Abstract  Cognitive research in the United States spans approximately 100 years. Most studies have occurred in primate centers, fewer at universities, and for a brief period, in home-based projects focused on enculturation. Historically, great apes living in zoos have been under represented. A shift has occurred that affects the future of the field. Studies at primate centers have significantly decreased, all university based projects have ended, and work in zoos is increasing. The Simon Skjodt International Orangutan Center at the Indianapolis Zoo provides an example of one stable, longitudinally based project. The primary areas of study at the Center are symbolic representation, numerical competency, social learning, memory, and strategic reasoning. All data collection sessions are conducted with visitors present. Cognitive studies in a zoo environment promote great ape welfare, offer a platform for transformational public education, and provide an effective means to advance support for \textit{in situ} conservation of great apes.

Key words: cognition, orangutans, great apes, welfare, mental enrichment, Indianapolis Zoo

1. Introduction

Investigations into the cognitive skills of the non-human great apes (orangutans, gorillas, chimpanzees and bonobos) are currently conducted \textit{in} and \textit{ex situ} and involve multiple academic disciplines. The field is vibrant and productive. Results continue to document the abilities of the great ape clade at a time when these species are either endangered or critically endangered in the wild (\url{iucnredlist.org}). While readily acknowledging the many valuable contributions from colleagues internationally, the purpose of this paper is to report only on the status of cognitive research conducted with great apes in the United States. This is not intended to be an exhaustive review of publications or topics that have been studied. Rather, the focus is on trends associated with prevailing perspectives on research with great apes, the institutions supporting it, how that has changed over time, and what appears likely for the future. For a thorough review of all primate cognition research through 1996, see Tomasello & Call (1997). Russon’s excellent (2004) review of the literature offers an evolutionary perspective on great ape intelligence.

The history of cognitive studies with great apes in the United States spans slightly more than 100 years (Parker & McKinney, 1999), beginning with studies by Robert M. Yerkes, known as both an evolutionist and behaviorist (Reed, 1987). The first report by Yerkes of...
cognitive research with a great ape (1916a) describes his study of “ideational behavior” in a young orangutan named Julius, which was conducted at the Franklin Field Station. Yerkes noted that his results included the “first curve of learning for an anthropoid ape”, and when compared to other mammals, may indicate “reasoning” on the part of the orangutan (Dewsbury, 2006; Yerkes, 1916a). Coincident with this research, Yerkes also promoted the concept of establishing an “anthropoid station” to benefit “the biological and sociological sciences and for human welfare” (1916a). Yerkes envisioned that the station would be “1) for the maintenance of various types of primates in normal and healthy condition; (2) for the successful breeding and rearing of the animals to many generations; (3) for systematic and continuous observation under reasonably natural conditions; (4) for experimental investigations from every significant biological point of view; (5) for profitable cooperation with existing biological institutes or departments of research throughout this country and the world” (Yerkes, 1916b). During the early years of his career, Yerkes studied chimpanzees and what is believed to be one bonobo in both zoos and private collections (Dewsbury, 2006). Results from these studies are compiled in Chimpanzee Intelligence and its Vocal Expressions (Yerkes and Learned, 1925), and Almost Human (Yerkes, 1925). Work with Congo, a male gorilla, is detailed in three separate monographs published on The Mind of a Gorilla (Yerkes, 1927a; Yerkes 1927b; Yerkes, 1928). In 1929, The Great Apes was compiled by Robert and Ada Yerkes. This classic volume reviewed all existing knowledge of apes, including behavior and mental abilities (Yerkes & Yerkes, 1929). Dewsbury (2006) suggests that the publication of The Great Apes was an influential factor that led to financial and philosophical support for Yerkes’ proposed anthropoid station. In 1929, the Rockefeller Foundation approved funding for the station, which opened in 1930 as the “Anthropoid Experiment Station of Yale University” located in Orange Park, Florida (Dewsbury, 2006). It was later referred to as the Yale Laboratories of Primate Biology (Finch, 1943). Yerkes served as the Director until he retired in 1941. The Station, renamed in honor of Yerkes, was moved to Atlanta in 1965. For an extensive review of the many research topics that were studied at Orange Park and then Atlanta through the mid 1970's, see Dewsbury (2006).

Following Yerkes, Parker and McKinney (1999) note that primate studies in the United States diverged along 2 distinct paths. The first focused on natural-history style observations of very young apes raised by humans. The general purpose of these studies was to document how immersion in a human cultural environment, sometimes with a married couple as “parents”, impacted the development of mental skills and abilities in great apes, including language comprehension and acquisition. Examples include the work of Luella and Winthrop Kellogg who raised a chimpanzee named Gua alongside their similarly aged human son Donald (Kellogg & Kellogg, 1933). Cathy and Keith Hayes home-reared a chimpanzee named Viki with a primary focus on understanding the emergence of vocal language (Hayes, 1951; Hayes & Hayes, 1952). Temerlin (1975) referred to a chimpanzee named Lucy as his daughter during the years-long study in which she lived as a member of the family (Fouts & Mellgren, 1976). Beatrice and Allen Gardner (1971) had the insight of using American Sign Language, rather than vocal language, in their work with a chimpanzee named Washoe which began in 1966 in Nevada. They were clear that this project was not intended to immerse their subject in a “human family-life”. Rather, the idea was to create a situation with rich and interesting opportunities for signed communication but managed with the rigor of a laboratory-based investigation (Gardner and Gardner, 1971). The project was moved to the Institute for Primate Studies in Norman, Oklahoma in 1970, and then ultimately based at Central Washington University in Ellensburg, Washington starting in 1980 (Fouts, 1997).
The second path for cognitive work with great apes focused on controlled studies in laboratory environments, usually based in established primate research centers (Parker and McKinney, 1999). The trend is illustrated by examples such as Spence (1937, 1938), Crawford (1941), Hayes et al. (1953), Ferster (1964), Mason (1965) Hayes and Nissen (1971), Menzel and Davenport (1962) and Menzel (1973). Spence (1937, 1938), working at Orange Park, pioneered an understanding of learning theory with chimpanzees. Crawford, working with seven chimpanzees at Orange Park, studied sequence learning, social learning, and cooperation. In retrospect, it is likely that this study also revealed abilities associated with Theory of Mind, a concept that did not exist in the great ape literature of the era. In one experiment during the study, the chimpanzees learned to operate electronically linked devices that delivered a food reward when engaged in the proper sequence. Naïve observers were housed next to an experienced demonstrator as a means of revealing socially cooperative behaviors. Crawford’s work (1941) is the first to employ technology-based stimuli in studies of cognition with apes (Martin, C. F., under review.). Hayes et al. (1953) studied discrimination learning set formation with 8 chimpanzees housed at Orange Park. Note that this group of subjects included Viki, who was home-raised by the Cathy and Keith Hayes (Hayes, 1951). Ferster performed “experiments in numerosity” (1964) with a pair of young chimpanzees named Dennis and Margie who were housed at the Institute for Behavioral Research in Silver Spring, Maryland. Mason investigated the social behavior of young chimpanzees at the Delta Regional Primate Research Center, and Hayes and Nissen (1971) published data from Viki describing “higher mental functions” that were collected at in Orange Park. Menzel and Davenport (1962) studied chimpanzees at Orange Park, focusing largely on social and cognitive development. Menzel is likely best known for his work with a group of chimpanzees who lived in a 1-acre compound at the Delta Regional Primate Center which allowed investigation of such topics as the organization of spatial memory (Menzel, 1973).

During the 1960s, universities began to take on a different role. Researchers since Yerkes had been employed by universities, but their work was generally conducted at a separate primate facility. The distinction that emerged was important: the researchers and their ape subjects came to be based at, not just affiliated with, a university. The first known example of this transition was made by David Premack who focused primarily on studying symbolic representation and its relationship to language acquisition (Premack & Premack, 1983). Starting at Orange Park in 1954, Premack moved to the University of Missouri in 1964 with two chimpanzees, Gussie and Sarah, who were housed on the campus. The project expanded over time with additional apes, eventually moved to the University of California, Santa Barbara, and finally to the University of Pennsylvania (Premack & Premack, 1983).

During this era, a small number of studies occurred with great apes living in zoos. Patterned string problems were studied by Riesen et al. (1953) with 3 very young gorillas housed at the Lincoln Park Zoo in Chicago, Illinois. Young gorillas were also the subjects in Fischer’s (1962) work on learning set formation. Her work was based at the Lincoln Park Zoo and utilized a standard Wisconsin General Testing Apparatus (Harlow, 1949) to present stimuli to the apes. Fischer and Kitchener (1965) compared the intelligence of orangutans and gorillas. The subjects were 2 juvenile orangutans, 2 infant orangutans, and 3 juvenile gorillas, all housed at the Lincoln Park Zoo. These apes were presented with patterned string problems, a spatial delay response task involving the location of a concealed food reward, and a delayed match-to-sample task (Fischer and Kitchener, 1965). Rumbaugh followed an unusual trajectory by starting at a zoo and then migrating to a primate research center. His early work drew heavily from data collected at the San Diego Zoo, but his most
significant accomplishments were based later at the Yerkes Regional Primate Center (Rumbaugh, 1971; Rumbaugh and Gil, 1973; Rumbaugh, 1977).

At this point in the history of behavioral and cognitive research with great apes in the United States, Parker and McKinney (1999) document a notable transition. The existing, foundational work had covered topics such as “tool use, space, number, logic and communication”, among others, but there had been little focus on development or developmental psychology (Parker & McKinney, 1999). The “third generation” of scientists in the field shifted towards an emphasis on comparative developmental psychology (Parker & McKinney, 1999). Exemplars include Boysen, who established the Comparative Cognition Project at The Ohio State University in 1983. Her work, which included Premack’s Sarah (Premack & Premack, 1983), largely defined the numerical abilities of chimpanzees at the time (Boysen & Berntson, 1990; Boysen et al., 1996). Sue Savage-Rumbaugh’s early career was dedicated to exploring symbolic representation in chimpanzees (Savage-Rumbaugh et al. 1978), with research based at the Yerkes Regional Primate Center. Later, her focus shifted exclusively to language-learning in bonobos living at the Language Research Center at Georgia State University (Savage-Rumbaugh, 1993). Contemporary developments in the study of language acquisition by great apes included Fouts, as previously mentioned, who studied chimpanzees at Central Washington University in Ellensburg, Washington (Fouts, 1997) and Terrace (1979), who was based at Columbia University. His project documented the failure of his chimpanzee Nim to learn American Sign Language (Terrace, 1979), and Terrace ultimately became a prominent critic of ape language work in general. Working at the University of Tennessee in Chattanooga, Miles was the first to teach American Sign Language to an orangutan (Miles, 1983; Miles, 1990).

The examples noted here illustrate some of the major contributions that were made by university-based projects. This important work contributed substantially to the understanding of cognitive abilities in great apes, particularly in the areas of anthropology, developmental psychology, comparative psychology, and linguistics. However, other academic domains were well represented by work conducted at primate centers. Examples include studies of social cognition with chimpanzees ( Tomasello et al., 1989) and observational learning in orangutans (Call & Tomasello, 1994), both at the Yerkes Regional Primate Center. Various capacities associated with Theory of Mind were explored by Povinelli et al. (1998) with chimpanzees at the New Iberia Research Center in New Iberia, Louisiana.

Despite the expanded focus and participation by a larger number of academic disciplines during this era compared to earlier decades (Parker and McKinney, 1999), a prevailing tendency is clear. The body of work produced was consistent with previous generations in that the majority relied on great apes living in primate centers, and to a lesser extent, university campuses. Great apes living in US zoos were not excluded but remained largely unrepresented. Exceptions can be found. For example, Patterson (1978) began her study of language acquisition with Koko the gorilla at the San Francisco Zoo, before moving to the campus of Stanford University, and finally to a private site in Woodside, California. Mitchell (1991) studied gorillas at the Woodland Park Zoo in Seattle, Washington, documenting their ability to hide, inhibit, and deceive as a means of social manipulation. However, a review of Zoo Biology supports the trend. Beginning with issue 1 in 1982 through the last issue of 1995, numerous applied studies with great apes related to areas such as reproduction and various aspects of husbandry were published. But, there were zero articles that explored the cognitive abilities of great apes in US zoos even though this subject is within the scope of the journal.

While there was no single event or coordinated effort that can be identified, the
landscape for cognitive research with great apes in the US began to shift during the mid-1990s and into the early 2000s. During this time, the field continued to be well supported by work produced at primate centers. The Living Links Center, part of the Yerkes Regional Primate Center, opened in 1997 with the purpose of studying “human evolution by investigating our close genetic, anatomical, cognitive, and behavioral similarities with great apes.” (http://www.emory.edu/LIVING_LINKS/index.shtml). The contribution to the field from Living Links is impressive, and results from studies into social cognition have been exceptionally rich. Topics such as visual kin recognition (Parr & deWaal, 1999), reconciliation (Preuschoft et al., 2002), facial perception (Plotnik et al., 2003), economic decision making (Brosnan et al., 2005), social diffusion of material culture (Hopper et al., 2007), and empathy (deWaal, 2012) substantially expanded the understanding of chimpanzee mental skills and abilities.

Through the late 1990s and into the beginning of the 21st century, universities continued to be important places for the study of great ape mental skills. The Language Research Center at Georgia State University supported research on such diverse topics as chimpanzee abilities to remember and communicate events to a naive human via lexigrams (Menzel, 1999), numerical competencies (Beran et al., 2011; Beran et al. 2013), and the expression of cognitive biases (Brosnan et al., 2012).

Independent of the work occurring at primate centers and universities, an impactful change was underway in the zoo community. In the early 1990s, the Smithsonian National Zoo developed a groundbreaking, permanent new exhibit. Unlike most previous zoo exhibits, the core concept revolved around a biological process, “thinking”, rather than any specific type of animal. Conceived by Benjamin B. Beck, a comparative psychologist, the plan was to design a zoo exhibit that included multiple different species from a variety of taxonomic groups. Interpretation and education for visitors would focus on the mental skills and abilities of these animals, ranging from simple to complex (Beck et al., 1993). As part of the exhibit, a longitudinal study of orangutan cognitive skills was initiated with one important distinction: data collection was conducted in front of zoo visitors in a demonstration format with live interpretation by the investigator. The exhibit, named “Think Tank”, opened in 1994 and was supported by both visiting and resident scientists. Topic areas of study included observational learning (Shumaker, 1997), object permanence (de Blois et al, 1998), mirror self-recognition (Shillito et al., 1999), magnitude discrimination and ordination (Shumaker et al., 2001), theory of mind (Shillito et al., 2005), and serial list learning (Swartz et al., 2007). The decision to fully embrace the process of scientific investigation as a core component for a permanent exhibit in a zoo was unprecedented. As a result, Think Tank changed the trajectory of cognitive research with great apes in the US.

In 2004, the Lincoln Park Zoo opened the Regenstein Center for Great Apes, which houses chimpanzees and gorillas (Ross, 2017). The facility focuses on comparative cognition, routinely presents cognitive tasks via touch-sensitive computer interfaces (Ross, 2009; Ross, 2017) and has explored topics including tool use (Ross et al., 2010), the impact of a social model on ape memory (Howard et al., 2017), social tolerance and sharing (Calcutt et al. 2014), and factors that impact the success of chimpanzee problem solving (Hopper et al., 2014). The philosophy of the Regenstein Center emphasizes welfare and structures all studies so that they are voluntary for the apes and conducted in view of visitors (Ross, 2017). Ross (2017) states that “research on display” offers the benefits of “transparency in the scientific methodology and promotes the importance of scientific research to a wide audience”.

Zoo Atlanta followed in 2007 with their “Learning tree”, which offered orangutans the opportunity to engage in cognitive tasks presented via a touch screen apparatus in front of visitors (https://zooatlanta.org/
An assessment of reactions by zoo guests revealed an overwhelmingly positive response (Perdue et al., 2012). Research with great apes at Zoo Atlanta occurs on exhibit with visitors present as well as in off-exhibit areas without visitors (Diamond et al., 2016; Gazes et al. 2017).

Research based in primate centers continues but is less frequent than in the past. Examples include Hopkins (pers. comm.) who studies auditory learning in chimpanzees at the Yerkes Regional Primate Center and the M. D. Anderson Cancer Center in Bastrop, Texas. Brosnan (pers. comm) also has an ongoing research program at M. D. Anderson studying decision-making in chimpanzees through experimental economics tasks. The Living Links Center is not active, and the future for this site is unclear.

As of early 2018, all university-based projects with great apes have closed. The Ape Cognition and Conservation Initiative (ACCI) in Des Moines, Iowa, houses the only ongoing study of bonobos in the US. The ACCI is focused on research that uncovers the “evolutionary origins of human language, cognition, and behavior” (http://apeinitiative.org/). This unique facility receives support from university-based investigators, and researchers regularly collaborate with zoos for data collection with their bonobos.

Currently, cognitive research projects with great apes are in residence at 4 zoos in the US. They are the Smithsonian National Zoo (Suda-King et al., 2013; Parrish et al, 2014.), Lincoln Park Zoo, Zoo Atlanta, and the Indianapolis Zoo. The project with orangutans started by Shumaker at the Smithsonian National Zoo’s Think Tank in 1993 (Beck et al., 1993; Shumaker et al., 2001) now resides at the Indianapolis Zoo and will be described in greater detail in the following section.

2. Factors promoting success with zoo-based cognitive research programs.

Virtually all modern, accredited zoos acknowledge the complex mental abilities that are present for great apes. Husbandry programs emphasize “environmental enrichment” as a means of providing cognitive stimulation. As categorized by Bloomsmith et al. (1991), enrichment typically falls into the categories of social, physical, nutritional, sensory, and occupational. While all are positive and offer species appropriate activities such as foraging or object manipulation, few to none of the usual forms of enrichment engage the intellectual potential of great apes (Meehan & Mench, 2007). To do this, Meehan and Mench (2007) suggest that frustration and stress are important elements that should be present, while Clark (2011) discusses “challenge” as the essential feature for a task to qualify as “cognitive enrichment”. A simpler and more useful description is that cognitive challenges for great apes must involve learning and problem solving. Additionally, the tasks should be self-paced, allowing the apes to continually progress based on their individual skills, abilities, and interests. When structured in this way, each ape is offered opportunities that are gradually and perpetually challenging, resulting in continuous interest and engagement. Ideally, opportunities to participate would be presented daily. Problem solving may, at times, include some level of healthy frustration that focuses attention and encourages interest. However, it is problematic and inaccurate to suggest that frustration and stress are required for a task to be mentally engaging. Further, measuring “frustration” or “stress” can be unreliable in this context. Metrics that document learning and problem solving are readily available through analysis of performance data on cognitive tasks. These provide a useful means of assessing the value of what is being presented to the ape.

Opportunities for great apes in US zoos to engage in mentally enriching tasks are becoming more common. Hopper’s (2017) review of the literature clearly illustrates that zoo-based cognitive research is increasing. Her analysis of publications from 15 coun-
tries shows that the largest increase has occurred in the US, and the most studied species by far are gorillas, orangutans, chimpanzees, and bonobos.

The Simon Skjodt International Orangutan Center at the Indianapolis Zoo, included in Hopper’s (2017) review, provides an example of a successful cognitive research program for great apes. The Center was conceptualized and designed with two main objectives in mind. The first was to maximize orangutan welfare. The second was to create an increased “connection” for visitors with orangutans that would result in greater concern for their conservation in the wild. The physical facilities, husbandry protocols, and all programs were created to advance these goals. To maximize welfare, it was assumed that the orangutans must have the ability to express a full range of physical, social, and mental behaviors. It was also assumed that witnessing this range of behaviors was the best way to maximize visitor engagement, create a “connection”, and generate concern for conservation in the wild. The dual goals of promoting ape welfare and engaging zoo visitors converged around design features that focus on three primary elements for the apes. These are 1.) promoting species-typical styles of locomotion, 2.) allowing travel for social choice, and 3.) regularly offering cognitive tasks that require learning and problem solving. No attempt was made to address these elements by constructing a facility that appeared to be an artificial forest. Rather, all efforts focused on creating an environment that was “functionally naturalistic” for the apes rather than “aesthetically naturalistic” from a human perspective.

Unlike the African great apes, orangutans are physically and behaviorally adapted for an arboreal lifestyle. Traditional zoo architecture has emphasized terrestrial locomotion for all great apes, which handicaps orangutans and prevents the expression of many species-typical behaviors. To maximize orangutan movement at the Center, indoor areas reach about 18 meters high with both fixed and movable affordances that promote locomotion on all surfaces. Outdoor spaces include an unenclosed tower and cable system reaching about 30 meters high that allows for travel between the 3 buildings and 2 outdoor yards that comprise the entire complex. The concept for this tower system originated with the Smithsonian National Zoo’s “O-Line” which opened in 1993 (Beck et al., 1993), and has been successfully replicated at a small number of other zoos including the Tama Zoo in Tokyo and the Guadalajara Zoo in Guadalajara. The layout of the buildings, yards, and tower system allows for individual choice and tremendous flexibility in social groupings. The apes can choose their location within the complex, as well as their social companions. Data collected over 289 days in 2015, when 7 individuals lived at the Center, revealed 47 different social groupings overall, with an average of 3.6 different social combinations each day. The Center currently houses 12 orangutans, ranging in age from 2 to 40 years old. A corresponding increase is social complexity has resulted.

Cognitive enrichment is structured around hypothesis driven research questions. A clear preference exists for longitudinal studies that include multiple subjects. The primary topics that are investigated at the Center are symbolic representation, numerical competency, social learning, memory, and strategic reasoning. Data collection is conducted by staff scientists and all sessions occur in a demonstration format that occurs with zoo guests in attendance. Most of the work takes place in the Solso Studio, which is equipped with two styles of touch-sensitive computer stations utilized by the apes. The first has a single response screen that requires an ape to work singly. The second is a version of the “arena system” (Martin et al., 2014) which has two adjacent and interconnected multi-touch monitors that function together. One is in the ape space, and the other is in the visitor area. This allows the presentation of diverse types of tasks including the ape working alone, in collaboration with a human partner, or with computer-generated respons-
es that move across the screens. Additionally, multiple other units are available, including a token operated vending machine, a button activated feeder, and a portable touch-panel system. The feeder and portable touch-panel system can be mounted in various locations indoors and outdoors within the complex, and are designed to present specific tasks that encompass research and enrichment, and also allow the apes to express preferences for certain tasks or desired foods and objects. The diverse types of apparatuses, as well as the different tasks that they can offer, have an important effect. All of the orangutans, regardless of age, location within the complex, experience level, or skill with cognitive testing, can engage in rewarding tasks that require learning and problem solving. Importantly, all cognitive work is voluntary for the apes, and based on positive reinforcement. Hunger is never used as a motivator, and all apes receive the same amount of food on the same schedule every day regardless of whether they choose to work or not. External researchers interested in cognitive topics are also hosted by the Zoo. Typically, this work has not been computer based and is characterized well by a series of studies conducted by Lameira et al. (2013; 2016) on vocal learning in orangutans.

Research with the orangutans has occurred daily since the opening of the Center in 2014, with rare disruptions resulting from such things as facility maintenance, repairs, or installation of new computer equipment. For all data collection sessions since 2014, voluntary participation by the apes has occurred 98% of the time, averaged across all individuals. These high rates of engagement, as well as the demonstrable learning, acquisition, and expansion of skills that have occurred, speak to the high levels of motivation that exist for the apes. There should be little surprise that orangutans (and great apes in general) seek out opportunities for mental exercise. Whether in the wild or a zoo, great apes have impressive mental skills. Russon (2014) makes the point succinctly and elegantly when she states that “great ape cognition requires powerful, sophisticated brains.”.

The goal of maximizing orangutan welfare at the Center is being achieved. But is this engaging zoo visitors in a way that advances a conservation ethic? As part of a summative evaluation of the Center, a survey assessing attitudes was implemented. Subjects were first-time visitors between the ages of 25 and 54 with children under the age of 16. A continuous random sampling method was used to select potential participants at the Zoo. A total of 68 groups agreed to participate. All respondents ranked their attitudes to the following 5 questions before their visit, as they exited the Center, and 6 to 8 weeks post visit:

- I am motivated to do something to protect wild orangutans (motivation)
- I feel a connection to orangutans (connection)
- My actions can help save wild orangutans (actions)
- I care about the future of wild orangutans (future)
- I think orangutan conservation matters (conservation)

For respondents who were exiting the Center, the results revealed statistically significant attitudinal changes in all the categories as a result of visiting the orangutan exhibit (Wilcoxon Signed Rank Test, P < .001). Attitudinal changes showed an increased “connection to orangutans” and all reported greater concern for field conservation.

In the follow-up survey 6 to 8 weeks later, attitudinal changes of respondents remained statistically higher than before their trip to the Zoo (Wilcoxon Signed rank with Bonferroni adjustments, P < .001), indicating a long-term effect of their visit to the orangutan Center. The “overall” category shown in Figure 2 includes the responses to all 5 survey questions.

Rates of voluntary participation and documented acquisition of skills demonstrate that orangutans of all ages are highly motivated
Figure 1. Guests who visited the Simon Skjodt International Orangutan Center all reported a positive shift in their attitudes about orangutans and the importance of their conservation.

Figure 2. Attitudinal changes were statistically significant for pre, post, and follow up responses.
to participate in cognitive tasks that require learning and problem solving. These opportunities provide one important means of maximizing great ape welfare in zoos. Guests that observe cognitive research have a stronger connection to orangutans and care more about their conservation in the wild. These effects persist after the zoo visit.

3. Summary

The history of cognitive research with great apes in the United States spans slightly more than 100 years, and began with Robert W. Yerkes. In his era, studies with great apes were overwhelmingly based in primate centers. After this founding generation of scholars, Parker and McKinney (1999) note that an important shift occurred in the field. Studies were largely based on two styles. The first relied on natural history style observations of young apes raised in human homes, with a primary focus on language acquisition. The second style involved research based in laboratory environments that was conducted under strictly controlled conditions. These studies were based in primate centers.

During the 1960s, universities began to host ape cognition projects on site, with Premack as a prime example (Premack & Premack, 1983). Apes living in zoos were not excluded from studies, but were largely unrepresented in the field.

A conceptual shift occurred when the “third generation” of scientists to study great ape cognition began to focus on development and developmental psychology (Parker and McKinney, 1999). As with past projects, this work was based primarily in primate centers, but some high-profile projects were based at universities. Zoo-based studies continued to be rare. What likely explanations exist for these trends?

Primate centers were a clear choice for several reasons. The ubiquity of a wide age range of potential subjects made these facilities well-suited for cognitive work. The largest number of chimpanzees in the US has historically been in laboratory environments, and it is no coincidence that the vast majority of research with great apes on all topics in the US has been conducted with chimpanzees. Research was the specific reason that labs were established, and it is the core of their institutional culture. Experimental work and the associated rigor was a comfortable fit in an environment that was managed at the executive level by scientists with the goal of accommodating other scientists to facilitate their research. These reasons also explain why cognitive research was rare in zoos. Numbers of apes in zoos were always much lower than in labs, and that remains true today. When research did occur in zoos, applied studies that enhanced husbandry and reproduction were prioritized over behavioral and cognitive investigations. Stated directly, theoretical research was largely peripheral to the historical purpose of most zoos, making it a difficult cultural fit. Investigators were also challenged by the nature of working in a zoo environment that allowed far less control compared to a laboratory. Also, the presence of visitors was resented. Patterson (1981) summarized perceptions about working in a zoo perfectly by stating that, “my enjoyment was tempered by the frustrations and crises of pursuing my work in front of gawking visitors”.

University-based projects have been highly visible and contributed significantly to the literature, although the number of great apes housed on university campuses has always been relatively small compared to primate centers and zoos. The mission fit with universities may have been strong, but concerns about expense, ape welfare, risk, and outside scrutiny have outweighed the benefits. Today, there are no apes living on university campuses, and this highly productive era has ended.

Influential work continues in primate centers with chimpanzees, but the number of active projects has significantly decreased. In general, these projects are short-term rather than longitudinal.

A significant shift occurred in the 1990s and cognitive research with zoo-living great
apes began to accelerate. A likely contributing factor included scientific interest in studying all species of great ape in response to a strong chimpanzee bias in the literature. More recently, the number of available great apes in laboratory environments declined as chimpanzees were retired and moved into sanctuaries (Kaiser, 2015), none of which host cognitive research. Modern zoos house species-typical social groupings for apes in enriched and behaviorally naturalistic environments, which is highly compatible with longitudinal studies. For studies of social cognition, these factors are particularly appropriate and desirable (de Waal, 1991). Perhaps most influentially, a culture shift occurred in the zoo community with the realization that cognitive challenges for great apes are valuable, enriching and in perfect alignment with husbandry goals. In contrast to primate centers and universities, zoos are the only sites where research focused on the mental abilities of the great apes is increasing.

Zoos offer a tremendous potential resource for investigators who are interested in great ape mental abilities. In fact, modern zoos meet all the criteria for an optimal research setting as envisioned by Yerkes (1916b). Several factors have proven to be highly beneficial for promoting the success of a zoo-based cognitive research program. Of primary importance are staff scientists and the institutional commitment to authentic mental enrichment as an essential element of care. Hypothesis based research involving learning and problem solving is the best way to provide the cognitive stimulation that great apes in zoos require and deserve.

Current trends suggest that zoos are essential for the future of cognitive research with great apes in the US. As described by de Waal (1991), the opportunity to compare results from zoos with data collected in other settings will provide converging evidence that advances that science of understanding great ape mental abilities. In addition, cognitive studies promote great ape welfare, offer a platform for transformational public education, and provide an effective means to advance support for in situ conservation of great apes.

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