more accurate reactions during trials with numerosities ranging from 1-3 because of *subitizing*, a process human and nonhuman animals are thought to use for rapid recognition of numbers less than about four (Murofushi, 1997), lending support to the postulation of an object-file system as a possible mechanism for the representation of number.

Another prominent theory for explaining the underlying mechanisms involved in nonverbal number representation is the approximate number system whereby number discrimination is approximated (Jones & Brannon, 2012). Although number can be conceptualized as a particular property of a set of discrete entities, numerical elements can be defined as a "continuous mental magnitude" (Brannon, 2006). This representation potentially allows for an estimation of which set may contain more or less. The main evidence for the approximate number system as mechanism for numerosity is that the ability to successfully discriminate more versus less obeys Weber's Law (Brannon, 2006). According to Weber's Law, the ratio rather than the absolute difference between tow values permits discriminability between two sets of differing numerosities (Dehaene, 1997; Feigenson & Carey, 2003; Gallistel, 1990; Jones et al., 2014; Lewis et al., 2005). As a result, the distinguishing characteristic of the approximate number system is its ratio dependence, and its effect has been demonstrated in many species (Brannon & Roitman, 2003). For example, mosquitofish (*Gambusia holbrooki*), who swim in aggregate groups (shoals) to reduce risk of predation, choose the larger shoal when given the option

between shoals that differ by ratios of 1:2 including those of 2:4, 4:8, and 8:16 (Agrillo, Dadda, & Bisazza, 2007).

Jones and Brannon (2012) suggest that the mechanism of numerical representation may not be an independent function of the object-file system or the approximate number system. During a food-choice task, 113 diurnal and cathermal lemurs from 15 different species housed at the Duke Lemur Center were allowed to choose between two differing sets of numerosities (e.g., 1 raisin versus 2 raisins). Results indicated that during small number discriminations (i.e., < 4), the object-file system was employed for precise judgments. On the other hand, lemurs relied on the approximate number system when given the choice between larger numerosities such that the discrimination was based upon estimation and precision decreased as the ratio approached one. Findings like these demonstrate the capacity for both mechanisms to be involved during numerical discriminations. In cases where numerosities are less than four, a limited object-file system may allow for implicit tracking of the numerosity. In situations dealing with larger numerosities, the approximate number system may allow estimations, with some accuracy, depending on the ratio between two quantities (Jones & Brannon, 2012). More research will lend clarification to the mechanisms of numerical representation.

Numerosity in Strepsirhine Primates

Non-human primate numerosity research has been almost exclusively conducted within haplorhine (humans, monkeys, apes, and tarsiers) species. Strepsirhini (lemurs, lorises, and galagos) split from the common ancestor of primates 47-54 million years ago (Yoder et al., 2013) and are the most varied group of primates as evidenced by the wide

range of ecological niches they occupy. Variability is so widespread that it persists not only between but also within taxa. Some species, for example, are diurnal, while others nocturnal; some arboreal, while others terrestrial (Ward, 1995). These niche occupations are thought to be more similar to ancestral primates than those of haplorhines making these primates, including bushbabies, an excellent model of the ancestral primate (Charles-Dominique, 1978).

Little is known about the cognitive abilities of strepsirhini. It may be that cognitive ability contains a similar level of variability as do ecological niches between these species. While numerical representation has been demonstrated in 15 species of diurnal and cathermal Malagasy primates (i.e., lemurs) (Jones et al., 2014; Jones & Brannon, 2012; Lewis et al., 2005; Merritt et al., 2011; Santos, Barnes, & Mahajan, 2005), no study to date has looked at this ability in either African strepsirhines or nocturnal primates. Furthermore, only two investigations have looked at the underlying mechanisms of numerosity in strepsirhini (Jones & Brannon, 2012; Lewis et al., 2005). As a result, insufficient evidence is available to make judgements on the numerical representation of strepsirhines, but initial investigations into the underlying mechanisms have been informative. As previously described, Jones and Brannon (2012), using a food-choice task with 113 diurnal and cathermal lemurs, provided evidence for use of the object-file system when representing small quantities, and the approximate number system when representing larger quantities. In another experiment, Lewis et al. (2005) employed a searching-task paradigm modeled after a similar experiment with human infants (Feigenson & Carely, 2003). Mongoose lemurs (*Eulemur mongoz*) observed an experimenter place grapes successively into an opaque bucket filled with shredded paper.

On some trials, grapes were placed into a hidden compartment preventing lemurs from accessing all grapes. Search time was measured and compared to trials in which lemurs were allowed to retrieve all grapes placed into the bucket. Lemurs searched longer only on trials that differed by ratios of 1:2, 2:4, and 4:8, but not 2:3 or 3:4, indicating that lemurs expected the hidden grapes depending on the size of the difference in ratio of accessible to non-accessible grapes, lending support to the approximate number system.

Current Study

It is necessary to further investigate numerosity to determine if there are characteristics specific to lemurs that allow for the representation of number or if it is a shared characteristic of strepsirhini. To examine the extent of numerical representation, this study tested a nocturnal African primate, Garnett's Greater Bushbaby (*Otolemur garnettii)* with the aims of investigating the underlying mechanisms of numerosity by testing the object-file versus the approximate number theories of numerosity. Garnett's bushbaby is a nocturnal, arboreal (Nash & Harcourt, 1986; Masters, Lumsden, & Young, 1988; Nash, Bearder, & Olsen, 1989) strepsirhine primate that occupies southeastern Africa (Olson, 1979). Their main diet is composed of fruits, insects, and small birds (Bearder & Doyle, 1974). While lemurs most often live in social groups (Curtis, 2003), female bushbabies live in small groups comprised of related females. Male bushbabies disperse and share overlapping ranges with several female territories (Bearder & Doyle, 1974; Charles-Dominique, 1978; Nash & Harcourt, 1986).

Radinsky (1974) demonstrated a similar brain sulcal pattern between *Otolemur* and some Malagasy lemurs like *Haplemur* and ring-tailed lemurs. Specifically, cerebral sucli in common "include coronal, lateral, orbital, sylvian, postsylvian, and calcarine."

This in conjunction with their close phylogeny (Yoder et al., 2013) supports the current hypothesis that Garnett's bushbaby will show results comparable to lemurs discriminating effectively at 1:2 ratios and declining in success as the ratio increases (Lewis et al., 2005). Therefore, we hypothesize support for the approximate number system in the bushbaby.

Table 1

Hypotheses

Evidence for Use Of Approximate Number System	Evidence for Use of Object File System	Duke's 15 Mixed Lemur Species	Mongoose Lemurs	Hypotheses for Garnett's Bushbaby
1:2 Yes	1:2 Yes	1:2 No	1:2 Yes	1:2 Yes
2:4 Yes	2:4 Yes	3:6 No	2:4 Yes	2:4 Yes
4:8 Yes	4:8 No	6:12 No	4:8 Yes	4:8 Yes
2:3 No	2:3 Yes	1:3 Yes	2:3 No	2:3 No
3:4 No	3:4 Yes	2:6 Yes	3:4 No	3:4 No
		4:12 Yes		

Note. Yes refers to longer search times when food should have remained in the pail

CHAPTER II – METHOD

Subjects

Subjects were thirteen captive born *Otolemur garnettii* (8 males, 5 females; Mean age = 7.64, Range = 1-16) housed at The University of Southern Mississippi Bushbaby Research Facility. Subjects were individually housed in plastic wire mesh cages (77 cm D x 77 cm W x 152 cm H) and maintained on a reverse light cycle set to approximate the natural day/night cycle. Light onset is at 1800 hours, and dark onset is at 700 hours. During the bushbabies' dark cycle, red lights are illuminated to accommodate experimental observations. The dark/light cycle was not modified during the course of this study. Animals were fed Purina high protein monkey chow (Diet #5045, Purina, St. Louis, MO) supplemented with fruit daily and insects on occasion. Water was available *ad libitum*. This project conformed to state, federal, and institutional guidelines and is approved by The University of Southern Mississippi's Institutional Animal Care and Use Committee (IACUC, 15081301; see Appendix C).

Testing Materials and Apparatus

Raisins (*Sun-Maid®, Stockton, CA*) were offered to assess the bushbabies' understanding of numerical concepts. Subjects retrieved raisins from a white plastic pail measuring 13.2cm H. The pail measured 11cm D at the top, and 9 cm D at the bottom because it is graduated such that it is slightly larger at the top than the bottom. Shredded paper within the pail obscured the raisins and a secondary compartment while each bushbaby foraged for raisins. Discrepancies between the number presented and the number available for retrieval were achieved by inconspicuously hiding a subset of raisins in a secondary compartment through a 2.54cm x 2.54cm opening located in the

bottom of the pail. The opening to the hidden compartment was designed such that a piece of duct tape effectively concealed it. As a result, no knowledge of hidden raisins was available to the animals.

Procedure

Using a modified searching-task paradigm set forth by Lewis et al. (2005), the raisins were presented to the subjects in one of 10 paired trials, with each pair consisting of one "honest" numerical presentation and one "deceitful" numerical presentation. In the "honest" presentations, the bushbabies were able to retrieve the number of raisins that were placed into the pail; in the "deceitful" presentations, the number of raisins accessible was fewer than the number placed into the pail. The deceitful trials were presented in ratios of 1:2, 2:3, or 3:4 with 1:2 consisting of three different levels (i.e., 1:2, 2:4, 4:8). Table 2 displays the ratios used in the honest and deceitful trials. No paired trials were presented together.

Table 2

Ratios for Honest Trials Versus Deceitful Trials

Honest Observed : Accessible	Deceitful Observed : Accessible
1 : 1	2 : 1
2 : 2	4 : 2
4 : 4	8 : 4
2 : 2	3 : 2
3 : 3	4 : 3

Testing Trials

The experimenter placed a number of raisins on the lid of the pail. After she was certain the bushbaby had viewed the raisins, she began consecutively placing each raisin individually into the pail. While placing the raisin into the pail, the experimenter reached inside where she either placed the raisin into the secondary compartment or released it into the shredded paper spread about the container. The experimenter closed the cage door and allowed the animal to retrieve all accessible raisins. After the animal finished eating the last accessible raisin, the experimenter started a stopwatch to allow for one-minute search time recording. After one minute, the camera was stopped.

Controls

Three control procedures optimized the likelihood of bushbabies relying only on number of raisin when searching. To prevent temporal cues, the number of seconds was standardized such that each raisin was placed into the pail in two seconds. Because the "amount of raisin" may be an important factor, the size of raisins was also standardized always weighing from 0.3 – 0.4 grams. Lastly, because of the highly developed olfactory system of the bushbaby (Beader & Doyle, 1974), it was necessary to control for odor. This was accomplished by rubbing all pails with raisins prior the initiation of the trials.

Data Collection

All trials were video-recorded and coded by two independent observers. Each observer recorded *search time* for a 30-second interval after all accessible raisins had been eaten. A bushbaby was considered searching if its head, hands and/or snout were moving about inside the pail. Search trials were terminated after 30 seconds. In addition, *orientation to raisins* as they were dropped into the pail was also coded. Bushbabies

were considered oriented to the raisin before placement in the pail if their heads and/or snouts were facing the raisins. A significant correlation between coder one (M = 4.35, SD = 3.37) and coder two (M = 5.50, SD = 3.81; r = 0.924) on search time was reached coding 20% of the trials (n = 26). Moreover, coders agreed every instance during the 26 trials that the bushbabies attended to the raisin being presented. A coding sheet with an ethogram is available in Appendix B.

Results

All analyses were accomplished using SPSS 23.0 statistical software. Potential important demographic variables were explored for their relationships with the multivariate composite of dependent variables. Although there were significant relationships of the composite dependent variable with age group and gene line, the introduction of age and then gene line into the model as independent variables did not change the outcome of the analysis so they were excluded from the main analyses. Results are presented in Table 3.

Table 3

Results for Demographic Variables

Variable		N	*M* Honest	*SD* Honest	*M* Deceit	*SD* Deceit	*F*	*p*-value
Age		13					$F(2,20) = 68.081$	0.015*
	Young	4	4.45	0.30	4.20	2.72		
	Mid	4	3.60	0.99	7.25	3.59		
	Old	5	4.48	2.11	6.24	2.97		
Sex		13					$F(2,10) = 0.700$	0.716
	Male	8	3.90	1.66	6.65	2.95		

Female	5	4.68	0.70	4.76	3.30		
Twin/Singleton	13					$F(2,10) = 1.371$	0.494
Twin	4	3.75	1.06	4.20	1.51		
Singleton	9	4.40	1.53	6.69	3.39		
Gene Line	13					$F(2,10) = 21.464$	0.045*
Memphis	6	4.20	1.83	3.30	3.57		
Hybrid	7	4.20	1.04	5.60	2.90		

Note: *Significant at 0.05 alpha level

Search times were analyzed in two ways. A Trial (1:2; 2:4; 4:8; 3:4; 2:3) X Condition (deceitful; honest) fully repeated measures analysis of variance (ANOVA) revealed a Trial X Condition interaction, $F(4,48) = 3.37$, $p = 0.011$.

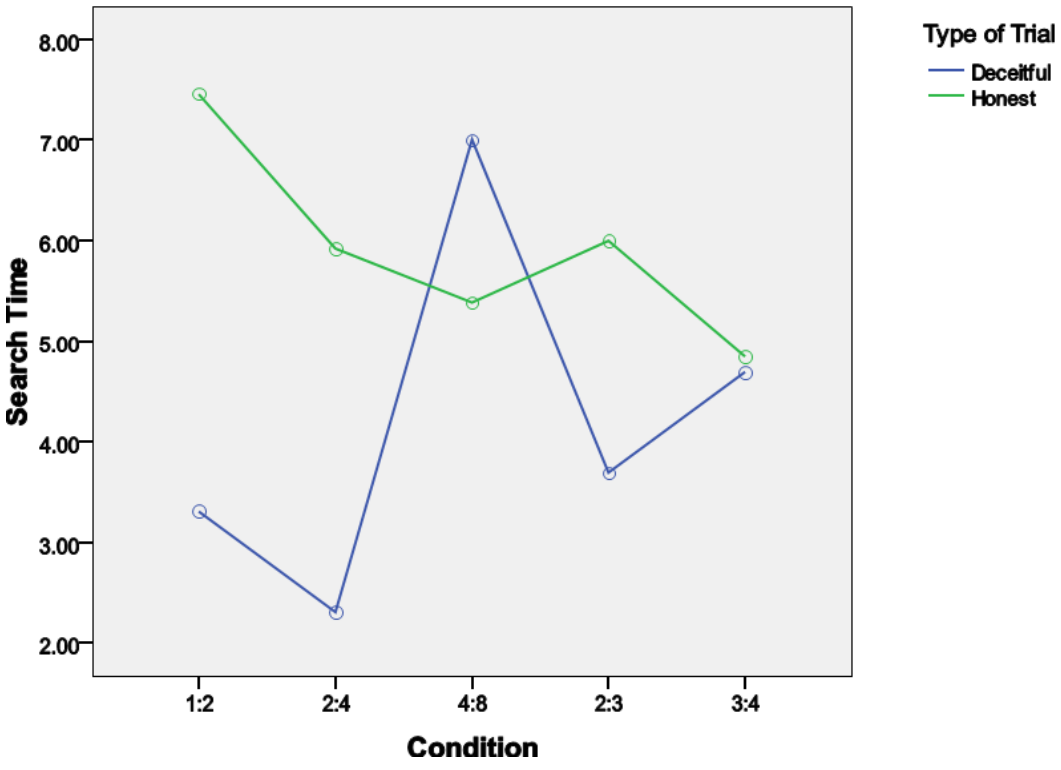


Figure 1. Search time differences for honest and deceitful trials for each ratio condition.

An analysis of simple effects of Condition at each level of Trial indicated that for 1:2 ratios, bushbabies searched longer on deceitful (M = 7.46, SD = 3.18) as opposed to honest trials (M = 3.31, SD = 3.28; $F(1,12) = 14.042$, $p = 0.003$). Similarly, for 2:4 ratios, bushbabies searched the pail longer on deceitful (M = 5.92, SD = 4.68) as opposed to honest trials (M = 2.31, SD = 2.75; $F(1,12) = 5.875$, $p = 0.032$). There was no difference in search time during 4:8 deceitful (M = 5.38, SD = 6.37) and honest trials (M = 7, SD = 4.16; $F(1,12) = 0.958$, $p = 0.347$), 2:3 deceitful (M = 6, SD = 4.53) and honest trials (M = 3.69, SD = 4.21; $F(1,12) = 2.278$, $p = 0.157$), or 3:4 deceitful (M = 4.85, SD = 3.91) and honest trials (M = 4.69, SD = 3.75; $F(1,12) = 0.010$, $p = 0.923$).

To test for higher versus lower time differences, search time also was analyzed by a series of five Sign Tests, one for each condition. Results indicated longer search times on trials that differed by a 1:2 ratio ($z(12) = -2.701$, $p = 0.007$), and 2:4 ($z(12) = -2.172$, $p = 0.030$), but not those that differed by ratios of 4:8 ($z(12) = -1.061$, $p = 0.288$), 2:3 ($z(12) = -1.633$, $p = 0.102$), or 3:4 ($z(12) = -0.045$, $p = 0.964$). Table 4 shows the results for the analysis of simple effects and the Sign Tests.

Table 4

Results of Analysis of Simple Effects and Sign Tests

Ratio	Analysis of Simple Effects	Sign Tests
1:2	$F(1,12) = 14.042$, $p = 0.003$*	$z(12) = -2.701$, $p = 0.007$*
2:4	$F(1,12) = 5.875$, $p = 0.032$*	$z(12) = -2.172$, $p = 0.030$*
4:8	$F(1,12) = 0.958$, $p = 0.347$	$z(12) = -1.061$, $p = 0.288$
2:3	$F(1,12) = 2.278$, $p = 0.157$	$z(12) = -1.633$, $p = 0.102$
3:4	$F(1,12) = 0.010$, $p = 0.923$	$z(12) = -0.045$, $p = 0.964$

Note: *Significant at 0.05 alpha level.

Figures for individual bushbabies are available Appendix A beginning with the youngest bushbaby.

Table 5 shows the results for bushbabies compared to previous strepsirhine studies in the theoretical framework of the approximate number and object-file systems.

Table 5

Theoretical and Comparative Results

Evidence for Use Of Approximate Number System	Evidence for Use of Object File System	Duke's 15 Mixed Lemur Species	Mongoose Lemurs	Garnett's Bushbaby
1:2 Yes	1:2 Yes	1:2 No	1:2 Yes	1:2 Yes
2:4 Yes	2:4 Yes	3:6 No	2:4 Yes	2:4 Yes
4:8 Yes	4:8 No	6:12 No	4:8 Yes	4:8 No
2:3 No	2:3 Yes	1:3 Yes	2:3 No	2:3 No
3:4 No	3:4 Yes	2:6 Yes	3:4 No	3:4 No
		4:12 Yes		

Note: Yes refers to longer search times when raisins should have remained in the pail

CHAPTER III - DISCUSSION

The results are incongruent with the author's hypothesis that Garnett's bushbabies would rely on the approximate number system. Instead, current results suggest bushbabies can only discriminate between numerosities that differ by 1:2 and 2:4 ratios. Several interpretations are available for these results.

Methodological Constraints

Even if bushbabies can make use of the object-file and approximate number systems, the particular task may have limited the use of these systems. If bushbabies employed the object-file system, all numerosities equal to or less than four should have been discriminable. Although 8 of the 13 bushbabies distinguished between 2 versus 3 and 7 of the 13 distinguished between 3 versus 4, the differences were nonsystematic and not significant.

If the task had been initiated with a perceptual ratio, as was the case for rhesus monkeys that were offered a choice between two groups of apple slices (Hauser et al., 2000), it is possible that the approximate number system would have been primed and the results may have been comparable to lemurs. In addition, both a perception and memory component rather than perception alone were required to effectively complete the task. The task itself, therefore, could have been more difficult for bushbabies than the mongoose lemur task. It remains unclear if bushbabies would make use of either the approximate number system, the object-file system, or both with a choice task. It should be noted that the task required the use of vision. Bushbabies may have discriminated more numerosities if tested under a primary modality such as olfaction.

On the other hand, as previously mentioned, strepsirhini are the most varied of primates (Ward, 1995). Therefore, conflicting results are not entirely unexpected. Garnett's bushbaby is a nocturnal African primate (Beader & Doyle, 1974) while mongoose lemurs are cathermal Malagasy primates (Curtis, 2003). It could be that the transition from nocturnal to cathermal allowed for the development of an approximation system. Numerosity investigations into owls may provide interesting clues for how nocturnality plays a role in number representation. Unfortunately, no numerosity research to the author's knowledge has been conducted with these animals.

The shift from the mainland of Africa to Madagascar could have required additional adaptations, or different adaptations may have occurred due to chance. It is important to note that it remains unclear if these adaptations would be species-specific, appearing intelligent but inflexible, or more advanced, with the animal having control over when to employ a particular numerical representation system. It is known that "increased flexibility requires a learning phase during the ontogeny of the species' infants" (Tomasello & Call, 1997). This suggests that parts of the system could be unlearned or modified.

The social intelligence hypothesis predicts that increases in social complexity drove the evolution of cognitive flexibility in primates. A more complex social group should require changes in cognitive abilities for successful navigation of the social system (MacLean, Barrickman, Johnson, & Wall, 2009). Mongoose lemurs live in social groups consisting of a female, her mate, and three or four of their offspring. Together the parents care for one additional offspring a year (Curtis, 2003). Bushbabies live in female groups of one matriarch and a few of her female offspring. The males disperse as they

reach sexual maturity. The males share overlapping territories with several females (Beader & Doyle, 1974). The difference in social group dynamics may have allowed the evolution of an estimation system, or the flexibility to choose which number system to use. Either way this approach would suggest that mongoose lemurs may be more cognitively advanced than Garnett's bushbabies assuming the social system of mongoose lemurs is more advanced.

Conclusion

While this study is not conclusive, we do now know that bushbabies discriminate between numerosities of 1 versus 2 and 2 versus 4 when engaging in a search task. We do not know whether bushbabies would rely on the object-file or approximate number system under a different set of circumstances or with different methodology, especially those taking into account different sensory modalities. Further research should vary the circumstances and methods to fully illuminate the capability of as well as the flexibility in number representation of this species. In addition, experimental designs should include a reaction time component to investigate subitizing in bushbabies to allow for Darwinian comparisons of rapid number recognition since it remains unclear if bushbabies make use of this process.

APPENDIX A - Individual Bushbaby Search Times

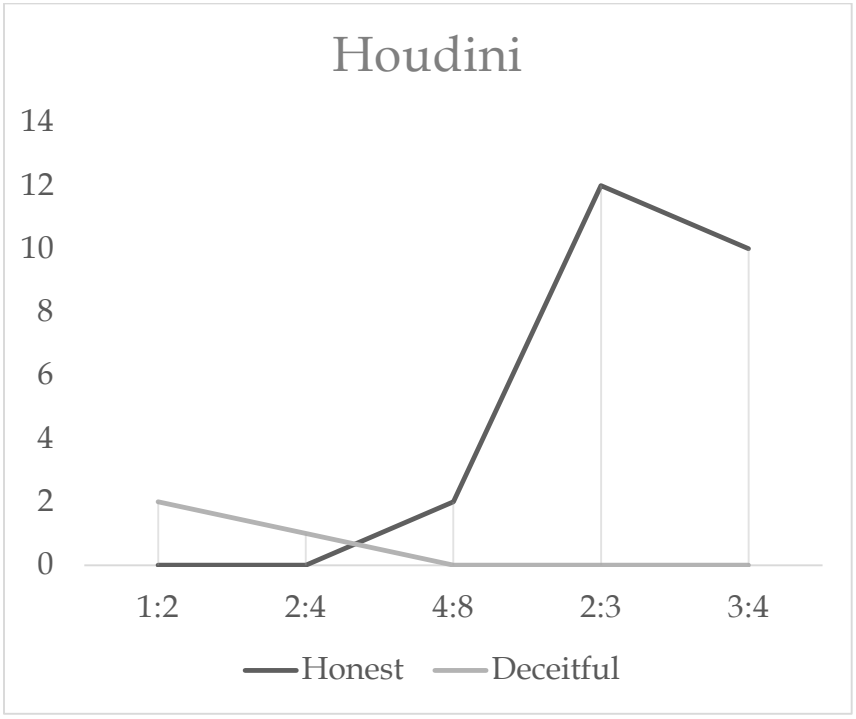


Figure A1. Houdini's search time during honest and deceitful trials.

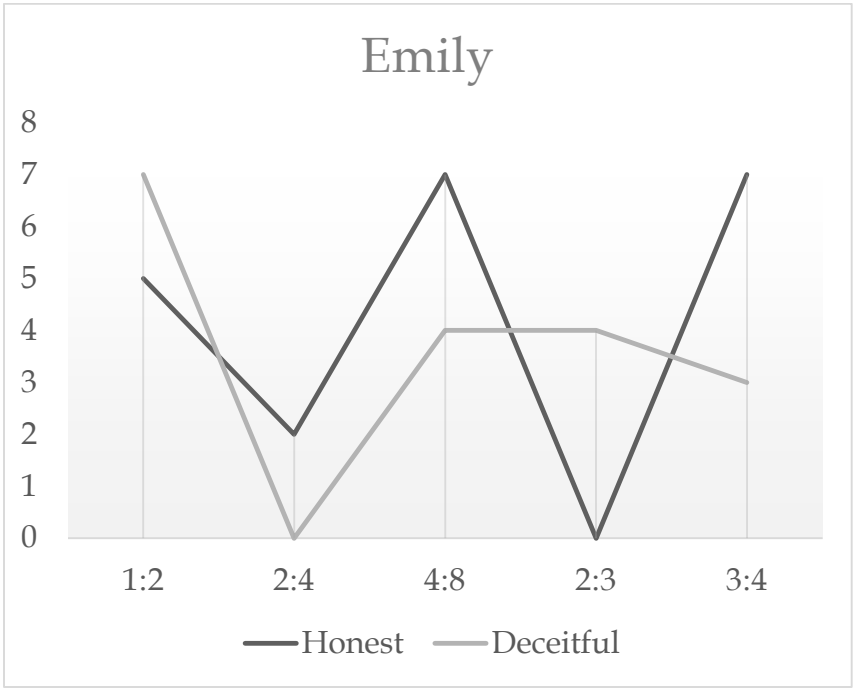


Figure A2. Emily's search time during honest and deceitful trials.

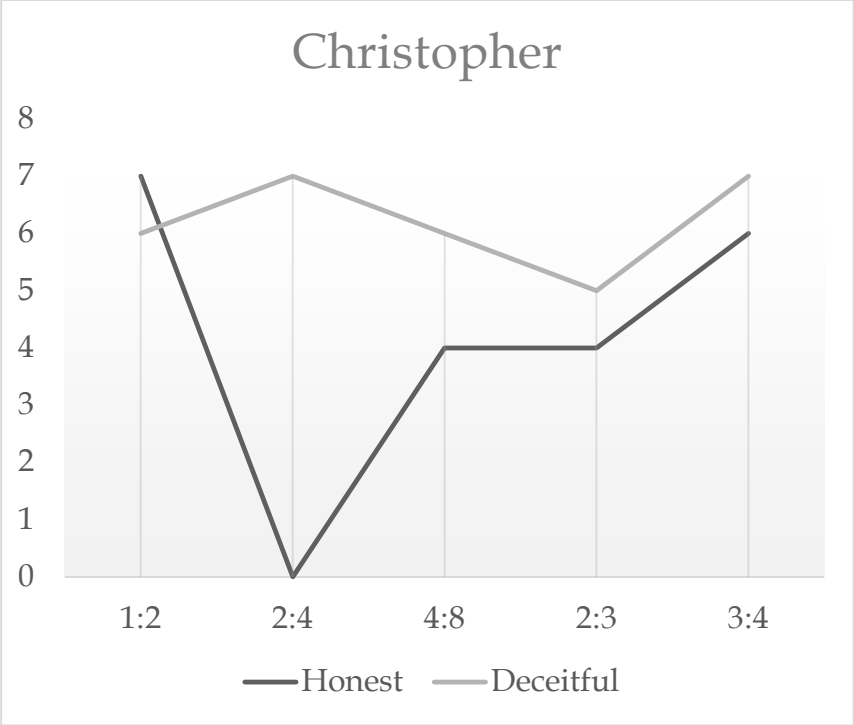


Figure A3. Christopher's search time during honest and deceitful trials.

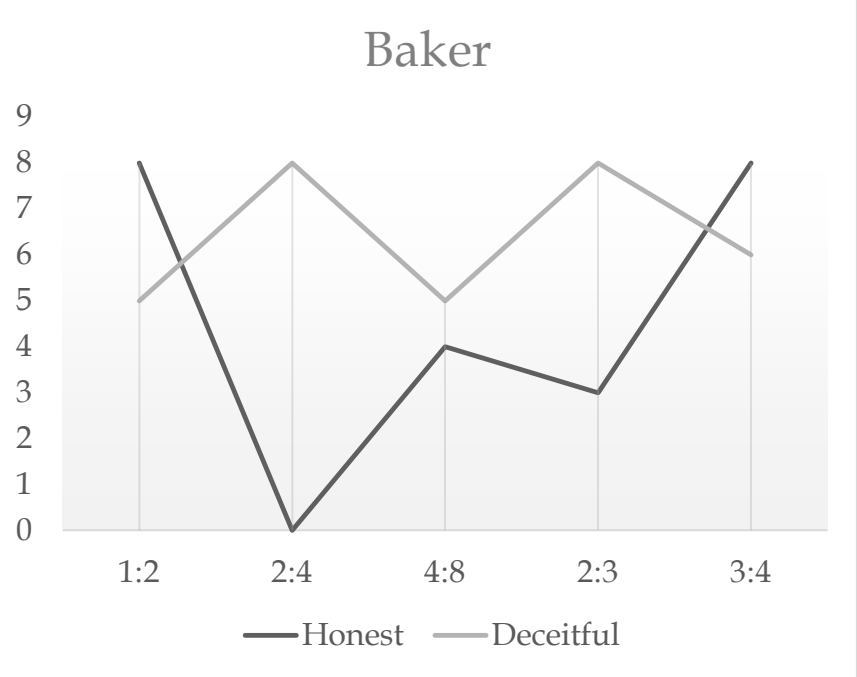


Figure A4. Baker's search time during honest and deceitful trials.

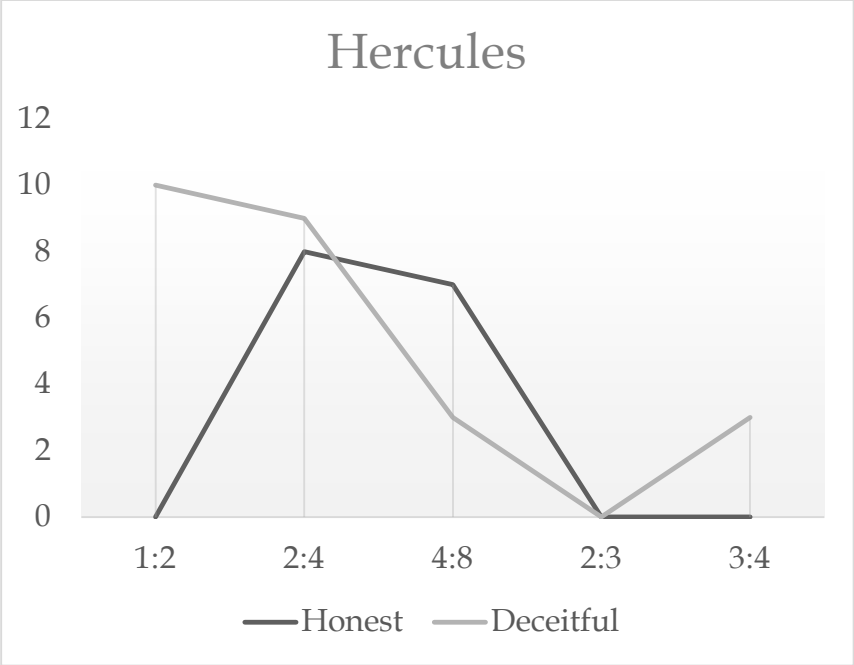


Figure A5. Hercules' search time during honest and deceitful trials.

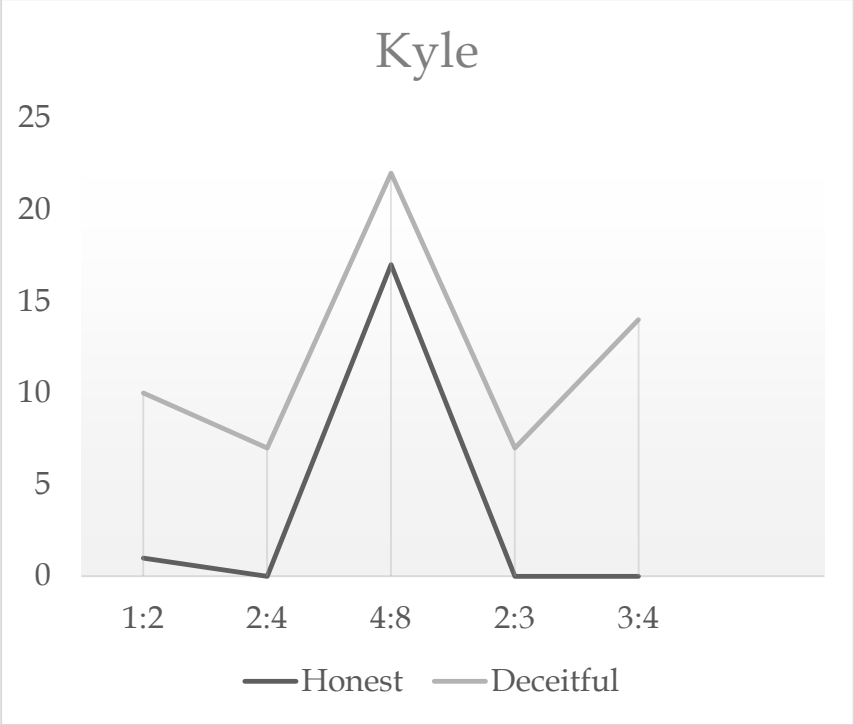


Figure A6. Kyle's search time during honest and deceitful trials.

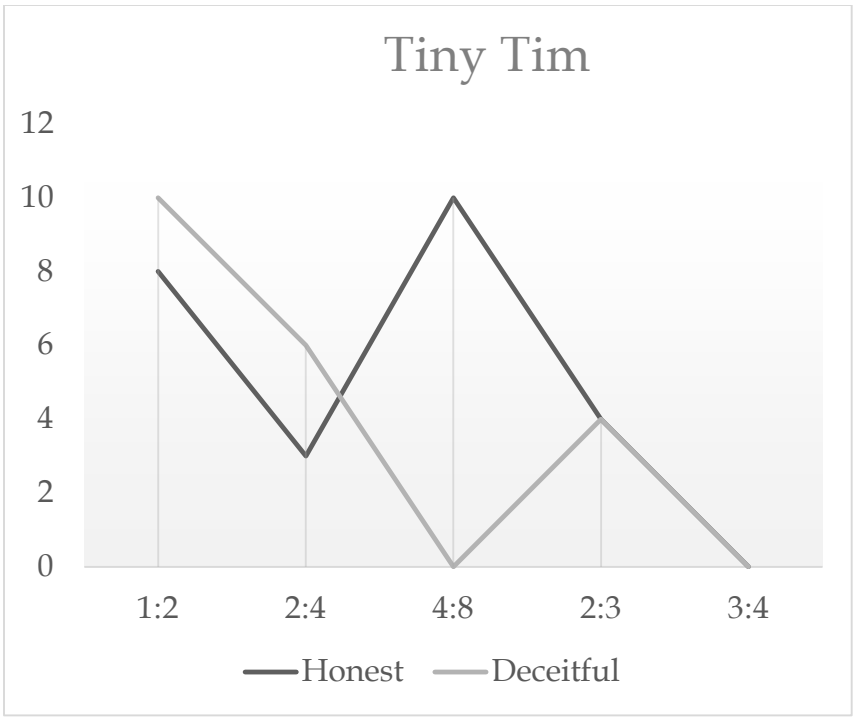


Figure A7. Tiny Tim's search time during honest and deceitful trials.

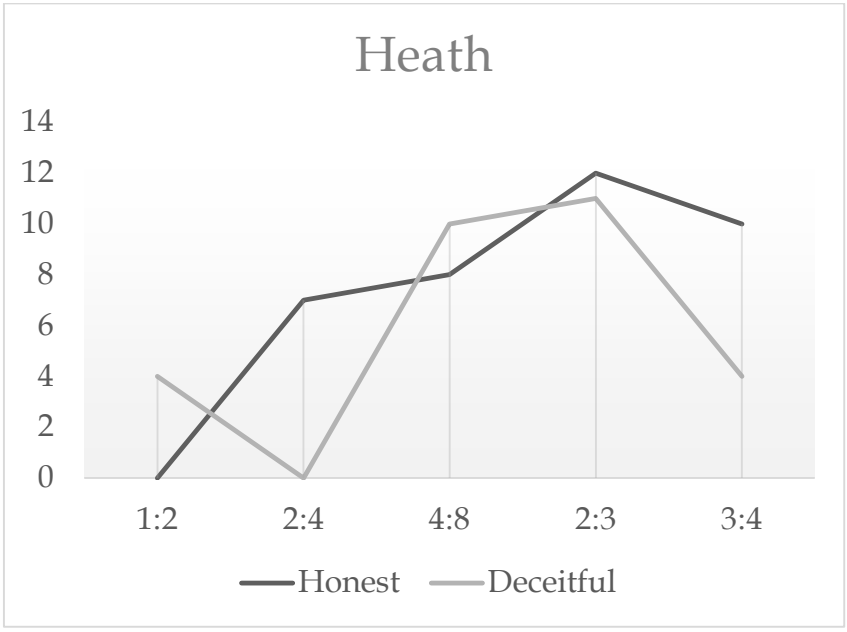


Figure A8. Heath's search time during honest and deceitful trials.

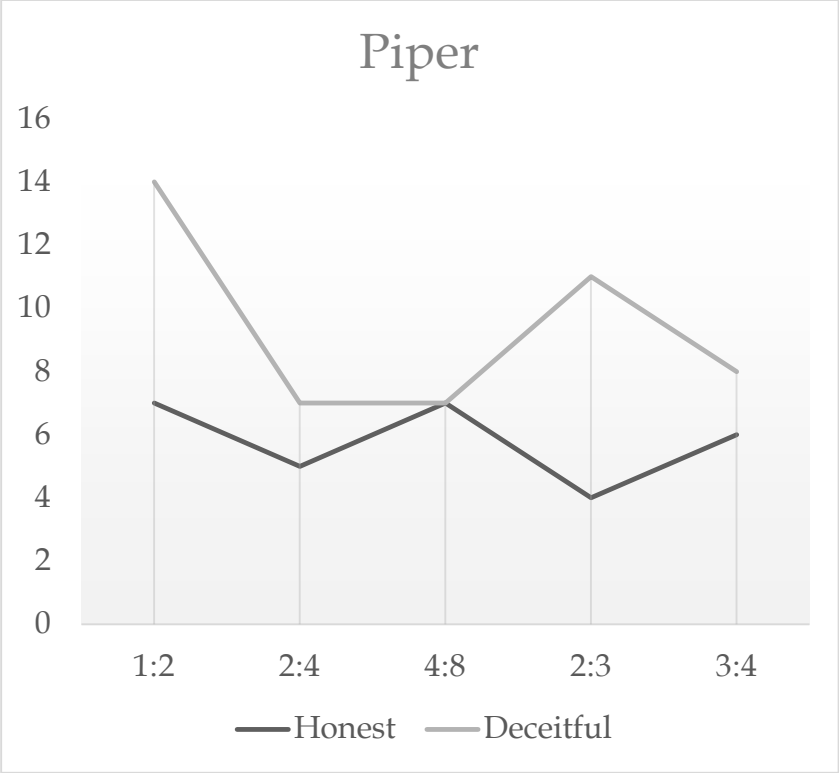


Figure A9. Piper's search time during honest and deceitful trials.

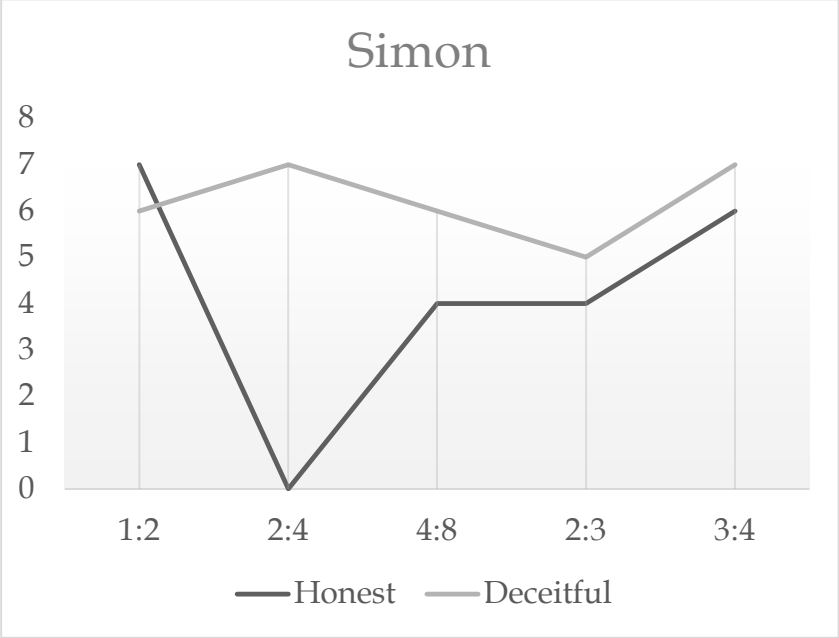


Figure A10. Simon's search time during honest and deceitful trials.

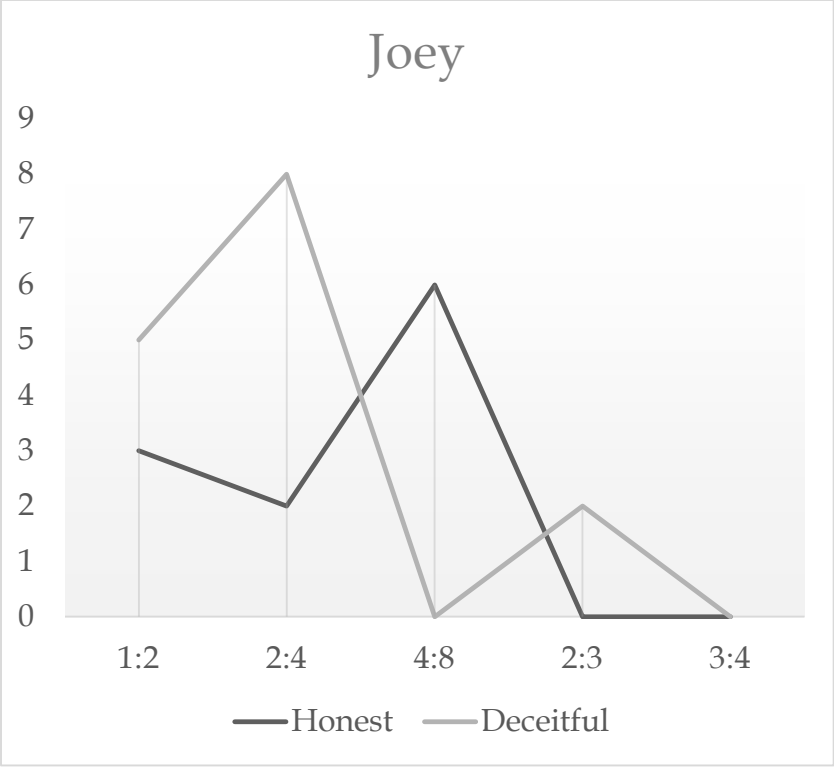


Figure A11. Joey's search time during honest and deceitful trials.

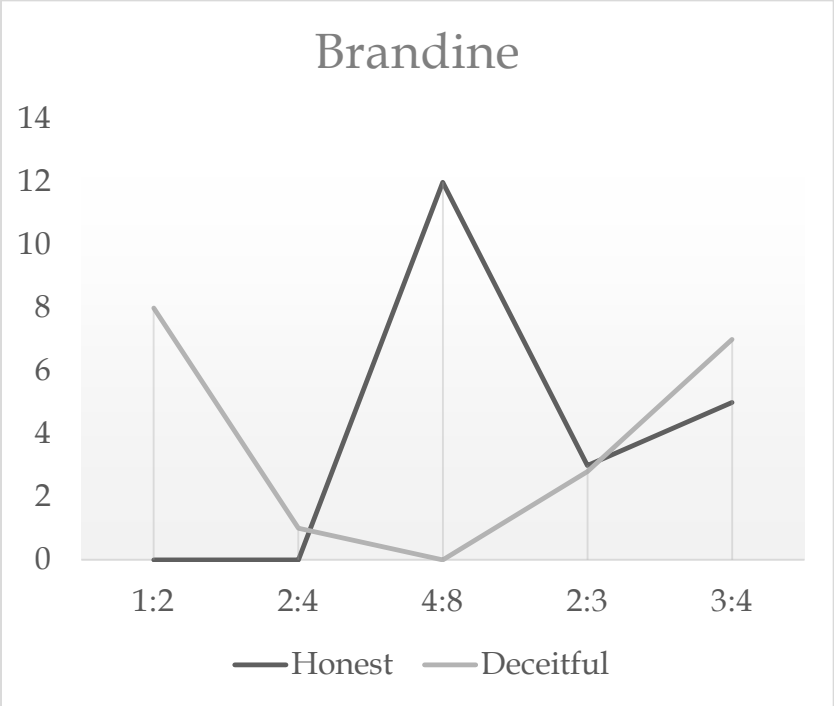


Figure A12. Brandine's search time during honest and deceitful trials.

APPENDIX B – Coding Sheet

Bushbaby: _____ Sex: _____ Age: _____ Coder: _____

Instructions: Code search time during the 30-second interval **following consumption of the last available raisin**.

- The numerator represents the number available for consumption to the bushbaby.
- The denominator represents the number placed in the pail by the experimenter.

Operational definitions:

- Searching- hands, head, and/or snout moving about inside the pail
- Orientation – head, eyes, and/or snout directed towards the raisins

1. Paired Trials: 1-1 versus 2-1 (1:2) Orientation (Y/N)

- 1/1 Honest_____ (Code after 1 raisin is consumed) _____
- 1/2 Deceitful_____(Code after 1 raisin is consumed) _____

2. Paired Trials: 2-2 versus 4-2 (2:4)

- 2/2 Honest_____(Code after 2 raisins are consumed) _____
- 2/4 Deceitful_____(Code after 2 raisins are consumed) _____

3. Paired Trials: 4-4 versus 8-4 (4:8)

- 4/4 Honest_____(Code after 4 raisins are consumed) _____
- 4/8 Deceitful_____(Code after 4 raisins are consumed) _____

4. Paired Trials: 2-2 versus 3-2 (2:3)

- 2/2 Honest_____(Code after 2 raisins are consumed) _____
- 2/3 Deceitful_____(Code after 2 raisins are consumed) _____

5. Paired Trials: 3-3 versus 4-3 (3:4)

- 3/3 Honest_____(Code after 3 raisins are consumed) _____
- 3/4 Deceitful_____(Code after 3 raisins are consumed) _____

APPENDIX C– IACUC Approval Letter

THE UNIVERSITY OF
SOUTHERN MISSISSIPPI

INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE

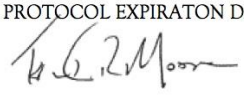
118 College Drive #5116 | Hattiesburg, MS 39406-0001
Phone: 601.266.6791 | Fax: 601.266.4377 | iacuc@usm.edu | www.usm.edu/iacuc

NOTICE OF COMMITTEE ACTION

The proposal noted below was reviewed and approved by The University of Southern Mississippi Institutional Animal Care and Use Committee (IACUC) in accordance with regulations by the United States Department of Agriculture and the Public Health Service Office of Laboratory Animal Welfare. The project expiration date is noted below. If for some reason the project is not completed by the end of the approval period, your protocol must be reactivated (a new protocol must be submitted and approved) before further work involving the use of animals can be done.

Any significant changes should be brought to the attention of the committee at the earliest possible time. If you should have any questions, please contact me.

PROTOCOL NUMBER:	**15081301**
PROJECT TITLE:	**Number Representation in the Small-Eared Bushbaby**
PROPOSED PROJECT DATES:	**08/2015 – 09/2017**
PROJECT TYPE:	**New**
PRINCIPAL INVESTIGATOR(S):	**Katie Smith**
DEPARTMENT:	**Anthropology & Sociology**
FUNDING AGENCY/SPONSOR:	**N/A**
IACUC COMMITTEE ACTION:	**Full Committee Approval**
PROTOCOL EXPIRATON DATE:	**September 30, 2017**



08/20/2015

Frank Moore, PhD
IACUC Chair

Date

REFERENCES

Agrillo, C., Dadda, M., & Bisazza, A. (2007). Quantity discrimination in female mosquitofish. *Animal Cognition, 10*, 63-70.

Bearder, S. K., & Doyle, G. A. (1974). Ecology of bushbabies, *G. senegalensis* and *G. crassicaudatus*, with some notes about their behavior in the field. R. D. Martin, G.

Beran, M. J., Smith, D. J., Redford, J., & Washburn, D. (2006). Rhesus macaques (*Macaca mulatta*) monitor uncertainty during numerosity judgments. *Journal of Experimental Psychology, 32*(2), 111-119.

Brannon, E. M. (2006). The representation of numerical magnitude. *Current Opinion in Neurobiology, 16*(2), 222-229.

Brannon, E. M., & Roitman, J. D. (2003). Nonverbal representation of time and number in animals and human infants. In W. H. Meck (Ed.), *Functional and neural mechanisms of interval timing* (143-182). Boca Raton, FL: CRC Press.

Charles-Dominique, P. (1978). Solitary and gregarious prosimians: Evolution of social structures in primates. In D. J. Chivers and K. A. Joysey (Ed.*), Recent advances in primatology* (139-149). New York, NY: Academic Press.

Coolidge, F. L. & Overmann, K. A. (2012). Numerosity, abstraction, and the emergence of symbolic thinking. *Current Anthropology, 53*(2), 204-225.

Curtis, D. J. (2003). Diet and nutrition in wild mongoose lemurs (*Eulemur mongoz*) and their implications for the evolution of female dominance and small group size in lemurs. *American Journal of Physical Anthropology, 124*(3), 234-247.

Dehaene, S. (1997). *The number sense: How the mind creates mathematics.* New York, NY: Oxford University Press.

Doyle, A., & Walker, A. C. (Eds.). *Prosimian biology* (109-130). London, UK: Duckworth Press.

Emmerton, J. (2001). Birds' judgments of number and quantity. R. G. Cook (Ed.), *Avian visual cognition* [On-line]. Available: www.pigeon.psy.tufts.edu/avc/emmerton/

Feigenson, L., Carey, S., & Hauser, M. (2002). The representations underlying infants' choice of more: Object files versus analog magnitudes. *Psychological Science, 13*(2), 150-156.

Feigenson, L., & Carey, S. (2003). Tracking individuals via object-files: Evidence from infants' manual search. *Developmental Science, 6*(5), 568-584.

Gallistel, C. R. (1990). *The organization of learning.* Cambridge, MA: Bradford Books/MIT Press.

Hauser, M. (2001). *Wild Minds: What Animals Really Think*. New York, NY: Henry Holt and Company.

Hauser, M. D., MacNeilage, P., & Ware, M. (1996). Numerical representation in primates. *Proceedings of the. National Academy of Sciences of the United States of America, 93*, 1514-1517.

Hauser, M. D., Carey, S., & Hauser, L. B. (2000). Spontaneous number representation in semi-free-ranging rhesus monkeys. *Proceedings of the Royal Society Biological Sciences, 267*, 829-833.

Jones, S. M., Pearson, J., DeWind, N. K., Paulsen, D., Tenekedjieva, A., & Brannon, E. (2014). Lemurs and macaques show similar numerical sensitivity. *Animal Cognition, 17*(3), 503-15.

Jones, S. M., & Brannon, E. M. (2012). Prosimian primates show ratio dependence in spontaneous quantity discriminations. *Frontiers in Psychology, 3*(550), 1-8.

Krumhansl, C. L. (1995). Music psychology and music theory: Problems and prospects, *Music Theory Spectrum, 17*(1), 53-80.

Le Floch-Prigent, P. (2008). The Vitruvian Man: an anatomical drawing for proportions by Leonardo Da Vinci. *Morphologie: Bulletin de L'Association des Anatomistes*. *92*(299), 204-209.

Lewis, K. P., Jaffe, S., & Brannon, E. M. (2005). Analog number representations in mongoose lemurs (*Eulemur mongoz*): evidence from a search task. *Animal Cognition, 8*, 247-252.

MacLean, E L., Barrickman, N. L., Johnson, E M., & Wall, C. E. (2009). Sociality, ecology, and relative brain size in lemurs. *Journal of Human Evolution, 56*, 471-478.

Masters, J. C., Lumsden, W. H. R., & Young, D. A. (1988). Reproductive and dietary parameters in wild greater galago populations. *International Journal of Primatology, 9*, 573-592.

Merritt, D., MacLean, E., Crawford, J. C., & Brannon, E. M. (2011). Numerical rule-learning in ring-tailed lemurs (*Lemur catta*). *Frontiers in Psychology, 2*(23).

Milliken, G. W., Stafford, D. K., Dodson, D. L., Pinger, C. D., & Ward, J. P. (1991). Analyses of feeding lateralization in the small-eared bushbaby (*Otolemur garnettii*): A comparison with the ring-tailed lemur (*Lemur catta*). *Journal of Comparative Psychology, 105*(3), 274-283.

Murofush, K. (1997). Numerical matching behavior by a chimpanzee (Pan troglodytes):

Subitizing and analogue magnitude estimation. *Japanese Psychological Research, 39*(3), 140-153.

Nash, L. T., Bearder, S. K., & Olson, T. R. (1989). Synopsis of galago species characteristics. *International Journal of Primatology, 10*(1), 57-80.

Nash, L. T. & Harcourt, C. S. (1986). Social organisation of galagos in Kenyan coastal forest: II. Galago garnettii. *American Journal of Primatology, 10*(4), 357-369.

Olson, T. R. (1979). *Studies on Aspects of the Morphology and Systematics of the Genus "Otolemur Coquerel", 1859 (Primates: Galagidae)* (Doctoral Dissertation, Faculty of Medicine, University of London, Department of Anatomy, St. Thomas's Hospital Medical School).

Radinsky, L. (1974). Prosimian brain morphology: Functional and phylogenetic implications. In R. D. Martin, G. A. Doyle, & A. C. Walker (Eds.), *Prosimian biology* (781-798). London, UK: Duckworth Press.

Reeder, S. L. (2007). Are We Golden? Investigations with the Golden Ratio. *Mathematics Teaching in the Middle School, 13*(3), 150–155. Retrieved from http://www.jstor.org.lynx.lib.usm.edu/stable/41182515

Santos, L. R., Barnes, J. L., & Mahajan, N. (2005). Expectations about numerical events in four lemur species (Eulemur fulvus, Eulemur mongoz, Lemur catta, and Varecia rubra). *Animal Cognition, 8*(4), 253-62.

Tomasello, M. & Call, J. (1997). *Primate Cognition*. New York, NY: Oxford University Press.

Uller, C., Jaeger, R., Guidry, G., & Martin, C. (2003). Salamanders (*Pletahodon cinereus*) go for more: rudiments of number in an amphibian. *Animal Cognition, 6*(2), 105-112.

Vallortigara, G. (2015). *Foundations of number and space representations in non-human species*. D. C. Geary, D. B. Berch, & K. M. Koepke (Ed.). New York, NY: Elsevier Inc.

Ward, J. P. (1995). Laterality in African and Malagasy prosimians. L. Alterman, G. A. Doyle, & M. K. Izard (1st ed.). *Creatures of the dark: The nocturnal prosimians* (293-307). New York, NY: Plenum Press.

Wier, S. K. (1996). Insight from Geometry and Physics into the Construction of Egyptian Old Kingdom Pyramids. *Cambridge Archaeological Journal, 6*, 150-163.

Yoder, A. D., Chan, L. M., dos Reis, M., Larsen, P. A., Campbell, C. R., Rasoloarison, R., Barrett, M., Roos, C., Kappeler, P. Bielawski, J., & Yang, Z. (2013). Molecular evolutionary characterization of a V1R subfamily unique to strepsirrhine primates. *Genome Biology and Evolution, 6*(1), 213-227.