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Spontaneous Preference for Primate Photographs in Sumatran Orangutans (*Pongo abelii*)

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Spontaneous looking preferences were assessed in six zoo-housed orangutans. Orangutans were presented with two photographs simultaneously on two identical laptop computers. Preference was measured by calculating the relative looking time for photographs from each stimulus category, over three studies. Orangutans exhibited moderate interest in looking at photographs, with four orangutans participating in Study 1 and Study 2, and six orangutans participating in Study 3. The results of Study 1 showed that orangutans preferred photographs of unfamiliar orangutans over unfamiliar humans. Study 2 results showed that orangutans preferred photographs of familiar orangutans over unfamiliar orangutans. In Study 3, preferences were assessed using photographs of the nine members of the participants' own orangutan social group. Orangutans preferred photographs of adults over infants, and males over females. Similar studies have reported varied preferences, and we propose that variation is a result of complex demographic and social factors.

Nonhuman primates exhibit intrinsic interest in pictures, and gaze at some pictures longer than others, a behavior that can provide insight into cognition and perception. Typically, animal cognition research employs designs based on trained behaviors or naturalistic observation. However, recording a subject's spontaneous responses to stimuli is an alternative option that involves no prior training and no extrinsic reinforcement, and can occur in a more controlled environment. This paradigm has been used successfully to assess preference for certain categories of pictures in chimpanzees (*Pan troglodytes*, Fujita & Matsuzawa, 1986), rhesus macaques (*Macaca mulatta*, Lacreuse, Martin-Malivel, Lange, & Herndon, 2007), and Bornean orangutans (*Pongo pygmaeus*, Hanazuka, Kurotori, Shimizu, & Midorikawa, 2012; Hanazuka, Shimahara, Tokuda, & Midorikawa, 2013). These results can be compared to experiments using training and food rewards that have shown categorization in great apes (*Sumatran orangutans*, Vonk & MacDonald, 2004; *chimpanzees*, Brown & Boysen, 2000; Tanaka, 2001). Similar outcomes across rewarded and spontaneous methodologies reinforce findings, and show that categorization is a cognitive ability that exists independent of training.

The preferential looking paradigm is a method in which the researcher presents multiple stimuli and measures looking time to assess untrained and unrewarded behavior (Winters, Dubuc, & Higham, 2015). Preferential looking methods were initially developed to assess visual acuity in human infants and animals (Fantz, 1965; Teller, Morse, Borton, & Regal, 1974). Looking time is used as an operational definition of preference, comparing the duration and frequency of looking at different stimuli. The term *preference* is used as an indication of interest or attention and is not synonymous with *liking* in this context. The subject may look at a picture because it is appealing, or because the picture is frightening, or to seek information (Bovet & Vauclair, 2000; Humphrey, 1972; Humphrey & Keeble, 1974). The preferential looking paradigm removes the confounding variable of training effects: when a subject is conditioned to respond to a characteristic of the target stimuli rather than the quality that the researchers are intending to study (Cacchione & Krist, 2004; D'Amato & Van Sant, 1988). Knowing about spontaneous preferences is also important as a basic starting point that takes into account any *a priori* bias that subjects may exhibit to some stimuli over others.

Researchers have consistently found that primates show spontaneous preference for pictures of animals. Humphrey (1972) reported that rhesus macaques preferred pictures of animate rather than inanimate objects, while Hanazuka and colleagues (2012) reported that a Bornean orangutan preferred pictures of mammals with four legs over pictures of inanimate objects. A chimpanzee preferred pictures with humans over pictures without humans (Fujita & Matsuzawa, 1986). Chimpanzees preferred video clips of daily activities of chimpanzees or humans rather than a blank screen (Bloomsmith & Lambeth, 2000). Breaux, Watson, and Fontenot (2012) found chimpanzees preferred pictures of chimpanzee body parts over objects. Preference for pictures of faces has been demonstrated across primate species (Parr, 2011) including capuchins, squirrel monkeys (*Saimiri sciureus*, Anderson, Kuwahata, Kuroshima, Leighty, & Fujita, 2005), a gibbon (*Hylobates agilis*, Myowa-Yamakoshi & Tomonaga, 2001), chimpanzees (Kano & Tomonaga, 2009), and human infants (Turati, Valenza, Leo, & Simion, 2005). Face preference has clear adaptive advantages for primate infants due to prolonged maternal dependency and complex social behavior.

When viewing pictures of their own species, nonhuman primates show preference for particular age/sex characteristics. Japanese macaques (*Macaca fuscata*) and Campbell's monkeys (*Cercopithecus campbelli*) showed spontaneous preference for pictures of infants over adults, which the authors argued was evidence of Konrad Lorenz's theory of hardwired attraction to infant-like "cuteness" characteristics (Sato, Koda, Lemasson, Nagumo, & Masataka, 2012). Preference for pictures of infants was also reported in rhesus macaques (Gerald, Waitt, & Maestripieri, 2006), and stumptailed macaques (*Macaca arctoides*, Demaria & Thierry, 1988). Preferences for different stimulus characteristics also vary across participant demographics. Waitt, Maestripieri, and Gerald (2007) found young nulliparous female rhesus macaques looked at pictures of infants longer than did older multiparous females, a finding consistent with juvenile female interest in allocare. Lacreuse and colleagues (2007) reported that female rhesus macaques in their pre-ovulatory cycle preferred pictures of male over female rhesus macaques. This difference was not seen when subjects were in other stages of the ovulatory cycle, and macaques did not exhibit preferences when presented with photos of male and female humans or chimpanzees at any time during their cycle.

Own-species preference has been found in other nonhuman primates, and would be predicted by evolutionary theories of other-species avoidance (Demaria & Thierry, 1988; Fujita & Watanabe, 1995; Parr, 2011). Fujita and Watanabe (1995) found four out of five species of macaques preferred pictures of their own species over other macaque species (*Macaca nigra*, *M. brunnescens*, *M. hecki*, *M. tonkeana*, and *M. maurus*), and the one species that did not show own-species preference was an isolated island species (*Macaca brunnescens*). Further evidence of hardwired own-species preference was demonstrated when rhesus macaques preferred pictures of their own-species despite being raised with individuals from another macaque species (Fujita, 1993). However, the same study found that Japanese macaques did not have preference for pictures of their own-species when young, it developed in adulthood and was mediated by experience (Fujita, 1993). Thus own-species preference may vary across species according to selection pressures and social factors.

An exception to own-species preference is sometimes seen in comparisons of own-species versus humans. Studies of chimpanzees have varied results in comparisons of humans and chimpanzees (Tanaka, 2003; Tanaka, 2007; Vonk & Vedder, 2013). Bloomsmith and Lambeth (2000) did not find a significant difference in chimpanzee preference for video of humans or chimpanzees. Tanaka (2003) found chimpanzees preferred pictures of humans over chimpanzees, and a follow-up study (Tanaka, 2007) suggested that preference for pictures of humans was a result of social exposure to humans. Eight adult chimpanzees with high human exposure preferred pictures of humans, whereas three young chimpanzees with less human

exposure had no preference or preferred pictures of chimpanzees (Tanaka, 2007). This variability demonstrates that preference must be assessed in multiple situations and contexts across species. Study 1 assessed preference for humans versus orangutans because species preference has not been reported in orangutans, and to add to the chimpanzee findings.

Unrewarded research on spontaneous preference has found some evidence of preference for pictures of familiar individuals over unfamiliar individuals across nonhuman primates, however results vary. A young human-raised gibbon showed preference for a photograph of its caregiver over a photograph of a human stranger (Myowa-Yamakoshi & Tomonaga, 2001). Chimpanzees showed developmental differences in tracking a picture of their mother over a picture of a comparison chimpanzee. Subjects only preferred a picture of their mother between 4-8 weeks of age, but younger (1-4 weeks) and older (8-18 weeks) showed no significant preference, and they also showed no preference for familiar human faces (Myowa-Yamakoshi, Yamaguchi, Tomonaga, Tanaka, & Matsuzawa, 2005). Analysis of neural activity of a conscious chimpanzee showed different event-related brain potentials when viewing pictures of familiar versus unfamiliar chimpanzees, but not familiar versus unfamiliar humans (Fukushima et al., 2013). Hanazuka and colleagues (2013) found an interesting pattern in an investigation of adult Bornean orangutan familiarity preference: individuals preferred pictures of unfamiliar orangutans over current familiar orangutans, but they preferred orangutans familiar from 10 years ago over unfamiliar individuals. However, comparisons could not be balanced for sex across current and former categories due to group constraints: three of four familiar orangutans were male versus all three former acquaintances were female, so the orangutans may have been avoiding current males rather than preferring unfamiliar individuals. Study 2 compared familiar and unfamiliar orangutans, omitting images of adult males at the request of the zoo. This could assess familiarity without aversion due to images of adult males, and contribute a few more subjects to the limited sample sizes characteristic of great ape research.

As discussed above, preference can be influenced by the demographic characteristics of the stimuli and participant (Demaria & Thierry, 1988; Gerald et al., 2006; Lacreuse et al., 2007; Sato, Koda, Lemasson, Nagumo, & Masataka, 2012; Waite et al., 2007). It is useful to compare these preferences across taxa and species characteristics. For example, group-living and solitary primates may show different preferences, or the prolonged maternal dependency of orangutans could be associated with an even more pronounced infant preference. For this reason, Study 3 assessed preference across pairs of all members of the orangutan social group to evaluate age/sex preferences and to account for complex demographic and relationship factors which may be overlooked in previous studies (e.g., using the participant's mother as a stimulus).

This study assessed spontaneous visual preferences in zoo-housed Sumatran orangutans. Orangutans provide a valuable comparison to humans, of particular interest due to our close phylogenetic relationship, sharing a common ancestor with humans 14 million years ago (Goodman et al., 1998). Orangutans are an interesting species to investigate sociality and face perception because they are semi-social semi-solitary, living alone or in mother-offspring dyads that make up loose communities (Singleton & van Schaik, 2002; van Schaik, 1999; van Schaik, Preuschoft, & Watts, 2004). Caregivers of captive orangutans often display pictures or videos, and zoos have recently incorporated touchscreens and iPads into orangutan enrichment programs (Boostrom, 2013; Perdue, Clay, Gaalema, Maple, & Stoinski, 2012), so the study of orangutan preference also has practical applications. Reports of orangutan preferences can aid in research design, to avoid any stimulus confounds due to *a priori* preference. Taken together, spontaneous preference data can shed considerable light on nonhuman primate social behavior, and how these species view their world.

Study 1: Orangutans versus Humans

The preferential looking paradigm was used to measure spontaneous preference for photographs of orangutans in comparison to photographs of humans. Two identical laptop computers presented simultaneous slideshows, one featuring photographs of unfamiliar orangutans and the other featuring photographs of unfamiliar humans. Orangutan looking behavior at each of the slideshows was coded as a measure of preference. We predicted that the orangutans would look preferentially at photographs of orangutans rather than at photographs of humans.

Method

Subjects

Eight orangutans at Toronto Zoo were available to participate but sample sizes fluctuated across Study 1, 2, and 3 due to circumstances and orangutan motivation. The orangutans included an adolescent female (Jahe), an adult male (Molek), and three mother-infant dyads: Puppe and Budi, Ramai and Jingga, Sekali and Kembali. Dinding, an older adult male, died before formal data collection began, but his data were included in the pilot phase. Age/sex and social characteristics are shown in Table 1. We collected data in the off-exhibit enclosures and play areas, and no changes were made to the orangutans' schedule or diet. In order to be included in the study the orangutans were required to remain in the front two meters of the enclosure, and look at each screen at least once during a set of stimuli. The two youngest orangutans, Jingga and Kembali, were often distracted and so did not meet this criterion during Study 1 and 2. Data from two adult female orangutans were excluded from all three studies. One (Puppe) had misaligned eyes so it was difficult to determine the direction of her gaze, and the other (Sekali) was not motivated to participate. We designed the research to concurrently serve as enrichment for the orangutans. Procedures complied with ethical guidelines of the Toronto Zoo and York University.

Table 1
Age/sex Characteristics and Social Relationships of the Subject Orangutans

| Subject | Sex | Age (yrs) | Experimental history | Rearing |
|--|-----|-------------|----------------------|--------------------------------|
| <i>Infants and nulliparous adolescent female</i> | | | | |
| Jingga | F | 1.5 | Naïve | Mother is Ramai |
| Kembali | M | 2 | Naïve | Mother is Sekali |
| Budi | M | 2.5 | Naïve | Mother is Puppe |
| Jahe | F | 11 | Cognitive studies | Mother is Puppe |
| <i>Adult females</i> | | | | |
| Sekali | F | 16 | Cognitive studies | Human and orangutan reared |
| Ramai | F | 23 | Cognitive studies | Captive born, orangutan reared |
| Puppe | F | 41 | Cognitive studies | Wild caught, age is estimated |
| <i>Adult males</i> | | | | |
| Molek | M | 30 | Cognitive studies | Captive born |
| Dinding | M | 50/Deceased | Cognitive studies | Wild caught, age is estimated |

Note. Age is age at time of study. Jahe, Sekali, Ramai, Puppe, Molek, and Dinding had all participated in several cognitive studies, for example rewarded touchscreen categorization experiments (Vonk & MacDonald, 2004; Marsh & MacDonald, 2008).

Materials

Apparatus. Photographs were presented on two identical Apple PowerBook G4 laptop computers with 30.5 cm screens using Microsoft® Office PowerPoint. The laptops were placed at a height of 28 cm from the ground, 30-60 cm apart, and 50-100 cm from the orangutans. Distances varied to optimize viewing angles for infant, adult female, and adult male subjects. Eye orientation was recorded by a video camera on a tripod located between the two screens. Two slideshows, each displaying photographs for five seconds,

were presented simultaneously to the individual subject. Preference was calculated as the proportion of time (in s) that the orangutan spent looking at the target photograph compared to the comparison screen.

Stimuli. The stimuli were color photographs resized to fill at least 50% of the screen. We obtained the stimuli from photographs taken by the research team, zoo staff and volunteers, and through internet searches. All stimuli in Study 1 featured unfamiliar individuals. Photographs of human infants and human adult females were compared to equal numbers of photographs of orangutan infants and orangutan adult females. At the request of the zookeepers, photographs of unknown adult male orangutans were excluded to minimize stress on the orangutans, particularly the adult male subject. Correspondingly, we omitted photographs of adult human males. The two simultaneous slideshows each contained 20 photographs resulting in a total of 40 photographs for each testing session. The 20 comparisons were separated into two units of 10 comparisons, so that a stimulus category displayed sequentially for 10 slides on one screen. This was done to mitigate the effect of any one photograph. We signaled the change of unit, and therefore changing content of slides, with a loud chime sound, two blank slides, and a brief pause. Presentation order was counterbalanced across trials, subjects, and left and right screen locations.

Measures. The data were coded from videotape by two trained coders who were blind to the content and order of the slideshows using TakLin SubTrak software (Takach & Lindtvedt, 2005). Interrater reliability had an overall Cohen's kappa of 0.83. Eye orientation was coded at 0.1s intervals, which was comparable to coding video frame-by-frame. From these data, the total duration of looking behavior and the mean looking time were calculated for each stimulus category. To build on this quantitative data, a second round of coding applied a qualitative code of preferred side for each unit. The coders watched the videotape in real-time and chose a preferred side using a forced-choice judgement of preference (Teller, Morse, Borton, & Regal, 1974) taking into account behavioral indicators of preference, such as leaning closer to one screen, body orientation, double-takes, facial expressions and vocalizations (Rijksen, 1978), as well as perceived looking behavior. Both quantitative and qualitative methods of coding were done with the coder blind to the content of the slideshows and blind to prior codes.

Procedure. We conducted the trials simultaneously for mother-infant pairs, and separately for individuals housed in single enclosures. We called the orangutans' names to alert them that a slideshow was about to begin, and began the testing session when an orangutan was within the front two meters of their enclosure. We did not provide any incentives or food rewards. We presented the slideshow until completion, but ended the slideshow early if the orangutan departed from the front two meters of the enclosure, or exhibited more than a few instances of agitation behavior (e.g., facial expressions and vocalizations). For individuals who did not complete the slideshow up to two additional attempts were provided. Data resulting from duplicated views were removed and only the first instance was used for analysis. Researchers remained hidden behind the apparatus to avoid cueing the orangutans and were blind to the stimuli and slideshow order.

The study was designed to measure spontaneous behavior, so a period of training was neither necessary nor desirable. Two practice slideshows were done to allow for calibration of the apparatus, initial technical difficulties, and orangutan habituation to the researchers and apparatus. Results from these two sessions were not included in the data analysis. Statistics were performed using SPSS v17.0. "Looking time" for categories of photographs was compared across orangutans using a paired sample *t*-test, and then compared within each subject using an Independent Samples *t*-test.

Results and Discussion

Four orangutans met the inclusion criteria. These orangutans looked at the screens on average 59% of the time (range: 27% - 81%), as shown in Table 2. We predicted that the orangutans would prefer photographs of orangutans over photographs of humans. The mean looking time for photographs of orangutans and humans was calculated and compared across subjects using a paired sample *t*-test. Subjects looked at photographs of orangutans, ($M = 1.36$, $SD = 0.38$), significantly longer than photographs of humans, ($M = 0.87$, $SD = 0.36$), $t(3) = 16.81$, $p < 0.001$ (one-tailed, Figure 1). Preference for pictures of orangutans over pictures of humans was compared for each subject using an independent samples *t*-test, with significant preference found in Jahe and Ramai (Table 2).

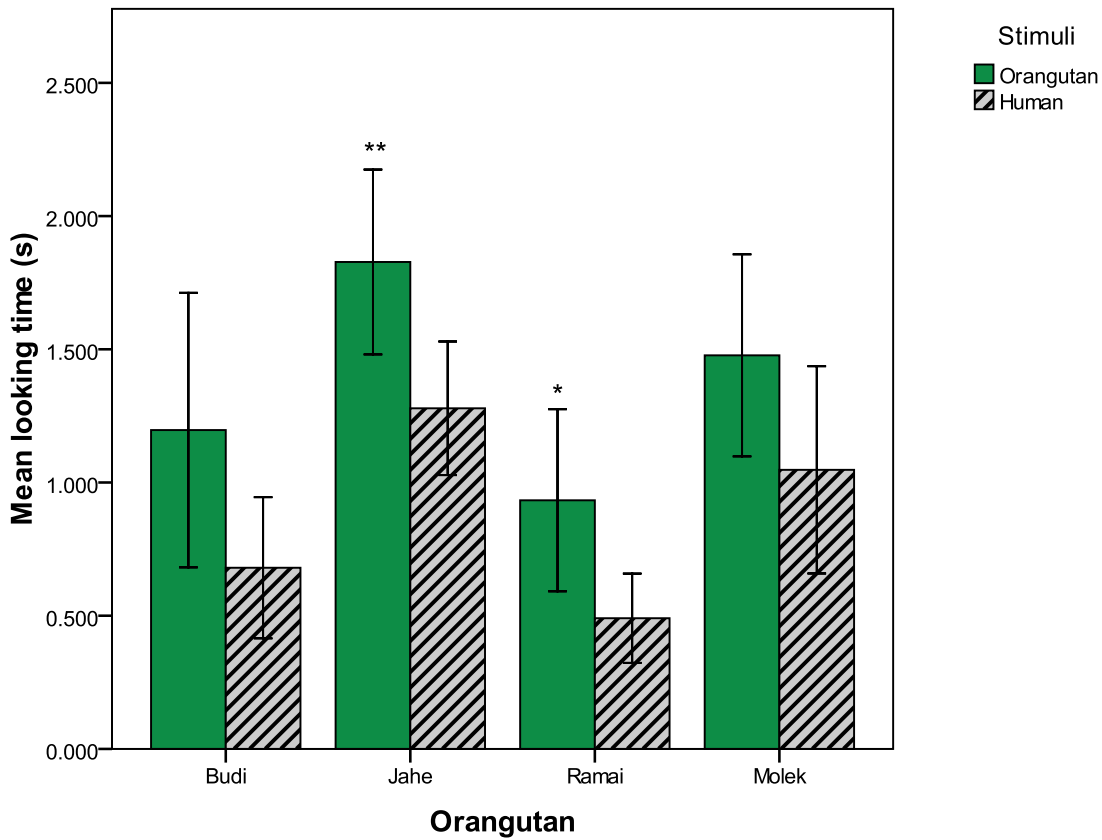


Figure 1. Mean time looking at photographs of orangutans and photographs of humans (* $p < 0.05$, ** $p < 0.01$, error bars indicate 95% confidence intervals).

Table 2
Participation and Looking Time (seconds) at Photographs of Orangutans and Humans

| Subject | Time looking | Orangutan <i>M (SD)</i> | Human <i>M (SD)</i> | <i>t(df)</i> | <i>p</i> (one-tailed) | Qualitative preference |
|---------|--------------|----------------------------|------------------------|--------------|--------------------------|------------------------|
| Budi | 50.3% | 1.20 (1.43) | 0.68 (0.48) | 1.36(45) | 0.091 | Orangutan |
| Jahe | 80.7% | 1.83 (1.26) | 1.28 (0.82) | 2.484(90.4) | 0.006** | Orangutan |
| Ramai | 27.0% | 0.93 (1.01) | 0.49 (0.45) | 2.364(50.1) | 0.011* | Orangutan |
| Molek | 70.7% | 1.48 (1.40) | 1.05 (1.29) | 1.578(98) | 0.059 | Orangutan |

Note. For the remaining analysis orangutan subjects are listed in order by age-sex group: infants, adolescent, adult females, adult male. Data only include times when the orangutans were within the first two meters of the enclosure, videotape was clear and unobstructed, photographs were present on both screens, and eyes were open (blinks removed).

* $p < 0.05$. ** $p < 0.01$

In this study, orangutans clearly preferred viewing photographs of orangutans over photographs of humans. This is consistent with own-species preference in macaques (Demaria & Thierry, 1988; Fujita & Watanabe, 1995; Parr, 2011), however it differs from studies of chimpanzees that found preference for images of humans over chimpanzees (Tanaka, 2003; Tanaka, 2007; Vonk & Vedder, 2013). This finding may differ from the chimpanzee studies due to species differences, or due to different conditions of captivity such as relationship to human caregivers. The Toronto Zoo setting places priority on maintaining social bonds among orangutans rather than with humans.

Study 2: Familiar versus Unfamiliar Orangutans

Method

Study 2 used the same method, apparatus, subjects, and procedure as Study 1 with the exception of the content of the stimuli. The stimuli featured photographs of familiar orangutans and unfamiliar orangutans, with the prediction that orangutans would prefer familiar orangutans. As with Study 1, each slideshow was composed of two units of 10 comparisons, for a total of 40 photographs shown, and we avoided the use of adult males. Photographs compared images of Jahe, an adolescent female member of the group, to one unfamiliar age-matched female orangutan, and photographs of familiar adult females with offspring to matched unfamiliar adult female orangutans with offspring.

Results and Discussion

Preference for familiar versus unfamiliar orangutans was calculated using the same methods as Study 1. The same four orangutans met the inclusion criterion, and average participation rate was 62%, range = 15% -97%, as shown in Table 3. Compared across subjects the mean looking time at familiar orangutans, ($M = 1.70$, $SD = 0.99$), was significantly longer than the unfamiliar orangutans, ($M = 0.93$, $SD = 0.58$), $t(3) = 2.621$, $p = 0.04$ (one-tailed, Figure 2). When compared for each subject using a one-tailed independent samples *t-test*, Budi and Jahe showed a significant preference for familiar orangutans (Table 3). The qualitative data codes matched all the quantitative measures of preference.

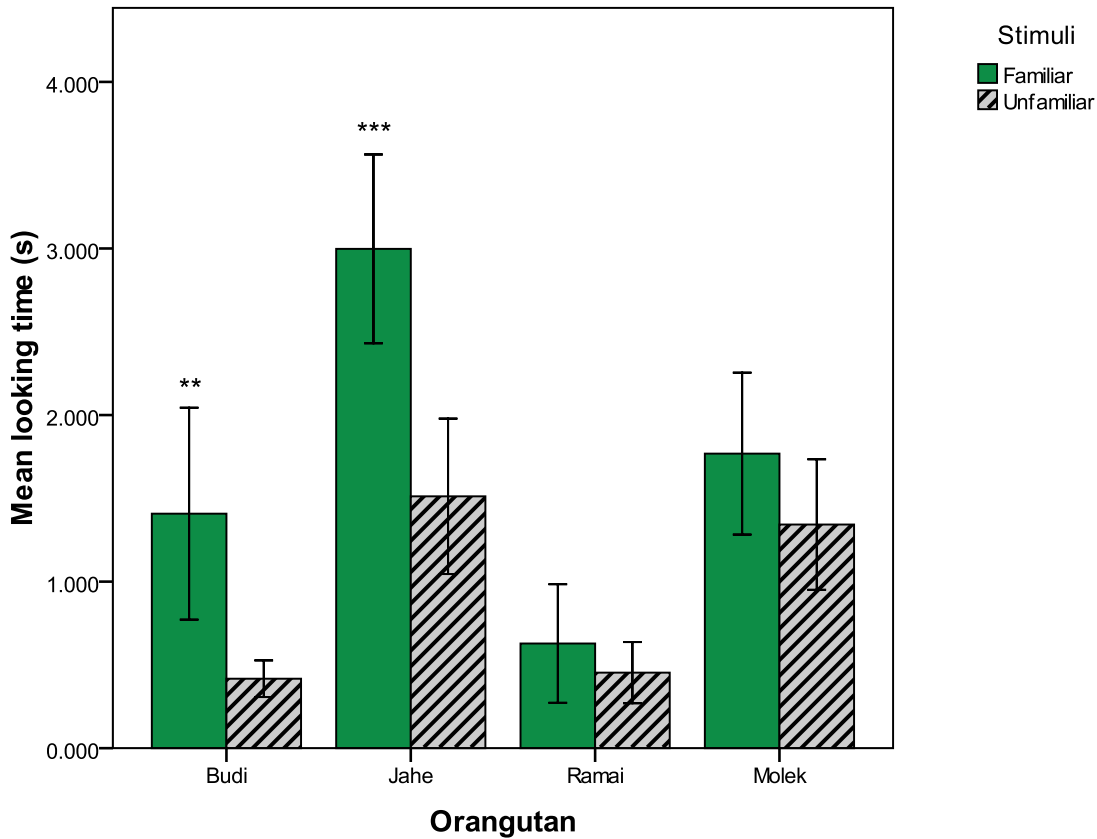


Figure 2. Mean time looking at photographs of familiar and unfamiliar orangutans (** $p < 0.01$, *** $p < 0.001$, error bars indicate 95% confidence intervals).

Table 3
Participation and Looking Time (seconds) at Photographs of Familiar Versus Unfamiliar Orangutans

| Subject | Time Looking | Familiar <i>M (SD)</i> | Unfamiliar <i>M (SD)</i> | <i>t(df)</i> | <i>P</i> (one-tailed) | Qualitative preference |
|---------|--------------|---------------------------|-----------------------------|--------------|--------------------------|------------------------|
| Budi | 29.1% | 1.41 (1.54) | 0.42 (0.26) | 3.167(25.4) | 0.002** | Familiar |
| Jahe | 96.9% | 3.00 (1.68) | 1.51 (1.13) | 4.135(59.0) | <0.001*** | Familiar |
| Ramai | 15.3% | 0.63 (0.50) | 0.45 (0.38) | 1.057(27) | 0.150 | Familiar |
| Molek | 83.7% | 1.77 (1.80) | 1.34 (1.39) | 1.355(104) | 0.089 | Familiar |

** $p < .01$, *** $p < .001$

Results showed a moderate preference for photographs of familiar orangutans over unfamiliar orangutans. Prior research using a matching-to-sample paradigm found that orangutans (*Pongo abelii*) could match photographs of familiar conspecifics, although it was unclear if this matching was due to physical features or recognition of familiar individuals (Vonk & Hamilton, 2014). Note that one of our subjects, Molek,

participated in a prior study (Vonk & MacDonald, 2004). This prior experience did not appear to bias Molek as he did not show significant familiarity preference in our study. Talbot, Mayo, Stoinski, and Brosnan (2015) also tested orangutan (*Pongo spp.*) matching-to-sample for conspecific faces and found that orangutans performed better with familiar conspecifics. As discussed in the introduction, many nonhuman primates have shown preference for images of familiar over unfamiliar individuals (Myowa-Yamakoshi & Tomonaga, 2001; Myowa-Yamakoshi, et al., 2005). Our results are not consistent with Hanazuka and colleagues (2013) who found preference for unfamiliar orangutans over current acquaintances. We propose that this difference is due to social, demographic, and relationship factors.

Context or social factors are likely relevant to familiar versus unfamiliar preferences, such as species characteristics and grouping patterns, for example solitary versus social, and stable versus fluctuating groups (Parr, 2011). Within species, individual differences and relationships may influence preferences. For example, kin may elicit looking behavior, and rivals could either elicit avoidance or vigilant looking. Preference research on familiarity is by nature confounded: comparisons pit preference for conspecifics against preference for novelty (Houston-Price & Nakai, 2004; Roder, Bushnell, & Sasseville, 2000). Further, adult orangutans may have conflicting preferences according to mating strategy, if familiar individuals are paired against potential novel mates and competitors. With the small sample sizes characteristic of great ape research, it is difficult to determine whether familiarity is the driver of behavior or whether other demographic characteristics, social dynamics, and kinship are responsible. The moderate preference for familiarity in the current study may reflect some of these complex social factors, which were further explored in Study 3.

Study 3: Age/sex Factors and Relationship Models

The method, apparatus, subjects, and procedure for Study 3 were identical to Study 1 and 2, however, the content of the stimuli and number of photographs differed. The stimuli were paired-comparisons of photographs of all nine resident orangutans at Toronto Zoo, so participants viewed photos of themselves and their close conspecifics. Each slideshow included 10 pairings of orangutan individuals. Each pairing showed five sequential comparisons of these individuals, for a total of 50 slides on each computer. Four testing sessions were required to show all 36 comparisons of individuals. We removed the background of the photographs using Adobe Photoshop so the stimuli displayed the orangutan on a white background.

We predicted orangutans would show different preferences according to the age/sex characteristics of both the subject (subject-orangutan) and the photo stimuli (stimulus-orangutan). We evaluated preference using comparisons of photographs of all of the orangutans at the zoo. The time spent looking at each stimulus-orangutan was calculated. We assessed age/sex classes of stimuli, comparing time looking at infants versus adults, and adult females versus adult males. We did not predict directional preferences, so two-tailed *p*-values were used. The adolescent Jahe was excluded from age comparisons because she was at an intermediate age, entering puberty at the time of testing.

Results and Discussion

Six orangutans met the inclusion criterion, including the young Jingga and Kembali. All subjects watched at least 30% of the time, ($M = 48.90\%$, $SD = 19.29$), range 31%-83%. Consistent with Study 1 and 2, Molek and Jahe had the highest participation. A paired samples *t*-test across subjects compared the proportion of time looking at photographs of infants versus adults, when displayed simultaneously. Proportionate time

looking at photographs of adults, ($M = 0.64$, $SD = 0.09$), was longer than time looking at photographs of infants, ($M = 0.36$, $SD = 0.09$), $t(5) = 3.94$, $p = .011$, $d = 3.11$, 95% CI [0.10, 0.47]. The mean duration of time spent looking at adults versus infants compared for each subject was not different, with the exception of Jahe who looked at adults ($M = 1.49$, $SD = 1.21$) for longer than infants, ($M = 1.00$, $SD = 0.71$), $t(154.78) = 3.28$, $p = 0.001$, $d = 0.49$, 95% CI [0.19, 0.78] (Figure 3).

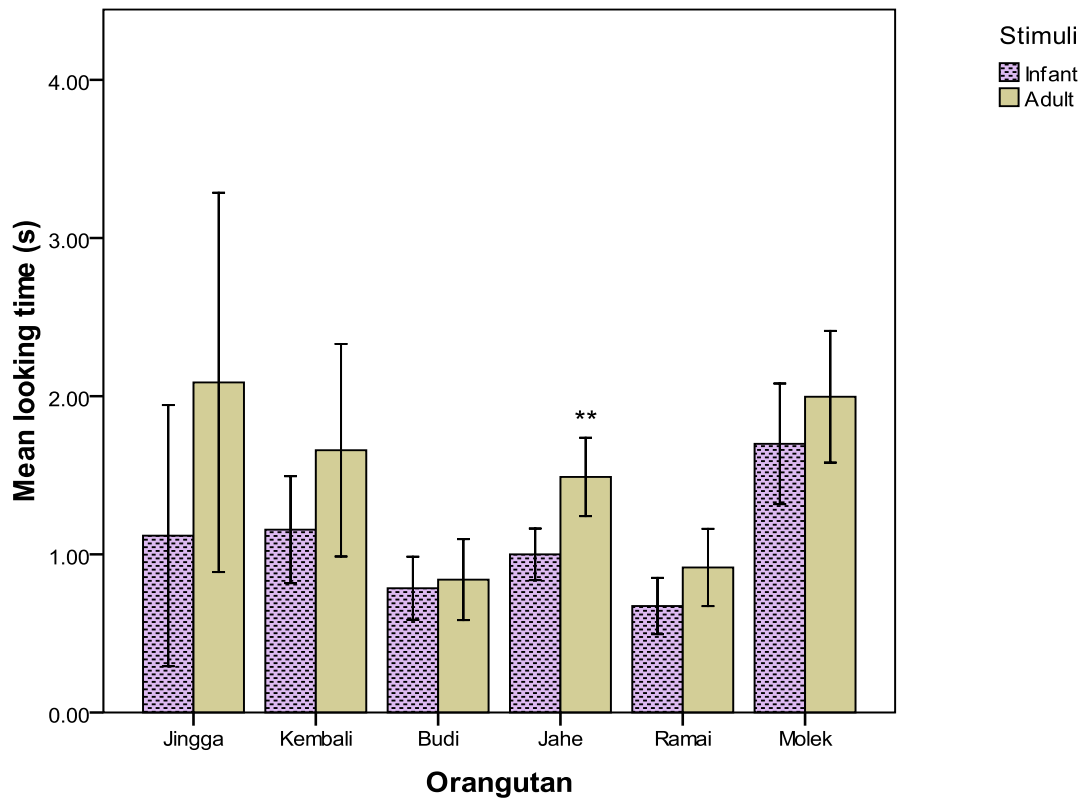


Figure 3. Mean time looking at photographs of infants or adults. Calculated using all simultaneous presentations of an infant and an adult (** $p < .01$, error bars indicate 95% confidence intervals).

When photographs of familiar female and male orangutans were presented, orangutans looked at photographs of males proportionately longer than females. A paired sample t -test across subjects compared the proportion of time looking at adult females versus time looking at adult males, when displayed simultaneously. The proportionate time looking at photographs of males, $M = 0.64$, $SD = 0.11$, was longer than time looking at photographs of females, ($M = 0.37$, $SD = 0.11$), $t(5) = 2.96$, $p = 0.03$, $d = 2.46$, 95% CI [0.04, 0.50]. When compared for each subject, Jahe looked longer at males, ($M = 2.17$, $SD = 1.82$), than females, ($M = 1.31$, $SD =$

1.09), $t(51.3) = 2.36, p = 0.02, d = 0.57, 95\% CI [0.13, 1.59]$, and Ramai also looked at males, $M = 2.66, SD = 2.10$, longer than females, ($M = 0.57, SD = 0.45$), $t(13.81) = 3.68, p = 0.003, d = 1.38, 95\% CI [0.87, 3.32]$ (Figure 4). After the age/sex differences were assessed for each stimulus-orangutan, we planned to assess preference across the age/sex characteristics of the subject-orangutans, relationships (i.e., mother and offspring), and interactions thereof. However, all subjects showed longer average looking time for adults over infants, and all but one subject (Kembali) preferred males over females.

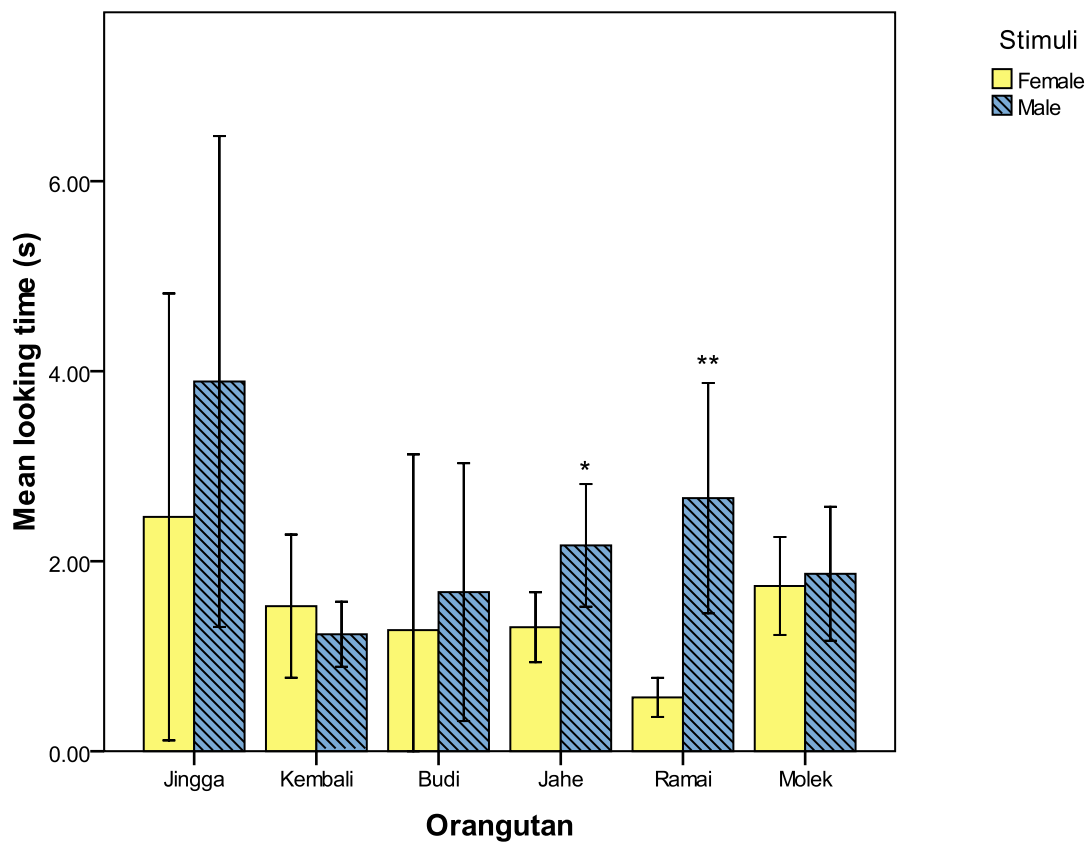


Figure 4. Mean time looking at photographs of females and males. Calculated using all simultaneous presentations of a female and a male (* $p < 0.05$, ** $p < 0.01$, error bars indicate 95% confidence intervals).

Orangutans spent more time watching the slideshows in Study 3 than the two previous studies. They demonstrated moderate preference for adults over infants, and males over females. Observed orangutan preference for photographs of adults over infants differed from research reporting preference for infants over adults in female rhesus macaques (Gerald et al., 2006), and Japanese macaques and Campbell’s monkeys (Sato et al., 2012). Our findings do not support the idea that orangutans have an evolved preference for “cuteness” as suggested by Sato and colleagues (2012), or it may be that interest in adult males outweighed the cuteness

effect. The preference for photographs of adult male orangutans over adult female orangutans was also in opposition to macaque research that reported preference for the opposite sex (Lacreuse et al., 2007), and prior observations with these orangutans (Marsh & MacDonald, 2008).

Different findings may reflect species-differences between orangutans and macaques, relating to species-typical patterns in dominance and social group organization, or may be a result of demographic and social characteristics of these particular individuals. We did not see differences in age preference between female and male subjects. Individual factors could also explain this discrepancy, e.g., prior social conflict between our adult females could have increased looking time at rivals, obscuring infant preference. Dinding's recent death could have influenced the higher looking time at adult males, however images of Molek were also preferred. Complex social and relationship factors make Study 3—and the results of previously published research—difficult to definitively interpret.

General Discussion and Conclusions

In Study 1 orangutans preferred photographs of their own species over photographs of humans, a result consistent with macaque own-species preference (Fujita & Watanabe, 1995; Parr, 2011) but differing from chimpanzee preference for pictures of humans over chimpanzees (Tanaka, 2003; Tanaka, 2007; Vonk & Vedder, 2013). In Study 2, orangutans showed a moderate preference for familiar over unfamiliar orangutans, similar to mixed reports of familiarity preference (Hanazuka et al., 2013; Myowa-Yamakoshi et al., 2005; Myowa-Yamakoshi & Tomonaga, 2001; Parr, 2011). In Study 3, the orangutans preferred photos of adults over infants which differs from reports of infant preference in other species (Gerald et al., 2006; Sato et al., 2012). The orangutans also preferred photos of males over females, which differs from previous reports of opposite sex preference (Lacreuse et al., 2007; Marsh & MacDonald, 2008).

The variability in findings across preference research likely reflects multiple interacting variables including species, social factors, and individual characteristics and experience. Preferences may vary across species, and the species niche such as diet and grouping pattern could select for a bias in attention to certain stimuli. Preferences may also depend on the situation and conditions of captivity and rearing, including amount and quality of relationships with humans and conspecifics, group dynamics, and housing. Finally, preference may depend on individual differences, temperament, and demographic characteristics of the subject. For example, Fujita and Watanabe (1995) found species preference was less pronounced in female macaques than males (*Macaca nigra*). Sekali (adult female) was excluded due to low participation rate, however her limited data differed from the other orangutans. This is interesting to note because she had been partially human-reared, potentially supporting the social exposure hypothesis of Tanaka (2007).

Unfortunately, small sample sizes in great ape research make it difficult to account for interactions across age, sex, and relationships of both the individual participating and the individual featured in stimuli. The three adult females were mothers of young offspring, which could be associated with different preferences; for example, avoidance of certain individuals due to infanticide risk. Relationship models would predict preference for some members of the social group over others; for example, mother-infant pairs may prefer pictures of each other. A supposed preference for females could be a preference for pictures of the subject's own mother, a distinction that is hard to assess with small samples. Study 3 was an attempt to account for relationship factors; however, no relationship trends were noted, and this may be too complex a question to assess with the small samples characteristic of great ape research. Nulliparous rhesus macaques showed higher infant preference than multiparous female macaques (Waite et al., 2007). Jahe, our only nulliparous adolescent

female, did not show infant preference. In some cases, social interests may cancel each other out: infants elicit looking behavior, but so do potential sexual partners and competitors. As discussed in the introduction, preference is not synonymous with liking: individuals may look longer at certain pictures due to fear, attraction, negative associations, or attachment. Preference may be influenced by further factors not measured, such as ovulatory cycle (Lacreuse et al., 2007). The varied research reports of preference likely reflect the complexity of the social factors, relationships, and demographics of captive primates.

The demonstrated preferences provide insight into the perceptual world of orangutans by showing what orangutans look at spontaneously. It is difficult to reveal inner mechanisms; for example, a demonstrated preference for own-species could employ sophisticated cognitive processes or it could be explained by more simple innate mechanisms. However, significant differences in looking time for different categories, such as humans versus orangutans, at minimum are evidence that some difference is perceived between these categories. Likewise, preference for either familiar or unfamiliar orangutans, regardless of which is preferred, is indicative of potential nonhuman primate ability to recognize familiar individuals from pictures without training. Ability to recognize individuals is likely important to successful group membership, and if a nonhuman primate can recognize a conspecific from a picture using two dimensional visual cues without other indicators, then this can inform our understanding of primate perception. These findings complement the findings of other experimental designs, such as matching-to-sample of familiar and unfamiliar conspecifics (*orangutans*: Talbot et al., 2015; Vonk & Hamilton, 2014; *chimpanzees*: Martin-Malivel & Okada, 2007; Parr, Siebert, & Taubert, 2011), and provides evidence that orangutans do not need training to distinguish these stimuli. Better understanding of picture perception is essential because of the prevalent use of pictures in research. DeLoache, Pierroutsakos, and Uttal (2003) argue overestimating pictorial competence of human infants is a methodological problem, and that use of pictorial versus real stimuli might explain some controversies in human infant research.

The participation rates of the orangutans varied, showing that this spontaneous looking paradigm is useful with some but not all subjects. The youngest individuals had low participation, instead choosing to engage in high energy active play. Jahe (adolescent female) and Molek (adult male) exhibited high rates of interest, watching the majority of the slideshows on all occasions. Overall the looking preference apparatus functioned as a source of enrichment, however, given the discrepant levels of interest and motivation across individuals and studies, caregivers should first assess individuals' interest before implementing an enrichment program (MacDonald & Ritvo, 2016; Ritvo & MacDonald, 2016).

The preferential looking paradigm is useful when there is a large preference effect size. However this method may not be useful to assess subcategories and smaller distinctions. For example, comparisons of high and low interest stimuli (e.g., animal versus non-animal) can be distinguished by looking time. The comparisons in the current research, particularly Study 3, both featured attractive photos making it difficult to detect differential looking at a marginally more attractive category. Difficulty in distinguishing preference with finer grained category differences was demonstrated in chimpanzees: they preferred video of humans and chimpanzees over a blank screen; however, there were no specific content preferences across comparisons of humans versus chimpanzees, or videos of different activities (Bloomsmith & Lambeth, 2000). Breaux and colleagues (2012) found that chimpanzees preferred pictures of chimpanzee body parts over inanimate objects, but did not find the predicted preference for specific characteristics of sexual body parts in comparison to other body parts. Finer grained distinctions may be particularly difficult if there are competing interests; for example, familiarity versus novelty. Human infant research reports looking preference both for familiar stimuli in some cases but there is also an established preference for novelty (Houston-Price & Nakai, 2004; Roder et al., 2000). These competing preferences must be accounted for in human infant research design. Novelty of stimuli could

influence research outcomes, for example, in the case of Breaux and colleagues (2012) chimpanzees did not prefer photos of the predicted pink sexual swellings over photos of (artificially created) green sexual swellings. Perhaps preference for a typical sign of sexual receptivity was obscured by the novelty of the artificial comparison stimuli. The complex patterns of preference in chimpanzees and orangutans (Hanazuka et al., 2013; Tanaka, 2007; Vonk & Vedder, 2013) are not surprising given their close phylogenetic relationship to humans. To our knowledge similar studies have not been conducted with human adults, but we would estimate that results may show similar complexity; that is, humans may show conflicting preference for cute infants versus attractive adults.

The preferential looking paradigm has limitations, however as discussed, it has advantages as it removes the risk of training effects and focuses on voluntary behavior (for a review of the looking time paradigm see Winters et al., 2015). Participation in this paradigm is solely motivated by intrinsic interest, so preference research is non-invasive and can concurrently function as enrichment. The paradigm provides a valuable alternative perspective to experiments based on extensive training or to naturalistic observation. Kano and Tomonaga (2009) demonstrated that eye-tracking technology could be used to measure looking time in chimpanzees. This avoids time-consuming coding so we hope that eye-tracker expense and feasibility will improve to allow use with free-moving untrained subjects from a wide range of species in non-laboratory settings.

It is important to document preferences to better understand how a species views their world, to inform cognition research, and to limit confounding variables in research that employs pictures as experimental stimuli. Spontaneous preferences, like those demonstrated here, show that orangutans are able to perceive and distinguish some aspects of photographs without training, which suggests that orangutans may look at photographs as humans do, with varied influence from social relationships, experience, and demographics.

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References

- Anderson, J. R., Kuwahata, H., Kuroshima, H., Leighty, K. A., & Fujita, K. (2005). Are monkeys aesthetists? Rensch (1957) revisited. *Journal of Experimental Psychology: Animal Behavior Processes*, *31*, 71–78.
- Bloomsmith, M. A., & Lambeth, S. P. (2000). Videotapes as enrichment for captive chimpanzees (*Pan troglodytes*). *Zoo Biology*, *19*, 541–551.
- Boostrom, H. (2013). *Problem-Solving with Orangutans (Pongo pygmaeus and Pongo abelii) and Chimpanzees (Pan troglodytes): Using the iPad to Provide Novel Enrichment Opportunities* (Doctoral dissertation, Texas A&M University).
- Bovet, D., & Vauclair, J. (2000). Picture recognition in animals and humans. *Behavioural Brain Research*, *109*, 143–165.
- Breaux, S. D., Watson, S. L., & Fontenot, M. B. (2012). A free choice task evaluating chimpanzees' preference for photographic images of sex swellings: Effects of color, size, and symmetry. *International Journal of Comparative Psychology*, *25*(2).
- Brown, D. A., & Boysen, S. T. (2000). Spontaneous discrimination of natural stimuli by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *114*, 392–400.
- Cacchione, T., & Krist, H. (2004). Recognizing impossible object relations: Intuitions about support in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *118*, 140–148.

- D'Amato, M. R., & Van Sant, P. (1988). The person concept in monkeys (*Cebus apella*). *Journal of Experimental Psychology: Animal Behavior Processes*, *14*, 43–55.
- DeLoache, J. S., Pierroutsakos, S. L., & Uttal, D. H. (2003). The origins of pictorial competence. *Current Directions in Psychological Science*, *12*, 114–118.
- Demaria, C., & Thierry, B. (1988). Responses to animal stimulus photographs in stumptailed macaques (*Macaca arctoides*). *Primates*, *29*, 237–244.
- Fantz, R. L. (1965). Visual perception from birth as shown by pattern selectivity. *Annals of the New York Academy of Sciences*, *118*, 793–814.
- Fujita, K. (1993). Development of visual preference for closely related species by infant and juvenile macaques with restricted social experience. *Primates*, *34*, 141–150.
- Fujita, K., & Matsuzawa, T. (1986). A new procedure to study the perceptual world of animals with sensory reinforcement: Recognition of humans by a chimpanzee. *Primates*, *27*, 283–291.
- Fujita, K., & Watanabe, K. (1995). Visual preference for closely related species by Sulawesi macaques. *American Journal of Primatology*, *37*, 253–261.
- Fukushima, H., Hirata, S., Matsuda, G., Ueno, A., Fuwa, K., Sugama, K., ... Hasegawa, T. (2013). Neural representation of face familiarity in an awake chimpanzee. *PeerJ*, *1*, e223.
- Gerald, M. S., Waitt, C., & Maestriperi, D. (2006). An experimental examination of female responses to infant face coloration in rhesus macaques. *Behavioural Processes*, *73*, 253–256.
- Goodman, M., Porter, C. A., Czelusniak, J., Page, S. L., Schneider, H., Shoshani, J., ... Groves, C. P. (1998). Toward a phylogenetic classification of primates based on DNA evidence complemented by fossil evidence. *Molecular Phylogenetics and Evolution*, *9*, 585–598.
- Hanazuka, Y., Kurotori, H., Shimizu, M., & Midorikawa, A. (2012). Visual discrimination in an orangutan (*Pongo pygmaeus*): Measuring preference. *Perceptual and Motor Skills*, *114*, 429–432.
- Hanazuka, Y., Shimahara, N., Tokuda, Y., & Midorikawa, A. (2013). Orangutans (*Pongo pygmaeus*) remember old acquaintances. *PLoS One*, *8*, e82073.
- Houston-Price, C., & Nakai, S. (2004). Distinguishing novelty and familiarity effects in infant preference procedures. *Infant and Child Development*, *13*, 341–348.
- Humphrey, N. K., & Keeble, G. R. (1974). The reaction of monkeys to "fearsome" pictures. *Nature*, *251*, 500–502.
- Humphrey, N. K. (1972). "Interest" and "pleasure": Two determinants of a monkey's visual preferences. *Perception*, *1*, 395–416.
- Kano, F., & Tomonaga, M. (2009). How chimpanzees look at pictures: a comparative eye-tracking study. *Proceedings of the Royal Society of London B: Biological Sciences*, *276*, 1949–1955.
- Lacreuse, A., Martin-Malivel, J., Lange, H. S., & Herndon, J. G. (2007). Effects of the menstrual cycle on looking preferences for faces in female rhesus monkeys. *Animal Cognition*, *10*, 105–115.
- MacDonald, S. E., & Ritvo, S. (2016). Comparative cognition outside the laboratory. *Comparative Cognition & Behavior Reviews*, *11*, 49–61.
- Marsh, H. L., & MacDonald, S. E. (2008). The use of perceptual features in categorization by orangutans (*Pongo abelli*). *Animal Cognition*, *11*, 569–585.
- Martin-Malivel, J., & Okada, K. (2007). Human and chimpanzee face recognition in chimpanzees (*Pan troglodytes*): Role of exposure and impact on categorical perception. *Behavioral Neuroscience*, *121*, 1145–1155.
- Myowa-Yamakoshi, M., & Tomonaga, M. (2001). Development of face recognition in an infant gibbon (*Hylobates agilis*). *Infant Behavior and Development*, *24*, 215–227.
- Myowa-Yamakoshi, M., Yamaguchi, M. K., Tomonaga, M., Tanaka, M., & Matsuzawa, T. (2005). Development of face recognition in infant chimpanzees (*Pan troglodytes*). *Cognitive Development*, *20*, 49–63.
- Parr, L. A. (2011). The evolution of face processing in primates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*, 1764–1777.
- Parr, L. A., Siebert, E., & Taubert, J. (2011). Effect of familiarity and viewpoint on face recognition in chimpanzees. *Perception*, *40*, 863–872.
- Perdue, B. M., Clay, A. W., Gaalema, D. E., Maple, T. L., & Stoinski, T. S. (2012). Technology at the zoo: The influence of a touchscreen computer on orangutans and zoo visitors. *Zoo Biology*, *31*, 27–39.
- Rijksen, H. D. (1978). A field study on Sumatran orang-utans (*Pongo pygmaeus abelii*, Lesson 1827): Ecology, behaviour and conservation (Doctoral dissertation). Wageningen (Netherlands): H. Veenman & Zonen.

- Ritvo, S. E., & MacDonald, S. E. (2016). Music as enrichment for Sumatran orangutans (*Pongo abelii*). *Journal of Zoo and Aquarium Research*, 4, 156–163.
- Roder, B. J., Bushnell, E. W., & Sasseville, A. M. (2000). Infants' preferences for familiarity and novelty during the course of visual processing. *Infancy*, 1, 491–507.
- Sato, A., Koda, H., Lemasson, A., Nagumo, S., & Masataka, N. (2012). Visual recognition of age class and preference for infantile features: Implications for species-specific vs universal cognitive traits in primates. *PLoS One*, 7, e38387.
- Singleton, I., & van Schaik, C. P. (2002). The social organisation of a population of Sumatran orang-utans. *Folia Primatologica*, 73, 1–20.
- Takach, S.G., & Lindtvedt, K. (2005). *TakLin SubTrak* Coding Program (Version 2.1) [Computer software], New York: College of Staten Island, Retrieved March 8, 2009, from www.TakLin.com.
- Talbot, C. F., Mayo, L., Stoinski, T., & Brosnan, S. F. (2015). Face discriminations by orangutans (*Pongo spp.*) vary as a function of familiarity. *Evolutionary Psychological Science*, 1, 172–182.
- Tanaka, M. (2001). Discrimination and categorization of photographs of natural objects by chimpanzees (*Pan troglodytes*). *Animal Cognition*, 4, 201–211.
- Tanaka, M. (2003). Visual preference by chimpanzees (*Pan troglodytes*) for photos of primates measured by a free choice-order task: Implication for influence of social experience. *Primates*, 44, 157–165.
- Tanaka, M. (2007). Development of the visual preference of chimpanzees (*Pan troglodytes*) for photographs of primates: Effect of social experience. *Primates*, 48, 303–309.
- Teller, D. Y., Morse, R., Borton, R., & Regal, D. (1974). Visual acuity for vertical and diagonal gratings in human infants. *Vision Research*, 14, 1433–1439.
- Turati, C., Valenza, E., Leo, I., & Simion, F. (2005). Three-month-olds' visual preference for faces and its underlying visual processing mechanisms. *Journal of Experimental Child Psychology*, 90, 255–273.
- van Schaik, C. P. (1999). The socioecology of fission-fusion sociality in orangutans. *Primates*, 40, 69–86.
- van Schaik, C. P., Preuschoft, S., & Watts, D. P. (2004). Great ape social systems. In A. E. Russon & D. R. Begun (Eds.), *The evolution of thought: Evolutionary origins of great ape intelligence* (pp. 190–209). Cambridge, England: Cambridge University Press.
- Vonk, J., & MacDonald, S. E. (2004). Levels of abstraction in orangutan (*Pongo abelii*) categorization. *Journal of Comparative Psychology*, 118, 3–13.
- Vonk, J., & Vedder, C. E. (2013). A zoo-housed chimpanzee's (*Pan troglodytes*) responses to potentially arousing stimuli. *International Journal of Comparative Psychology*, 26(3).
- Vonk, J., & Hamilton, J. (2014). Orangutans (*Pongo abelii*) and a gorilla (*Gorilla gorilla gorilla*) match features in familiar and unfamiliar individuals. *Animal Cognition*, 17, 1089–1105.
- Waite, C., Maestripieri, D., & Gerald, M. S. (2007). Effects of parity and age on female attraction to faces of infants and neonates in rhesus macaques. *Primates*, 48, 164–167.
- Winters, S., Dubuc, C., & Higham, J. P. (2015). Perspectives: The looking time experimental paradigm in studies of animal visual perception and cognition. *Ethology*, 121, 625–640.

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