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Systems of Quantity Judgment in Various Species: A Meta-Analysis

Tiffany A. Woodard Baker
University of Southern Mississippi

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SYSTEMS OF QUANTITY JUDGMENT IN VARIOUS SPECIES: A META-ANALYSIS

by

Tiffany Alycia Woodard Baker

A Dissertation
Submitted to the Graduate School,
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Approved by:

Tammy Greer, Committee Chair
Alen Hajnal
Elena Stepanova
Lawrence Patihis

_____   _____   _____
Dr. Tammy Greer   Dr. D. Joe Olmi   Dr. Karen S. Coats
Committee Chair   Department Chair   Dean of the Graduate School

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ABSTRACT

An abundance of behavioral and neuroimaging literature supports the presence of two cognitive systems for quantity judgments (Agrillo & Bisazza, 2014). In particular, small quantities are thought to be guided by the object-file system, a precise system that uses mental files to map onto real world objects, and large quantities by the approximate number system, an imprecise, estimation system (Dehaene, 1997). Evidence supporting both systems exists in a variety of species including nonhuman primates (Boysen & Hallberg, 2000), birds (Garland, Low, & Burns, 2012), amphibians (Uller, Jaeger, Guidry, & Martin, 2003), and fish (Agrillo, Dadda, Serena, Bisazza, 2009), but support may depend on species and on method of assessment. The purpose of this meta-analysis was to examine differences in the extent of support for object-file versus the approximate number systems, to determine whether type of task affects quantity judgment, and to delineate species differences in abilities to distinguish quantities. Results revealed some success in both large and small set sizes and in both large and small ratio manipulation categories and supported the use of both the approximate number system and the object file system across species. Moderator analyses revealed no effect of the type of task on the proportion of correct judgments during quantity discrimination tasks. Findings support the overall hypothesis that there is not one single quantity judgment system, but rather there is a combination of the approximate number and object file systems plus a role of experience with the environment. Species differences are discussed.

ACKNOWLEDGMENTS

DEDICATION

For the countless hours by my side, I dedicate this dissertation to Kylie Baker.

Thank you for always being positive and never complaining. You truly have been a

dedicated partner invested in my success throughout this endeavor. I will forever be

grateful. Thank you.

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CHAPTER I - INTRODUCTION

Preverbal and verbal humans as well as nonhuman animals possess a sense of number, or an "intuition" for numbers independent of counting (Dehaene, 1997; Feigenson, Dehaene, & Spelke, 2004; Parish & Beran, 2017). Number sense systems afford the ability to perform the most basic mathematical operations such as simple arithmetic, judging the numerosity of a set, and quantity discrimination, without any formal education, culture, or language. These abilities vary by individual and have been shown to predict mathematical performance in human children (Aunio & Niemivirta, 2010; Mazzocco, Feigenson, & Halberda, 2011). The current meta-analysis will compare evidence for two number sense systems involved in quantity judgments.

Historical Developments in Research Regarding Quantity Discrimination

The study of number sense and, in particular, quantity discrimination dates back as early as the late 19th century (Jevons, 1871). In 1871, W. Stanley Jevons, an economist and logician, published "The Power of Numerical Discrimination" in *Nature*. Participating as his own subject across 1,027 trials, Jevons estimated the count of similar sized black beans tossed on a plain, white surface. He argued that, for most people, perfect discrimination does not occur beyond the limit of five objects (Jevons, 1871), providing initial evidence for a distinction between large and small number discriminations as well as inherent large number restrictions during quantity judgments.

Francis Galton (1880) compared many personal accounts of how individuals visualize number. He determined that everyone viewed numbers relative to the position on a mental number line most often visualized from left to right. Vallortigara (2012) later hypothesized that this may be due to a phenomenon called *pseudoneglect*, a tendency to

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attend to objects located on the left hemispace, potentially resulting in a bias to process numerical information from left to right. In addition, Galton noted that, for the individuals involved in his study, smaller numbers on the mental number line were a lot clearer and more distinct than larger numbers, allowing easier differentiation while mentally comparing quantities of smaller numbers as opposed to larger numbers (Galton, 1880). For example, it is much easier to visualize the difference between numbers one and ten than between numbers 100 and 110.

Kinnaman (1902) explored numerical cognition using the first primate model. His attempts were to perform the first of what he referred to as "rigorous examinations of the number notions of lower animals" (i.e. relative to humans, p.173). Two captive rhesus monkeys (*Macaca mulatta*), one male participating 2,700 times and one female participating 1,260 times, were compared to two human children, a three-year old and a five-year old tested a combined total of 140 times. Kinnaman (1902) simultaneously presented twenty-one bottles covered with paper to conceal the inside of the bottles. Subjects were to select the food bottle among the series of twenty-one bottles. This bottle remained in the same position across thirty trials, and then switched to a different position for the subsequent thirty trials, and so on. Results suggested that monkeys had difficulty selecting the correct food bottles placed in positions higher than six in the series. However, previous experience with the food bottle when located at positions one through six may account for the results as those positions were tested first, although not in any particular order. The male rhesus monkey chose the food bottle only if it was in positions one through six. The female rhesus monkey, on the other hand, chose the food bottle only if it was in positions one through three. Comparable to the female monkey,

the five-year old child chose the correct bottle when it was in positions one through three, and the three-year old child chose the correct bottle only in the first and second positions. Kinnaman (1902) believed that the cognitive processes used by monkeys and children during correct bottle judgments were independent of numeration (i.e., counting). Instead he claimed judgments were based upon a process that allowed for discrimination between a greater or lesser quantity. For further explanation, Kinnaman (1902) referred to Lloyd Morgan's *An Introduction to Comparative Psychology* (1894). In his textbook, Morgan (1894) hypothesizes that:

> the raw materials of numerical relations, as of those of space and time, are given in our daily experience, and are marginally sensed long before they are focally perceived. The child, long before he can count, senses the difference between one thing and two things, between two and three, between three and several, between several and many. (p.232)

Behaviorism and Quantity Discrimination Research

Research started shifting forms as a new school of thought, known as behaviorism, slowly started to dominate partly in response to John B. Watson's "Psychology as the behaviorist view it" published in *Psychological review* in 1913. Before behaviorism could reach its height in the 1950s and 1960s, a mathematician named T. Dantzig proposed a philosophy similar to that of Morgan (1894) and Kinnaman (1902). In his book concerning the evolution of number, Dantzig (1954) first gave *Number Sense* a more solidified definition as a "faculty permitting recognition of a change in a small collection when, without direct knowledge, an object was added or removed from the group" (p. 1). Although he did not investigate his hypotheses

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empirically, Dantzig argued that nonhuman animals and human infants both possess a sense of number, independent from counting. This sense of number affords quantity discrimination via a perceptual system that allows for the persistence of objects over time during visual encounters. Dantzig believed it was this system that allowed for accuracy during small quantity judgments rather than knowledge of quantitative information (Dantzig, 1954). This system was later termed the object-file system by Treisman & Kahneman (1992).

Behaviorism dominated the scientific mindset during the 1950s and 1960s. It occurred as a rebellion against prevailing structuralist and functionalist schools of thought that centered around the use of introspection, a methodology involving the reporting of current experiences by trained individuals with introspective reports being the foci of scientific investigation. In contrast, behaviorism advocated for behavior as the foci of investigation. As such, the investigation of mental acts was prohibited and only observable behavior was of interest. Introspection, therefore, became an unacceptable methodology. Experimental psychologists such as John B. Watson, the father of behaviorism, argued that it was only in this manner that psychology could be an objective science akin to biology and physics (Miller, 2003).

The shift in zeitgeist posed difficulties for research surrounding a number sense. In addition, behaviorism brought a new language restricting words that indicated "use of mental acts such as perception, memory, or language replacing them with behavior-centric terms like discrimination, language, and verbal behavior" (Miller, 2003, p. 141). Nevertheless, a few animal psychologists, during the 1950s and 1960s, developed new experimental paradigms that conformed to current behavioristic standards by

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investigating behavioral response characteristics during numerical tasks. For example, Mechner (1958) first attempted to identify the number of responses that should be used as a criterion for an effective discriminative stimulus. Mechner (1958) required rats to press a right-lever a certain number of times (N) before receiving a reward after a left-lever response. Using the formula $p(R_{Tn}$ given $R_N)$ to determine the function whereas p = the probability that the run will be terminated, R_{Tn} = left-lever response, and R_N = the Nth response in a run, Mechner (1958) determined that the probability of a rat making a left-lever response as a function of the number of responses on the right-lever was fairly symmetrical on a linear scale with a maximum probability near the criterion N. In addition, as the value of N increased, the variability of the distribution also increased. However, time responding on the right-lever could have been the discriminative stimuli instead of number of right-lever responses, since time responding and N was positively correlated. Mechner and Guevrekian (1962) showed that water deprivation increased the rate of responding but did not change the function relating the probability of a left-lever response to the number of right lever responses. Moreover, Laties (1972) duplicated these results when rats were administered methamphetamine and found that the rate of responding increased but the probability function was unaltered.

The Cognitive Revolution and Quantity Discrimination Research

Acceptance of theoretical models that emphasized explanations including cognitive processes along with its behavioral counterpart emerged. The Cognitive Revolution, a quiet movement that became apparent in the mid-1950s, emphasized interdisciplinary studies and, thus, Cognitive Science was born in 1956 (Miller, 2003). Cognitive scientists represent a variety of disciplines including, but not limited to,

psychology, biology, and computer science. Today, number sense research and abilities including quantity discrimination are studied by a variety of scientists from diverse backgrounds including comparative cognition, developmental psychology, cognitive psychology, psychophysics, computer science, and neuroscience (Feigenson, Dehaene, & Spelke, 2004).

Psychologists Moyer & Landauer (1967) asked what type of process, either perceptual or cognitive, underlies what they called numerical inequality judgments. To examine the type of process, Moyer and Landauer (1967) measured time required for judging the larger of two single digit numerals (1-9) for ten female undergraduates at Stanford University. Participants were to respond correctly as quickly as possible. If a cognitive process such as counting was responsible for accuracy when making inequality judgments, the authors expected larger distances to require longer reaction times. However, Moyer & Landauer (1967) discovered reaction time was significantly shorter when the distance between two numerals was large. Moreover, ratio was more important during inequality judgments than the absolute difference between the two numerals. The authors concluded that a "reasonable fit" (p. 1520) would be to apply the common interpretation for discrimination reaction times to that of physical quantities (i.e., pitch of tone and length of line; Moyer & Landauer, 1967). After the stimulus numerals are cognitively transformed to a mental magnitude, a comparison is completed between those mental magnitudes. Moyer & Landauer (1967) applied Welford's (1960) proposed formula for product-moment correlation in such situations: $RT = K \log$ (larger/larger-smaller). The formula yielded a product-moment correlation of 0.75, and as the authors expected, mimicked that of other of physical quantities supporting the mental magnitude

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theory. Not only is this important because Moyer & Landauer (1967) laid initial groundwork pertaining to the importance of the ratio between two quantities during judgments as opposed to the absolute difference, but they also made contributions to a future theory now known as the approximate number theory, also referred to as the analog magnitude theory.

Research regarding number sense abilities flourished in the 1980s (Boysen & Capaldi, 1993), and empirical topics explored number as a core system. Meck and Church (1983), Church and Broadbent (1990), Dehaene and Changeux (1993) first attempted to characterize aspects of core number systems responsible for the ability successfully distinguish between quantities. From these studies three common principles emerged. First, number representation imprecision is positively correlated with cardinal value (Spelke & Kinzler, 2007). Second, information about quantity can be received through any sensory input (Spelke & Kinzler, 2007). For example, adult female lions (*Panthera leo*) faced with audio recordings of distant lions, a potential territorial threat were more likely to approach the sound of one lion than three lions. If the lions did choose to approach, a more cautious approach was employed (McComb, Packer, & Pusey, 1994). Third, comparisons and simple arithmetic operations such as addition and subtraction are available through a core number system (Spelke & Kinzler, 2007). Uller et al. (2001) suggested that cotton-top tamarins (*Saguinus oedipus*) used addition and subtraction rules when viewing 1+1 events with consistent (1+1 = 2) and inconsistent outcomes (1+1=1, 3, or 1 large). Monkeys demonstrated longer looking times during the inconsistent outcomes of 1, 3, or 1 large, as opposed to the consistent outcome of 2 demonstrating the cotton-top tamarins did recognize simple addition rules.

Culture, Language, and Number Sense

The presence of core number systems suggests that number sense should be available regardless of culture (Spelke & Kinzler, 2007) or language (Gordon, 2004; Starkey, Spelke, & Gelman, 1990). To address the effect of culture and language, researchers have investigated number sense abilities in remote tribes with few number words. For example, the language of the Pirahã, an Amazonian tribe, contains only words that translate to *one*, *two*, and *many*. The Pirahã consists of approximately 200 hunters and gatherers living across small villages of ten to twenty people. Experimenters asked Pirahã individuals to match items into a one-to-one correspondence while there were time constraints. Participants performed well up to a set-size of three items, after which performance dropped significantly (Gordon, 2004).

The language of Mundurukú contains exact words for numbers up to five. After five, individuals show no consistency when describing quantity using various words that translate into *some*, *many*, or *small quantity*, as well as *more than one hand*, *two hands*, and *some toes*. This language is spoken by the Tupi family, consisting of about 7,000 people living in an autonomous territory in the Pará state of Brazil. When Tupis were presented with two sets of 20 to 80 dots, with density, space and size controlled, and were asked to point to the set containing more, they did so consistently above chance in all groups (minimum was 70.5% correct in the youngest group). In fact, Tupis performed similar to their French counterparts during varying ratios. Response times were faster for numbers with larger differences for both sets of participants. Results from number discrimination tasks indicate that the Piraha and Tupis can discriminate with quantities

far beyond the range for which they have number words supports the presence of a core number system that is independent of culture and language.

Neurological Correlates of Quantity Discrimination

Gallistel (1990) proposed that "evolutionary pressures must have led to the internalization of numerical representations in the brain of various animal species". In fact, during quantity judgments, neuroscientists uncovered activation of both the parietal cortex as well as the subcortex, an evolutionarily older brain structure, in human and nonhuman animals (Bueti & Walsh, 2009; Collins, Park, & Behrmann, 2017; Dehaene, 1993; Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004). The parietal cortex is involved during visuomotor activities such as eye movements, reaching and grasping, processing action-related information such as object shape and orientation regardless of whether or not an action is performed (Culham & Valyear, 2006) and the perception of magnitudes such as time and space (Bueti & Walsh, 2009). Collins et al. (2007) hypothesized that perception of magnitude is responsible for judgments during more versus less tasks independent of counting or the use numerical symbols. Furthermore, the authors propose that this magnitude perception makes up the rudiments of mathematical thinking.

The dawn of neuroscience provided much needed technological advancements leading to novel opportunities for studying the neural correlates of quantity judgments using different neuroscience methods, eventually providing convergent evidence involving the parietal cortex during number cognition (Dehaene, Piazza, Pinel, & Cohen, 2003). Roland and Friberg (1985) uncovered parietal and frontal region metabolism increases during mathematical thinking using single photon emissions. To date,

activation of the parietal cortex has been replicated across different neuroimaging techniques (fMRI, Burbaud, et al., 1999; Rueckert et al., 1996; PET, Dehaene et al., 1996; Pesenti, Thioux, Seron, & De Volder, 2000; Zago et al., 2001). Typical experiments investigating the activation of the parietal cortex involve the presentation of arrays during numerical tasks such as a same-different task. During presentations, human or nonhuman participants, show activation in the parietal cortex supporting species continuity of the involvement of the parietal cortex (Piazza et al., 2004).

Involvement of the subcortex during quantity judgments was recently identified using a "psychophysical method" that capitalizes on monocular visual signals. During a typical experiment, human adults judged quantities of two images of dot arrays presented sequentially. During some trials, the images were presented monocularly, while other trials the images were presented dichoptically. If the subcortex was activated during quantity judgments, then participants were expected to perform better during monocular presentations as incoming visual information reaches the same subcortical structure during monocular presentations only. Results indicated activation of the subcortex when discriminating quantities in larger (4:1 or 3:1) ratios, but no activation when discriminating smaller ratios. Given the evolutionarily ancient subcortex and its presence across the animal kingdom, Collins et al. (2017) speculated that "core number knowledge that is both related to phylogenetic numerical competence and serves as the foundation on which more complex ontogenetic numerical skills may be built" is housed within the subcortex (p. 2806). Research of the subcortex in other animal species will shed light to the full involvement of the subcortex.

Interspecific Number Sense

Human numerical abilities are unique in that numbers are represented symbolically and, generally, used to compute complex mathematical equations. These abilities are attributed to the development of uniquely human language and culture (Dehaene, 1997; Feigenson et al. 2004). Evidence exists, however, that humans along with nonhuman species, possess a sense of number that does not require learning, allows for the discrimination of quantities and provides access to simple arithmetic skills (Agrillo & Bisazza, 2014).

Advantages of Number Sense

What Dantzig termed *Number Sense* has now been defined several different ways but "reputedly constitutes an awareness, intuition, recognition, knowledge, skill, ability, desire, feel, expectation, process, conceptual structure, or a mental number line" (Berch, 2005, p. 333). The possession of a number sense is advantageous and plays a major role when discriminating between two sets of quantities. A sense of number also aids in the navigation of the world (Piazza & Dehaene, 2004). For example, correct quantity judgments maximize potential while foraging (Emmerton, 2001), maximize survivability in anti-predator behaviors (Gomez-Laplaza & Gerlai, 2011) and in fight or flee decisions (Hauser, 2001). It even maximizes efficiency when deciding which check-out line at the supermarket is shorter. Acknowledgement of these advantages that a sense of number may proffer has led researchers to ask if different species share mechanisms that allow for quantity judgments, and if, in a rudimentary sense, human and nonhuman animals discriminate quantities following the same patterns (Butterworth, 1999; Dehaene, 1997; Piazza & Dehaene, 2004).

Phylogenetic Groups

Currently, an abundance of behavioral and neuroimaging literature supports the involvement of at least two cognitive number sense systems allowing for quantity discrimination (Agrillo & Bisazza, 2014; Feigenson et al., 2004) in eight broad phylogenetic groups in Kingdom Animalia (see Figure 1) including human (Lipton & Spelke, 2003) and nonhuman primates (Boysen & Hallberg, 2000), birds (Garland, Low, & Burns, 2012), amphibians (Uller, Jaeger, Guidry, & Martin, 2003, and fish (Agrillo, Dadda, Serena, Bisazza, 2009).
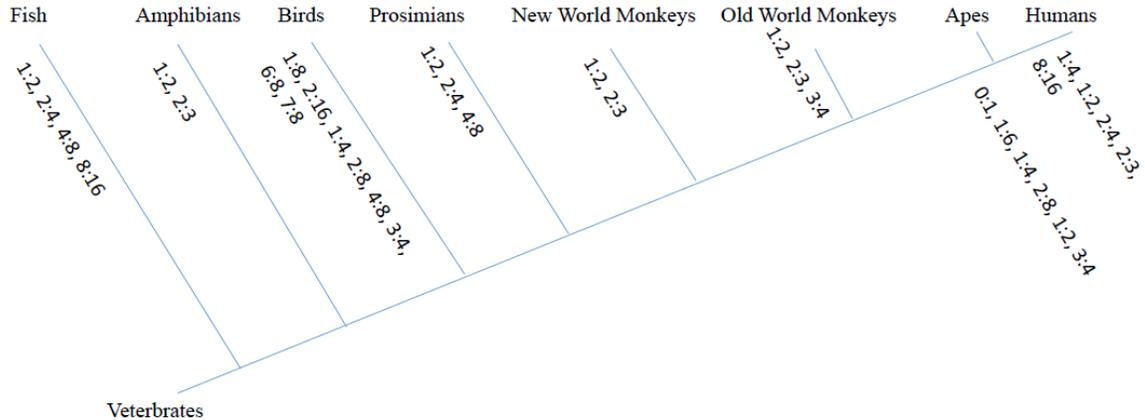
Figure 1. Eight broad phylogenetic groups in Kingdom Animalia used in quantity judgment experiments.

Note: Phylogenetic groups are ordered by their approximate first appearance on Earth. Ratios listed have been tested and have some support.

Object-File System

Regarding the object-file system, object-files are considered perceptual tools that aid in the understanding and navigation of the environment, and are updated constantly according to changes such as those in quantity (Green & Quilty-Dunn, 2016). For discrete quantity judgments, object-files are assigned to each object within a set such that there is a one-to-one correspondence between each mental file and a tangible object.

These mental files are then compared to determine differences such as which set contains more or less (Feigenson & Carey, 2005). Because of the strenuous nature of the system, however, only a limited number of files can be deployed. This limitation, often occurring at a set size of four, has become known as the "set-size limitation" (Green & Quilty-Dunn, 2016; Halberda, Simons, & Wetherhold, 2004; Luck & Vogel, 1997; Uller et al., 2003). Experimenters integrate the set-size limitation into tests for number sense that behave in accordance with the object-file system. Researchers often expect performance that is accurate up to the set-size limitation, and then declines rapidly for any greater numbers. Subitizing, the "quick and accurate enumeration of numerosities 1-4" (Clements, 1999; Feigenson et al., 2004, p. 310), is also affected by the set-size limitation and has been proposed as further evidence for the object-file system (Trick & Pylyshyn, 1994). However, it is unknown if this system is employed when number is used symbolically (Cordes, Gelman, & Gallistel, 2001; Gallistel & Gelman, 2000; Hyde, 2011).

Empirical Investigation of the Object-File System

During tests of quantity judgments, the critical question for the object-file system is if subjects will discriminate between quantities of two sets containing up to about four objects each, and then fail with larger numerosities (Feigenson, Carey, & Hauser, 2002). To allow testing, stimuli is presented in varying ratios. In tests of non-human primates and other animals, subjects are expected to choose the set containing more items to maximize food intake (Agrillo & Bisazza, 2014; MacAuthor & Pianka, 1966; Pyke, Pulliam, & Charnov, 1977; Stephens & Krebs, 1986). During a choice task that allowed for the spontaneous choice between two quantities of apple slices, rhesus monkeys

(*Macaca mulatta*) have demonstrated the signature set-size limitation during trials that differed by 1:2, 2:3, and 3:4 ratio levels, but failed with 4:5, 4:6, 4:8, and 3:8 ratios (Hauser, Carey, & Hauser, 2000). A set size of three rather than four has been clearly demonstrated in infants using a habituation paradigm where 10- and 12-month-old infants reliably discriminated on trials that differed by 1:2 and 2:3 ratios, but not 3:4, 2:4 or 3:6, even though the last two ratios are highly favorable (Feigenson et al., 2002). A set-size limitation of three also has been replicated with 10- to 12-month old infants allowed to search for ping pong balls in an opaque box (Feigenson & Carey, 2003). Salamanders (*Plethodon cinereus*) performed the same as human infants, discriminating between the number of flies available for food consumption during presentations that differed by 1:2 and 2:3 ratios but not 3:4 or 4:6.

Approximate Number System

Number sense regarding large quantities differs from that regarding small quantities in that number abilities with large quantities are thought to rely on the approximate number system - an imprecise, estimation system. Quantities are thought to be represented by a "fluctuating mental magnitude, akin to a number line" (Feigenson et al., 2004, p. 308). Mathematicians have devised two distinct mathematical formulations of the number line with similar behavioral predictions (Figure 2).
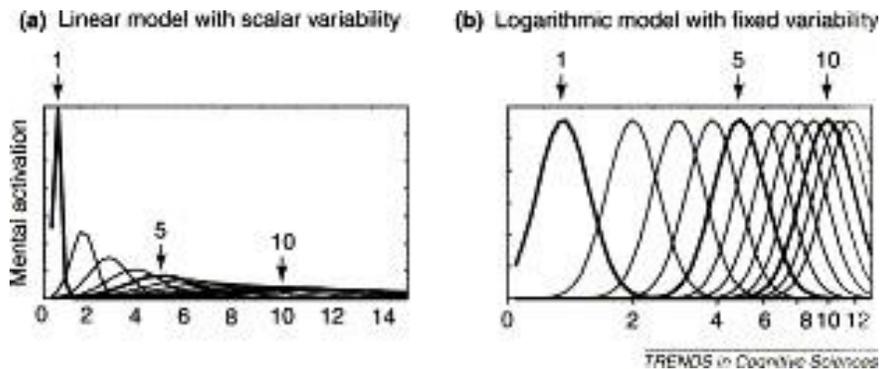
Figure 2. Two mathematical formulations of the number line.

Both models predict that the representation of larger numerosities overlap increasingly

with neighboring numerosities making the likelihood of confusing more similar

numerosities greater with larger numerosities than with smaller numerosities (Feigenson

et al., 2004). As a result, the approximate number system is ratio dependent, with

precision during quantity judgments for large numbers decreasing as the ratio approaches

one. Because the discrimination of quantities is ratio dependent, it is thought to be

modulated by Weber's Law, as this nonlinear law has well-established ratio effects.

According to Weber's Law, it is the ratio rather than the absolute difference between two

quantities that allows for the discrimination between two differing sets (Dehaene, 1997;

Feigenson et al., 2004; Feigenson & Carey, 2003; Gallistel, 1990; Jones et al., 2014;

Lewis, Jaffe, & Brannon, 2005).

Empirical Investigation of the Approximate Number System

The critical question when testing the approximate number system is whether or

not discrimination shows a ratio dependent pattern. Experimenters have demonstrated

that 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). Results are similar in human infants. Starr, Libertus, and Brannon (2013) found that 6-month old infants reliably discriminated numerosities differing by 1:2, 2:4, and 8:16 instead of exhibiting a limitation of size. Furthermore, reaction time and accuracy has been shown to be modulated by ratio in an addition task given to college students and monkeys (Cantlon & Brannon, 2007).

Experimental Procedures

"Although the specter of Clever Hans still looms within the field of comparative psychology, more rigorous and creative paradigms have been developed over past decades" (Boysen & Hallberg, 2000, p. 423-424). Quantity judgment experiments generally have been composed of three common sets of procedures: the simultaneous choice task, the sequential choice task, and the search task (Figure 3).

(a) Simultaneous choice task   (b) Sequential choice task

(c) Searching task
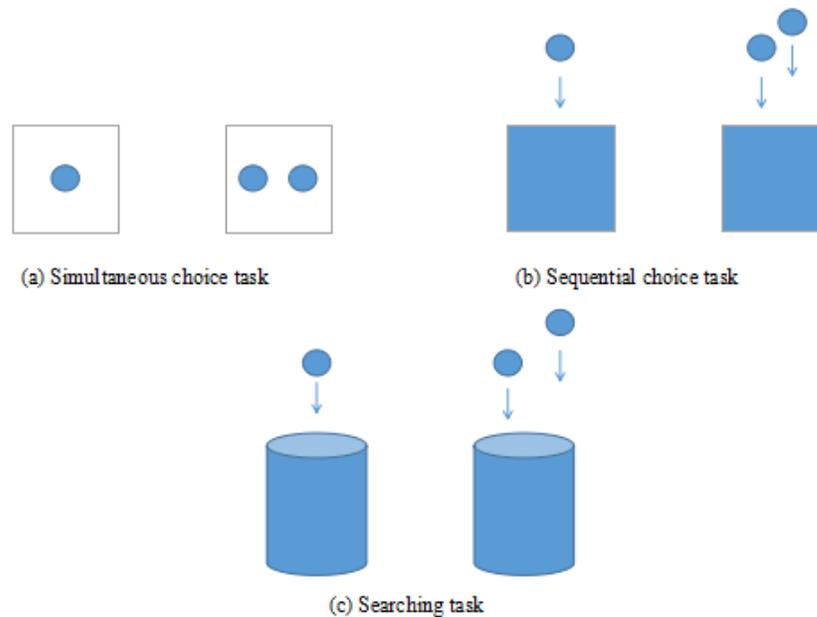
Figure 3. Three common procedures in quantity judgment experiments.

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Simultaneous Choice Task

The *simultaneous choice task* involves allowing subjects to make a spontaneous choice between two sets of objects when all items in the sets are in view simultaneously. However, presenting stimuli simultaneously requires careful control of other continuous cues (Agrillo, Petrazzini, Piffer, Dadda, & Bisazza, 2012). Instead of relying on the number of items, for instance, subjects could rely on the amount of space occupied by the object, confounding density with number of objects.

Sequential Choice Task

Second, the *sequential choice task* involves the presentation of stimuli sequentially to eliminate some continuous cues by avoiding the opportunity for a global view of the sets to be discriminated. Subjects must attend to each item individually and represent the set as the aggregate of items that comes sequentially into view. Next, the process must be repeated for the second set. Only then can subjects compare the two representations (Agrillo, Petrazzini, Piffer, Dadda, & Bisazza, 2012). The nature of this task, though, requires the careful control of the potentially confounding variable of time, as the more time it takes to present items, the more items the set may contain. In addition, tasks that require memory such as the sequential choice task may not properly engage the quantity discrimination system for human and nonhuman animals that do not have sophisticated visual short-term memory capabilities (Luria, Sessa, Gotler, Jolicoeur, & Dell'Acqua, 2009). For example, Geary (2003) demonstrated that children with mathematics disabilities score low on tests involving working memory.

Searching Task

A third common procedure is the *searching task* which, although first developed with infants (Feigenson & Carey, 2003), can be used to mimic natural foraging behaviors (Baker, 2016). Subjects watch as an experimenter successively places items inside an opaque pail containing shredded paper. On half of the trials, a subset of items is placed into a hidden compartment. Search time is measured during trials that allow for retrieval of all items (honest trials) and compared to trials where a subset of items remain hidden (deceitful trials). Subjects are expected to search longer on deceitful trials. However, much like the sequential choice task, searching tasks require subjects to attend to each individual item being placed in the pail, remember it as having been placed in the pail, aggregate future items to represent the whole set, and then discriminate expected versus observed quantities available for retrieval. The cognitive load is potentially large during searching tasks and may, similar to the sequential choice task, interfere with attention and discriminability for human and nonhuman animals with low working memory capacities (Downing, 2009).

Issues Regarding Procedures

Comparisons using the simultaneous and sequential choice tasks as well as searching tasks have led to mixed results regarding both the object-file and approximate number systems (Agrillo & Bisazza, 2014). Because procedures vary in demands, method of assessment may factor in the use of the object-file system, approximate number system, or the inability to access or use either system. Reinforcing the idea that differences in procedures may underlie the differences observed between species within the same broad phylogenetic group, Agrillo and colleagues (2008) have demonstrated identical results for both small and large quantity judgments using the same apparatus

and procedures when testing different species of fish (Agrillo et al. 2008). In contrast, after researchers altered procedures, quantity judgment among Asian elephants (*Elephas maximus*) but not African elephants (*Loxodonta africana*) appeared to be unaffected by ratio (Irie & Hasegawa, 2012; Irie-Sugimoto, Kobayashi, Sato, & Hasegawa, 2009; Perdue, Talbot, Stone, & Beran, 2012), although these animals are known to have a highly developed brain and memory (Shoshani, Kupsky, & Marchant, 2006). In cases such as these, it appears that number sense findings may differ as a function of task type. However, it is difficult to make an assessment based upon any single study. Meta-analytic techniques will be helpful when addressing this issue.

Issues Regarding Species

Sometimes phylogenetically similar species perform differently during the same task raising questions if support for either the object-file or approximate number system may also depend on species. Among the prosimian primates, for example, mongoose lemurs (*Eulemur mongoz*; Lewis et al., 2005) and small-eared bushbabies (*Otolemur garnettii*; Baker, 2016) were tested using a searching task. Lemurs searched longer on trials that differed by ratio levels of 1:2, 2:4, and 4:8, but not 2:3 or 3:4, showing the hallmark ratio pattern of the approximate number system (Lewis et al., 2005). On the other hand, bushbabies searched longer only on trials that differed by 1:2 and 2:4, but not 2:3, 3:4, or 4:8 lending no support to either the object-file system or the approximate number system. It is possible that the task demanded too much for bushbabies as both perception and memory, rather than perception alone, was required to effectively complete the task. However, it could be differences between species that accounted for better quantity judgments for mongoose lemurs. For example, mongoose lemurs are

cathemeral and more social (Curtis, 2003) than the nocturnal, semi-solitary bushbabies (Bearder & Doyle, 1974). Furthermore, species from different phylogenetic groups have shown support for the object-file system, as opposed to the approximate number system, during a searching task. Human infants (*Homo sapiens*) ranging from 12 to 24 months old searched for ping pong balls in an opaque container following the object-file system's signature set-size limitation of three, identical to the set-size limitation found in infants during a habituation task.

<div align="center">Current Study</div>

Because a substantial body of data now exists, it is valuable to compile information on the object-file and approximate number system using meta-analytical techniques to provide some guidance to future studies. In addition, animal researchers and those who study infants often rely on small sample sizes (Jennions & Pape Moller, 2003; Oakes, 2017) so that an aggregation of effect sizes is needed to provide for the detection and delineation of differences regarding number abilities that may be due to procedures, species or an interaction of the two variables.

Goals of the Current Study

There are four goals for this meta-analysis: 1) to determine overall differences in the extent of support for the object-file versus approximate number systems, 2) to delineate species differences in abilities to distinguish quantities, 3) to determine whether specific procedural differences affect performance on quantity judgment tasks, and 4) ascertain procedural effects that differ for different species.

Hypotheses of the Current Study

It is hypothesized that

1. large quantity judgments for all species will be ratio dependent and, therefore, support the use of the approximate number system.

2. quantity judgments with small numerosities will have a set-size limitation of four, rapidly declining thereafter, and comport with the object-file system.

3. species with low attention and/or short-term memory will have a set-size limitation of three rather than four or will use the approximate number system across the entire number range.

4. procedural differences such as simultaneous versus sequential item presentation will affect performance in that performance will be enhanced with simultaneous presentation.

5. species will interact with procedural differences such that species with low attention and short-term memory capacity will not perform as well as species with high attention and short-term memory capacity on tasks that sequentially present items versus those that simultaneously present items.

CHAPTER II – METHOD

Article Identification

PsycINFO (1887-2018), PubMed (1809-2018), Google Scholar (1677-2018), and Proquest Dissertations and Theses Global (1743-2018) databases were searched using the keywords *quantity discrimination*, *quantical representation*, *numerosity*, *spontaneous numerosity, number task*, and *number representation*. Two hundred forty-two potential articles were obtained and those articles as well as the references within those articles were checked for relevance according to the Initial Screening for Relevance form (see Appendix A). Internet-based conference proceedings spanning 2013-2017 of the Comparative Cognition Society, known to have a numerosity session, were searched resulting in four obtained articles. In addition, because there is a publication bias for studies with statistically significant findings (File Drawer issue), statistics (N, M, SD, F, Z, p, number of choices, and number of more choices) from unpublished data generated by eleven authors with colonies of animals and/or multiple publications were requested by electronic mail. Finally, unpublished data was requested through electronic mailings and social media platforms of the American Psychological Association, Animal Cognition, American Society of Primatologists, and Comparative Cognition Society. All responders were given 60 days to complete the Unpublished Data Form and gently prompted on a weekly basis during the 60 days to maximize responses (see Appendix B). Obtained articles were assigned a Report Identification (ID) Number and then year, source, subject, and method were recorded for descriptive purposes.

Article Inclusion

To be included in the meta-analysis, obtained articles must have met the following criteria:

1. Spontaneous numerosity, rather than learned (i.e., trained), was some part of the investigation (Habituation to the task did not qualify as learning but rather as an adjustment period.)

2. If human infants were participants in the study, the infants must have been preverbal.

3. The task must have involved either a binary choice or a violation of expectancy while searching for or looking at tangible objects in a set.

4. Presentation of stimuli must have varied in ratio.

5. Confounding variables (e.g., time and space) must have been controlled.

All available statistics were then recorded for effect size calculation directly into Microsoft Excel and then transferred to the Comprehensive Meta-Analysis program.

Final Sample

Of the 242 obtained articles, 26 articles met the inclusion criteria. Most of the 242 articles (216) were not included because animals were trained prior to the discrimination task. Two of the remaining 26 articles were discarded because the necessary data was unavailable. This resulted in 24 final articles for this meta-analysis. Within these 24 articles, 162 independent experiments were conducted with a total of 3,137 subjects. Of those subjects, 204 were infants, 0 were apes, 135 were old world monkeys, 24 were new world monkeys, 273 were prosimians, 558 were birds, 270 were amphibians, and 1673

were fish. Study dates ranged from to 2000-2017. Articles included are denoted by * in the reference section.

Coded Variables

Two independent raters coded articles for ratio, task type, species, and all available statistics. One rater coded 100% of the 24 included studies while the other rater coded 20% of the studies which were chosen at random (random.org).   This resulted in 21.6% coding overlap in the 162 experiments. Reliability of codings was 100% for the two raters.

The statistical package Comprehensive Meta-analysis (CMA, version 3) was used to accomplish all effect sizes and analyses. If a study involved multiple experiments, each data set within the study was considered separate experiments when the samples from each data set were independent. Additionally, if separate studies involved the same animals, the study with the largest number of participants was included.

Dependent Variables and Effect Size Transformations

Authors often did not report complete statistics. Most authors, however, did report the number of correct choices (i.e., number of times the set containing more was chosen) or presented graphs allowing the extrication of the proportion of correct choices. Therefore, the proportion of correct choices was analyzed[1].

Descriptive Data

Data were collected from 162 experiments overall. Table 1 displays the overall number of experiments with correct choices at different levels.

Table 1

Overall Number of Correct Choices

Choices	Number
Less than 50%	17/162
50% or More	145/162
Greater than 60%	98/162
Greater than 70%	55/162

[1] Programmers of Comprehensive Meta Analysis were contacted to insure this was the best option for the data

Table 1 (continued).

Greater than 80%	26/162
Greater than 90%	7/162

Of the 162 overall experiments, 44 manipulations of ratios were investigated by researchers using simultaneous choice tasks, sequential choice tasks, or searching tasks with infants, prosimians, birds, amphibians, or fish. Old world monkeys and new world monkeys only had data available from one experiment. Therefore, these species were not included in any of the analyses. Table 2 shows the number of experiments for each of the 44 manipulations of ratio for the five species under investigation.

Table 2

Number of Experiments for each Ratio by Species

Ratio	Infants	Prosimians	Birds	Amphibians	Fish	Total
1:2	4	4	3	1	5	17
2:4	1	2	1	0	2	6
4:8	0	2	4	0	0	12
2:3	2	4	3	3	6	18
3:4	2	2	4	1	6	15
4:6	0	0	3	2	4	9
4:5	0	0	1	0	4	5
6:8	0	0	4	0	2	6
3:9	0	0	0	0	2	2
5:8	0	0	0	0	1	1
5:9	0	0	0	0	1	1
6:9	0	0	0	0	1	1
3:7	0	0	0	0	1	1
5:10	0	0	0	0	1	1
6:12	0	1	0	0	0	1
12:16	0	0	1	0	0	1
24:32	0	0	1	0	0	1
28:32	0	0	1	0	0	1
32:64	0	0	1	0	0	1
8:64	0	0	1	0	0	1
4:32	0	0	1	0	0	1
2:16	0	0	2	0	0	2

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Table 2 (continued).

2:8	0	0	2	0	2	4
2:6	0	1	0	0	2	3
1:8	0	0	2	0	0	2
1:3	0	1	0	0	2	3
5:6	0	0	0	0	4	4
4:10	0	0	0	0	2	2
4:7	0	0	0	0	1	1
6:7	0	0	0	0	2	2
4:12	0	1	0	0	1	2
4:16	0	0	0	0	1	1
3:6	2	1	0	0	3	6
3:12	0	0	0	0	1	1
3:5	0	0	0	0	3	3
8:10	0	0	1	0	0	1
14:16	0	0	2	0	0	2
7:8	0	0	2	0	0	3
8:16	0	0	2	1	1	4
8:12	0	0	1	1	1	3
1:4	1	0	2	0	4	7
16:32	0	0	1	0	1	2
16:64	0	0	1	0	0	1
8:32	0	0	1	0	0	1
Total	12	19	48	9	74	162

Table 3 shows the number of experiments for each of the 44 ratio manipulations for each of the three task types: simultaneous choice, sequential choice, and searching tasks.

Table 3

Number of Experiments for each Ratio by Task

Ratio	Simultaneous	Sequential	Searching	Total
1:2	7	7	3	17
2:4	3	1	2	6
4:8	7	3	2	12
2:3	9	6	3	18
3:4	9	4	2	15
4:6	7	1	1	9
4:5	4	1	0	5
6:8	4	2	0	6

Table 3 (continued).

3:9	2	0	0	2
5:8	1	0	0	1
5:9	1	0	0	1
6:9	1	0	0	1
3:7	1	0	0	1
5:10	1	0	0	1
6:12	0	1	0	1
12:16	1	0	0	1
24:32	1	0	0	1
28:32	1	0	0	1
32:64	1	0	0	1
8:64	1	0	0	1
4:32	1	0	0	1
2:16	1	1	0	2
2:8	3	1	0	4
2:6	2	1	0	3
1:8	1	1	0	2
1:3	2	1	0	3
5:6	4	0	0	4
4:10	2	0	0	2
4:7	1	0	0	1
6:7	2	0	0	2
4:12	1	1	0	2
4:16	1	0	0	1
3:6	4	2	0	6
3:12	1	0	0	1
3:5	3	0	0	3
8:10	0	1	0	1
14:16	1	1	0	2
7:8	2	1	0	3
8:16	3	1	0	4
8:12	3	0	0	3
1:4	5	2	0	7
16:32	1	0	0	1
16:64	1	0	0	1
8:32	1	0	0	1
Total	109	40	13	162

Table 4 shows the number of experiments for each of the five species (infants, prosimians, birds, amphibians, fish) by the type of task (simultaneous choice, sequential choice, searching).

Table 4

Number of Experiments for each Task by Species

	Infants	Prosimians	Birds	Amphibians	Fish	Total
Simultaneous	1	0	27	9	72	109
Sequential	11	9	18	0	2	40
Searching	0	10	3	0	0	13
Total	12	19	4	9	74	162

To utilize more fully the available data sets, ratios that had similar characteristics were combined to reflect whether they were equal to or below the set size limitation and double or more in the ratio. For example, 1:2, 1:3, 1:4, and 2:4 are ratios containing sets less than the set size limitation and double or more in ratio and so those ratios were grouped and categorized as "Below Set Size $\geq$ Double Discrepant". Ratios were divided based on whether 1) the ratio was below or above the set size limitation and 2) the ratio between objects in the two sets were at least double discrepant (e.g., 4:8 or greater) or less than double discrepant (e.g., 2:3). Table 5 shows the division of ratios into four categories.

Table 5

Division of Ratios into Categories

	$\geq$ Double Discrepant	< Double Discrepant
Below Set Size	1:2, 2:4, 1:3, 1:4	2:3, 3:4
Above Set Size	3:6, 4:8, 5:10, 6:12, 8:16, 16:32, 32:64, 2:6, 3:9, 4:12, 8:32, 3:7, 1:8, 2:16, 4:32, 8:64, 2:8, 4:10, 4:16, 3:12, 16:32	24:32, 5:9, 8:12, 12:16, 28:32, 4:7, 5:8, 6:9, 3:5, 4:6, 6:8, 8:10, 14:16, 4:5, 5:6, 7:8, 6:7

Table 6 shows the final number of experiments in each of the four ratio categories by the type of task.

Table 6

Number of Experiments for Ratio Category by Task

Ratio Category	Simultaneous	Sequential	Searching	Total
Below Set Size $\geq$ Double Discrepant	17	11	5	33
Below Set Size $<$ Double Discrepant	18	10	5	33
Above Set Size $\geq$ Double Discrepant	37	12	2	51
Above Set Size $<$ Double Discrepant	36	7	1	45
Total	108	40	13	162

Table 7 displays the final number of experiments for each species in each of the four ratio categories.

Table 7

Number of Experiments for Ratio Category by Species

Ratio Category	Infant	Prosimians	Birds	Amphibians	Fish	Total
Below Set Size $\geq$ Double Discrepant	6	7	6	1	13	33
Below Set Size $<$ Double Discrepant	4	6	7	4	12	33
Above Set Size $\geq$ Double Discrepant	2	6	19	1	23	51
Above Set Size $<$ Double Discrepant	0	0	16	3	26	45
Total	12	19	48	9	74	162

Table 8 relates the ratio categories to the approximate number system and the object file system.

Table 8

Ratio Dependent Evidence for the Approximate Number versus Object File Systems

Ratio Category	Ratio	ANS	OFS
Below Set Size ≥ Double Discrepant	1:2	Yes	Yes
	2:4		
	1:3		
	1:4		
Below Set Size < Double Discrepant	2:3	No	Yes
	3:4		
Above Set Size ≥ Double Discrepant	3:6	Yes	No
	4:8		
	5:10		
	6:12		
	8:16		
	16:32		
	32:64		
	2:6		
	3:9		
	4:12		
	8:32		
	3:7		
	1:8		
	2:16		
	4:32		
	8:64		
	2:8		
	4:10		
	4:16		
	3:12		
	16:64		
Above Set Size < Double Discrepant	24:32	No	No
	5:9		
	8:12		
	12:16		
	28:32		
	4:7		
	5:8		
	6:9		
	3:5		
	4:6		
	6:8		
	8:10		
	14:16		

Table 8 (continued).

	4:5
	5:6
	7:8
	6:7

Note: 'Yes' refers to ability to discriminate whereas 'No' refers to lack of ability to discriminate

Overall Results

The first goal was to test the hypotheses that large quantity judgments for all species are ratio dependent and, therefore, support the use of the approximate number system and that quantity judgments with small numerosities have a set-size limitation of four, rapidly declining thereafter, and comport with the object-file system. A series of meta-analyses measuring the effect of the four ratio manipulation categories was conducted using the proportion of correct choices.

Overall Results for Ratio Category

The Below Set Size $\geq$ Double Discrepant category had 7/33 ratio manipulations with significantly higher proportions of correct choices compared to chance (0.50) while 26/33 ratio manipulations had a null effect. Meta-analytic results revealed that subjects chose correctly at a rate significantly above chance responding during Below Set Size $\geq$ Double Discrepant ratio manipulations. The computed random-effects weighted mean effect size was 0.684, 95% confidence interval (CI) [0.642, 0.722], $Z = 8.187$, $p = .001$, which suggests a medium effect size in favor of success during the Below Set Size $\geq$ Double Discrepant ratio manipulations. Finally, the fail-safe N estimated that 657 missing studies would be needed to bring the *p*-value to greater than alpha.

The Below Set Size $<$ Double Discrepant had 4/33 ratio manipulations with significantly higher proportions of correct choices than chance (0.50) while 29/33 ratio

manipulations had a null effect. Meta-analytic results revealed that subjects chose correctly during Below Set Size < Double Discrepant ratio manipulations significantly greater than chance. The computed random-effects weighted mean effect was 0.610, 95% CI [.568, .650], $Z = 5.120$, $p < 0.001$, which suggests a medium effect size in favor of success during Below Set Size < Double Discrepant ratio manipulations. Finally, the fail-safe N estimated that 241 missing studies would be needed to bring the p-value to greater than alpha.

The Above Set Size $\geq$ Double Discrepant had 9/51 ratio manipulations with significantly higher proportions of correct choices than chance (0.50) while 42/51 ratio manipulations had a null effect. Meta-analytic results revealed that subjects chose correctly during Above Set Size $\geq$ Double Discrepant ratio manipulations significantly greater than chance. The computed random-effects weighted mean effect was 0.639, 95% CI [0.602, 0.674], $Z = 7.094$, $p < 0.001$, which suggests a medium effect size in favor of success during Above Set Size $\geq$ Double Discrepant ratio manipulations. Finally, the fail-safe N estimated that 974 missing studies would be needed to bring the p-value to greater than alpha.

The Above Set Size < Double Discrepant had 3/45 ratio manipulations with significantly higher proportions of correct choices than chance (0.50) while 42/55 ratio manipulation had a null effect. Meta-analytic results revealed that subjects chose correctly during Above Set Size < Double Discrepant ratio manipulations significantly greater than chance. The computed random-effects weighted mean effect was 0.573, 95% CI [0.539, 0.607], $Z = 4.133$, $p < 0.001$, which suggests a medium effect size in favor of success during Above Set Size < Double Discrepant ratio manipulations. Finally,

the fail-safe N estimated that 123 missing studies would be needed to bring the *p*-value to greater than alpha.

Overall Results for Type of Task

The next goal was to identify whether the type of task moderated the variability among effect sizes for the overall proportion of correct choices during ratio categories. An inverse variance weight random effects meta-regression on the *Z*-distribution with the logit event rate revealed no effect of type of task. Results are displayed in Table 9.

Table 9

Type of Task Moderator Analysis

Level				
		Model Overall		
Moderator	*Q*	*df*	*Z*	*p*
Overall	1.07	2	.5871	
Simultaneous Choice Task versus				
Sequential Choice Task			.3000	.7661
Searching Task			1.0100	.3104

Species Results

The final goal was to determine whether species abilities differed with regard to their use of the approximate number and object file systems.

Infant Results

The Below Set Size ≥ Double Discrepant category had 4/6 ratio manipulations with significantly higher proportions of correct choices than chance (0.50) while 2/6 ratio manipulations had a null effect, and 4/6 experiments had proportions greater than 0.50. Meta-analytic results revealed that infants correctly chose during Below Set Size ≥ Double Discrepant ratio manipulations at a rate significantly greater than chance. The computed random-effects weighted mean effect size was 0.683, 95% (CI) [0.577, 0.773],

34

$Z = 3.289$, $p = .001$, which suggests a medium effect size in favor of success during

Below Set Size $\geq$ Double Discrepant ratio manipulations.

The Below Set Size $<$ Double Discrepant had 2/4 ratio manipulations with

significantly higher proportions of correct choices than chance (0.50) while 2/4 ratio

manipulations had a null effect, and 2/4 experiments had proportions greater than .50.

Meta-analytic results revealed that infants did not choose correctly at a rate greater than

chance during the Below Set Size $<$ Double Discrepant ratio manipulations. The

computed random-effects weighted mean effect was 0.628, 95% CI [0.488, 0.749], $Z =$

1.796, $p = 0.073$.

The Above Set Size $\geq$ Double Discrepant had 1/2 ratio manipulations with

significantly higher proportions of correct choices than chance (0.50) while 1/2 ratio

manipulations had a null effect, and 1/2 experiments had proportions greater than 0.50.

Meta-analytic results revealed that infants did not choose correctly at a rate above chance

during Above Set Size $\geq$ Double Discrepant ratio manipulations. The computed random-

effects weighted mean effect was 0.609, 95% CI [0.183, 0.915], $Z = 0.447$, $p = 0.655$.

Prosimian Results

The Below Set Size $\geq$ Double Discrepant category had 2/7 ratio manipulations

with significantly higher proportions of correct choices than chance (0.50) while 5/7 ratio

manipulations had a null effect, and all experiments had proportions greater than 0.50.

Meta-analytic results revealed that prosimians chose correctly at a rate significantly

greater than chance during Below Set Size $\geq$ Double Discrepant ratio manipulations. The

computed random-effects weighted mean effect size was 0.710, 95% CI [0.608, 0.794], Z

= 3.862, *p* < .001, which suggests a medium effect size in favor of success during Below Set Size ≥ Double Discrepant ratio manipulations.

The Below Set Size < Double Discrepant ratio condition had 0/6 ratio manipulations with significantly higher proportions of correct choices than chance (0.50) with all experiments having a null effect, and 3/6 experiments having proportions of success greater than 0.50. Meta-analytic results revealed that prosimians did not chose correctly at a rate significantly greater than chance during the Below Set Size < Double Discrepant ratio manipulations. The computed random-effects weighted mean effect was 0.522, 95% CI [0.408, 0.633], *Z* = 0.376, *p* = 0.707.

The Above Set Size ≥ Double Discrepant condition had 2/6 ratio manipulations with significantly higher proportions of correct choices than chance (0.50) while 4/6 had a null effect, and 4/6 experiments had proportions greater than 0.50. Meta-analytic results revealed that prosimians chose correctly at a rate significantly above chance during Above Set Size ≥ Double Discrepant ratio manipulations. The computed random-effects weighted mean effect was 0.632, 95% CI [0.525, 0.728], *Z* = 2.394, *p* = 0.017.

Bird Results

The Below Set Size ≥ Double Discrepant category had 2/6 ratio manipulations with significantly higher proportions of correct choices than chance (0.50) while 4/6 ratio manipulations had a null effect, and all experiments had proportions greater than 0.50. Meta-analytic results revealed that birds chose correctly at a rate significantly above chance during Below Set Size ≥ Double Discrepant ratio manipulations. The computed random-effects weighted mean effect size was 0.819, 95% (CI) [0.694, 0.90], *Z* = 4.282,

$p < .001$, which suggests a large effect size in favor of success during Below Set Size $\geq$ Double Discrepant ratio manipulations for birds.

The Below Set Size $<$ Double Discrepant condition had 2/7 ratio manipulations with significantly higher proportions of correct choices than chance (0.50) while 5/7 ratio manipulations had a null effect. All experiments had proportions of correct choices greater than 0.50. Meta-analytic results revealed that birds chose correctly at a rate significantly greater than chance during the Below Set Size $<$ Double Discrepant ratio manipulations. The computed random-effects weighted mean was 0.789, 95% CI [0.680, 0.868], $Z = 4.587$, $p < .001$, which suggests a medium effect size in favor of success during Below Set Size $<$ Double Discrepant ratio manipulations.

The Above Set Size $\geq$ Double Discrepant had 4/19 ratio manipulations with significantly higher proportions of correct choices than chance (0.50) while 15/19 ratio manipulations had a null effect, and 16/19 experiments had correct proportions greater than 0.50. Meta-analytic results revealed that birds chose correctly at a rate significantly better than chance during Above Set Size $\geq$ Double Discrepant ratio manipulations. The computed random-effects weighted mean effect was 0.714, 95% CI [0.644, 0.775], $Z = 5.567$, $p < .001$, which suggests a medium effect size in favor of success during Above Set Size $\geq$ Double Discrepant ratio manipulations.

The Above Set Size $<$ Double Discrepant condition had 0/19 ratio manipulations with significantly higher proportions of correct choices than chance (0.50) while 19/19 ratio manipulations had a null effect. 10/19 experiments had proportions greater than 0.50. Meta-analytic results revealed that birds did not choose correctly at a rate greater than chance during Above Set Size $<$ Double Discrepant ratio manipulations. The

computed random-effects weighted mean effect was 0.568, 95% CI [0.493, 0.640], $Z =$ 1.790, $p = .073$.

Amphibian Results

The Below Set Size $\geq$ Double Discrepant condition had 1/1 ratio manipulations with significantly higher proportions of correct choices than chance (0.50). Meta-analytic procedures were not performed because there was only one experiment in the category. The Below Set Size $\geq$ Double Discrepant single experiment effect size was 0.733, 95% CI [0.550, 0.861], $Z = 2.45$, $p = .014$, which suggests a medium effect size in favor of success during Below Set Size $\geq$ Double Discrepant ratio manipulations.

The Below Set Size $<$ Double Discrepant condition had 0/4 ratio manipulations with significantly higher proportions of correct choices than chance (0.50) while 4/4 ratio manipulations had a null effect. 3/4 experiments had proportions greater than 0.50. Meta-analytic results revealed that amphibians did not choose correctly at a rate greater than chance during Below Set Size $<$ Double Discrepant ratio manipulations. The computed random-effects weighted mean effect was 0.589, 95% CI [0.498, 0.675], $Z =$ 1.925, $p = .054$.

The Above Set Size $\geq$ Double Discrepant condition had 0/1 ratio manipulations with significantly higher proportions of correct choices than chance (0.50). 1/1 experiments had proportions greater than 0.50. Meta-analytic procedures were not performed because there was only one experiment in the category. The Above Set Size $\geq$ Double Discrepant single experiment effect size was 0.567, 95% CI [0.388, 0.729], Z $=0.728$, $p = .467$.

The Above Set Size < Double Discrepant had 2/3 ratio manipulations with significantly higher proportions of correct choices than chance (0.50) while 1/3 ratio manipulations had a null effect, and 2/3 experiments had proportions greater than 0.50. Meta-analytic results revealed that amphibians chose correctly at a rate greater than chance during Above Set Size < Double Discrepant ratio manipulations. The computed random-effects weighted mean effect was 0.626, 95% CI [0.513, 0.728], $Z = 2.171$, $p = .030$.

Fish Results

The Below Set Size ≥ Double Discrepant category had 1/13 ratio manipulations with significantly higher proportions of correct choices than chance (0.50) while 11/13 ratio manipulations had a null effect, and 13/13 experiments had proportions greater than 0.50. Meta-analytic results revealed that fish chose correctly significantly greater than chance during Below Set Size ≥ Double Discrepant ratio manipulations. The computed random-effects weighted mean effect size was 0.649, 95% CI [0.591, 0.703], $Z = 4.845$, $p < .001$, which suggests a medium effect size in favor of success during Below Set Size ≥ Double Discrepant ratio manipulations.

The Below Set Size < Double Discrepant condition had 0/12 ratio manipulations with significantly higher proportions of correct choices than chance (0.50) while 12/12 ratio manipulations had a null effect. All experiments had proportions of correct choices greater than 0.50. Meta-analytic results revealed that fish chose correctly at a rate significantly greater than chance during the Below Set Size < Double Discrepant ratio manipulations. The computed random-effects weighted mean effect was 0.600, 95% CI

[0.539, 0.658], $Z = 3.169$, $p = .002$, which suggests a medium effect size in favor of success during Below Set Size < Double Discrepant ratio manipulations.

The Above Set Size ≥ Double Discrepant had 4/23 ratio manipulations with significantly higher proportions of correct choices than chance (0.50) while 19/23 ratio manipulations had a null effect, and 19/23 experiments had proportions correct greater than 0.50. Meta-analytic results revealed that fish did choose correctly during Above Set Size < Double Discrepant ratio manipulations at a rate significantly greater than chance. The computed random-effects weighted mean effect was 0.615, 95% CI [0.571, 0.658], Z = 5.036, $p < .001$, which suggests a medium effect size in favor of success during Above Set Size ≥ Double Discrepant ratio manipulations.

The Above Set Size < Double Discrepant condition had 1/26 ratio manipulations with significantly higher proportions of correct choices than chance (0.50) while 25/26 ratio manipulations had a null effect, and 24/26 experiments had proportions correct greater than 0.50. Meta-analytic results revealed that fish did choose correctly at a rate significantly greater than chance during the Above Set Size < Double Discrepant ratio manipulations. The computed random-effects weighted mean effect was 0.568, 95% CI [0.526, 0.608], $Z = 3.181$, $p = .001$, which suggests a medium effect size in favor of success during Above Set Size < Double Discrepant ratio manipulations.

Results Summary

Table 10 reveals whether ratio manipulation category effects significantly differed from chance (.05) overall and for each species.

Table 10

Revealed Significant Effects for Ratio Categories

Ratio Category	Infant	Prosimians	Birds	Amphibians	Fish	Overall
Below Set Size ≥ Double Discrepant	Yes	Yes	Yes	X	Yes	Yes
Below Set Size < Double Discrepant	No	No	Yes	No	No	Yes
Above Set Size ≥ Double Discrepant	No	Yes	Yes	X	Yes	Yes
Above Set Size < Double Discrepant	X	X	No	Yes	Yes	Yes

Note: 'Yes' refers to significant differences revealed and 'No' refers to no differences

Each ratio manipulation category is displayed in Tables 11 - 14 along with its computed random-effects weighted mean effect size and its 95% confidence interval along with the results of a *Z*-test indicating whether the proportion of correct choices was significantly greater than chance (0.50).

Table 11

Below Set Size ≥ Double Discrepant

Species	Mean Effect Size	95% CI	Z	p
Infant	.683	.577 - .733	3.289	p = .001*
Prosimian	.710	.608 - .794	3.862	p < .001**
Bird	.810	.694 - .900	4.282	p < .001**
Amphibian	X	X	X	X
Fish	.649	.591 - .703	4.845	p < .001**
Overall	.684	.642 - .722	8.187	p = .001*

Note: * indicates significance at a .05 alpha level and ** indicates significance at a < .001 alpha level

Table 12

Below Set Size < Double Discrepant

Species	Mean Effect Size	95% CI	Z	p
Infant	.628	.488 - .749	1.796	p = .073
Prosimian	.522	.408 - .633	0.376	p = .707
Bird	.789	.680 - .868	4.587	p < .001**
Amphibian	.589	.480 - .675	1.925	p = .054
Fish	.600	.539 - .658	3.169	p = .002*
Overall	.610	.658 - .650	5.120`	p < .001**

Note: * indicates significance at a .05 alpha level and ** indicates significance at a < .001 alpha level

*Ta*ble 13

Above Set Size ≥ Double Discrepant

Species	Mean Effect Size	95% CI	Z	p
Infant	.609	.183 - .915	0.447	p = .655
Prosimian	.632	.525 - .728	3.862	p < .001**
Bird	.714	.644 - .775	5.567	p < .001**
Amphibian	X	X	X	X
Fish	.615	.571 - .658	5.035	p < .001**
Overall	.639	.602 - .674	7.094	p = .001*

Note: * indicates significance at a .05 alpha level and ** indicates significance at a < .001 alpha level

Table 14

Above Set Size < Double Discrepant

Species	Mean Effect Size	95% CI	Z	p
Infant	X	X	X	X

Table 14 (continued).

Prosimian	X	X	X	X
Bird	.568	.493 - .640	1.790	p = .073
Amphibian	.626	.513 - .728	2.171	p = .030*
Fish	.568	.526 - .608	3.181	p = .001*
Overall	.537	.532 - .607	4.133	p < .001**

Note: * indicates significance at a .05 alpha level and ** indicates significance at a < .001 alpha level

CHAPTER IV – DISCUSSION

The current meta-analysis synthesized and examined experiments on quantity judgment in five different species across three different tasks with a variety of set size and discrepancy ratio manipulations. Results revealed some success in both large and small set sizes and in both large and small ratio manipulation categories and supported the use of both the approximate number system and the object file system across species.

Success in the Below Set Size $\geq$ Double Discrepant ratio manipulation category and the Above Set Size $\geq$ Double Discrepant ratio manipulation category supported the hypothesis that large quantity judgments for all species are ratio dependent and, therefore, supported the use of the approximate number system. Furthermore, success in the Below Set Size $<$ Double Discrepant ratio manipulation category during quantity judgments with small numerosities comported with the object-file system. Because the Above Set Size $<$ Double Discrepant ratio manipulation category was above the set size limitation and does not share ratio characteristics with the Above Set Size $\geq$ Double Discrepant category, success in this most complex category suggested that experience may have played a role in quantity judgment tasks. These results combined supported the overall hypothesis that there was not one single quantity judgment system, but rather there was a combination of the approximate number and object file systems plus a role of experience with the environment.

Combinations of ratio manipulations into categories did not allow for direct testing of the hypothesis that species with low attention and/or short-term memory would have a set-size limitation of three rather than four. However, species differences were

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uncovered over the course of this study. Specifically, infants successfully discriminated between sets of quantities the poorest, only having success in the Below Set Size $\geq$ Double Discrepant ratio manipulation category. This may be because all other species were at least juveniles when tested and may have had much more experience navigating the environment. Having this experience may have allowed the systems guiding quantity judgment of other species to become more efficiently calibrated.

Prosimians had success during both the Below Set Size $\geq$ Double Discrepant and the Above Set Size $\geq$ Double Discrepant ratio manipulation categories while engaging in quantity discrimination tasks. This pattern of results mimics the hallmark signature of the ratio dependent approximate number system and supported the previous hypothesis that prosimians make use of the approximate number system (Lewis et al., 2005).

Birds were successful at discriminating quantities in the Below Set Size $\geq$ Double Discrepant, Below Set Size < Double Discrepant, and the Above Set Size $\geq$ Double Discrepant manipulations of ratio categories supporting the presence of both the approximate number system and the object file system. Being flock animals may have played a role in the observed success of birds across most conditions.

Amphibians had success only in the most difficult ratio manipulation category, the Above Set Size < Double Discrepant condition. Amphibians are unique in that their food is often moving targets (e.g., flies). Success in the most difficult category may be accounted for by this. However, if more amphibian studies become available these results may change.

Success for fish was revealed in the Below Set Size $\geq$ Double Discrepant, Above Set Size $\geq$ Double Discrepant, and the Above Set Size < Double Discrepant ratio

manipulation categories, but not the Below Set Size < Double Discrepant. This supported the use of the approximate number system as opposed to the object file system. Success in the most difficult ratio manipulation category, the Above Set Size < Double Discrepant condition, may have occurred because fish depend on shoaling to reduce the risks of predation.

Regarding the effect of procedural differences, the moderator analysis revealed no differences in the proportion of correct choices across all three types of task. Although it has been suggested that the cognitive load is potentially large during searching tasks and may, similar to the sequential choice task, interfere with attention and discriminability for human and nonhuman animals with low working memory capacities (Downing, 2009), this did not seem to be the case. Perhaps memory does not play as big of a role as hypothesized. These results suggest that if a particular task such as a searching task is better matched with a species than a choice task (e. g., to mimic foraging), then the best procedure should be chosen for that species.

Lastly, it was hypothesized that species will interact with procedural differences such that species with low attention and short-term memory capacity would not perform as well as species with high attention and short-term memory capacity on tasks that sequentially present items versus those that simultaneously present items. Although having a global view of all objects in a set seems easier intuitively, the proportion of correct choices remained the same for both simultaneous and sequential choice tasks. Because using the same task makes comparative examinations cleaner, it is suggested that future researchers employ the sequential choice task, because performance is not task

based, and the sequential choice task allows for control of continuous variables such as surface area by preventing the global view of all objects in a set.

Methodological Constraints and Future Research

A major constraint to this study was prevalent incomplete statistical reporting (i.e., not reporting means and standard deviation; only reporting *p*-values from unknown analyses) throughout the quantity judgment literature. This only allowed for event rate data to be tested.

Another major constraint was the lack of consistency in ratios tested in all the different experiments. This led to 20/44 ratios having only one experiment, and the creation of ratio manipulation categories. Future research should test the same ratios to allow for direct comparisons across experiments.

To allow for a more complete evolutionary picture, more studies are needed from different species within each of the phylogenetic groups including apes, old world monkeys, and new world monkeys. Furthermore, more studies that involve spontaneous quantity judgments rather than trained quantity judgments are needed.

Summary and Implications

In summary, quantity judgment articles using five different species across three different tasks with a variety of set size and discrepancy ratio manipulations were synthesized and examined. Results revealed some success in both large and small set sizes and in both large and small ratio manipulation categories and supported the use of both the approximate number system and the object-file system across species. Furthermore, successful discrimination during complex ratios not comport with either the approximate number or the object-file system suggests a role of the environment which

may allow for quantity judgment abilities to become better calibrated with experience. Limited success for infants further supports this hypothesis because they were the most inexperienced of all subjects. Finally, subjects performed the same regardless of task type.

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1. What is the Report ID number? _____

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    1 = Background
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    e. Review of previous research _____
    f. Other (specify) _____

APPENDIX C – Unpublished Data Form

Author(s): _____

Year: _____

Subjects: _____ If human infants, age: _____

Method Type: _____

A, Spontaneous Choice Task with Sequential Presentation

B. Spontaneous Choice Task with Simultaneous Presentation

C. Searching Task

D. Other. Briefly describe. _____

_____

If applicable, Type of Controls: _____

_____

Ratio _____ Total # of Choices _____ Total # of More Choices _____

Ratio _____ Total # of Choices _____ Total # of More Choices _____

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Analysis_____

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SD _____

T _____

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Z _____

p _____

Other_____

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