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A Comparison of Chimpanzee (Pan Troglodytes) Responses to Caregiver Use of Positive Reinforcement Training (PRT) and Species-Specific Behaviors (SSB)

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A COMPARISON OF CHIMPANZEE (*PAN TROGLODYTES*) RESPONSES TO CAREGIVER USE OF POSITIVE REINFORCEMENT TRAINING (PRT) AND SPECIES-SPECIFIC BEHAVIORS (SSB)

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ABSTRACT

A COMPARISON OF CHIMPANZEE (*PAN TROGLODYTES*) RESPONSES TO CAREGIVER USE OF POSITIVE REINFORCEMENT TRAINING (PRT) AND SPECIES-SPECIFIC BEHAVIORS (SSB)

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The present study compared the effects of positive reinforcement training (PRT) and unstructured interactions (UI) on chimpanzee (*Pan troglodytes*) behavior. In the PRT condition, a caregiver interacted with a chimpanzee to condition behaviors for 10 min. In the UI condition, a caregiver interacted without PRT for 10 min. Participants were five chimpanzees in a sanctuary setting. Chimpanzees were also videotaped for 10 min after trials (PTP) and for 10 min in a matched control (MC) period on a different day. From these videotapes experimenters coded chimpanzee behaviors and calculated durations in behavioral contexts. Chimpanzees spent a significantly higher proportion of time in the Affinitive context during PRT and UI than during PTP and MC. Chimpanzees interacted with the caregiver equally often in both PRT and UI conditions. While PRT is useful in husbandry applications, the caregiver's use of chimpanzee behaviors in UIs promotes well-being equally well.

Keywords: positive reinforcement training, operant training, captive chimpanzees, caregiver interaction

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INTRODUCTION AND LITERATURE REVIEW

Introduction

The Animal Plant Health Inspection Service of the U.S. Department of Agriculture (2013) states that captive environments housing nonhuman primates must have management programs that include environmental enhancement to promote psychological well-being. The environmental enhancement plan must include social grouping of all non-exempt individuals and environmental enrichment that encourages species-typical behaviors. For chimpanzees in the wild, the most commonly occurring species-typical behaviors include sleeping, foraging, resting, traveling, and socializing (Pruetz & McGrew, 2001). Enrichment programs provide stimuli to captive nonhuman primates to encourage these behaviors. Physical enrichment can include climbing structures, foraging opportunities, manipulable objects, sensory stimulation, and occupational activities (Brent, 2001). Social interactions with conspecifics or caregivers also serve as enrichment (Brent). Chimpanzees are highly social and those relationships extend to human caregivers (Fouts, Abshire, Bodamer, & Fouts, 1989; Jensvold, 2008).

Opportunities for unstructured interactions between captive nonhuman primates and caregivers have several benefits. Unstructured interactions provide captive individuals with social stimulation, help develop a positive relationship between captive individuals and caregivers, and allow caregivers to be better able to detect changes in individuals that may need to be addressed (Brent, 2001). Studies that further explore the benefits of various types of interactions with caregivers are described below.

Effects of Unstructured Interaction with Caregivers

While there are benefits of unstructured interactions between chimpanzees and caregivers, previous studies have mixed findings on the exact benefits. Baker (2004) conducted a study in which caregivers increased interactions with 12 laboratory chimpanzees by approximately 10 min per chimpanzee per weekday. Interactions included play, grooming, serving food, and talking. The researcher recorded the chimpanzees' behavior for the 30 min after the interaction ended. The interactions were followed by a significant decrease in regurgitation, reingestation and other abnormal oral behaviors, agonistic displays, and inactivity compared to baseline. The interactions also increased grooming behaviors and the chimpanzees were less reactive to the vocalizations and displays of others.

Chelluri, Ross, and Wagner (2013) examined the effect of unstructured interactions between caregivers and zoo-living chimpanzees and Western lowland gorillas (*Gorilla gorilla gorilla*). They compared the amounts of time the apes spent in six behavioral categories during interactions to a matched control period when no direct caregiver interaction had occurred. During trials, 1 of 12 caregivers engaged the apes in play, spontaneous feeding, and other affinitive interactions. Chimpanzees showed significantly higher levels of agonism and attention to the caregiver area, and significantly lower levels of self-directed and prosocial behavior in play, feeding, and positive interaction sessions with caregivers than in matched control periods. Chimpanzees showed no significant differences in abnormal or sexual behavior between the experimental and control periods. Gorillas also showed significantly higher levels of agonism and attention to the caregiver area, and significantly lower levels of self-directed and abnormal behavior in caregiver interaction conditions than in matched control periods. Gorillas showed no significant differences in social or sexual behavior between the experimental and control periods. There was no significant difference in rates of wounding for both chimpanzees and gorillas between interaction and matched control conditions. The results of this study show a significant effect of unstructured interactions with caregivers on changes in chimpanzee and gorilla behavior. They suggest that unstructured interactions with caregivers have an arousing effect, particularly for chimpanzees. The increase in agonism during interactions, although comprising a much lower proportion of their behavior overall, compared to matched control periods, suggests that caregivers can be a source of stress.

The behaviors employed by caregivers during interactions with captive nonhuman primates may influence the quality of the interaction and relationship. Jensvold (2008) compared caregivers' use of chimpanzee behaviors versus human behaviors during 10-min interactions with three zoo-living chimpanzees. The researcher coded video-recorded data of three chimpanzees for behavioral contexts during the interactions. Two of the chimpanzees spent significantly more time interacting with caregivers during the chimpanzee behavior condition than during the human behavior condition. Results varied by chimpanzee, but in the chimpanzee behavior condition chimpanzees spent more time in affinitive social, grooming, play, and serving (food) contexts than in the human behavior condition. In the human behavior condition chimpanzees spent significantly less time interacting with caregivers than in the chimpanzee behavior condition. The types of behaviors caregivers use in interactions with chimpanzees have an effect on chimpanzee well-being, as expressed by the amount of time chimpanzees spend in certain behavioral contexts.

Jensvold, Buckner, and Stadtner (2011) compared the responses of three sanctuary chimpanzees to caregivers' use of either chimpanzee behaviors or human behaviors. The sanctuary chimpanzees' usual interactions with caregivers included the use of chimpanzee behaviors. In this study, caregivers refrained from using chimpanzee behaviors in the human behavior condition. In the human behavior condition, Tatu spent significantly more time in Affinitive Social/Greet and Feeding contexts, Loulis spent significantly more time in Play and Feeding contexts, and Dar spent significantly more time in Groom, Non-Interactive, and Feeding contexts. In the chimpanzee behavior condition, Tatu spent significantly more time in Non-Interactive and Play contexts, Loulis spent significantly more time in Affinitive Social/Greet and Groom contexts, and Dar spent significantly more time in Affinitive Social/Greet and Play contexts. These results indicate that, although individual differences exist, chimpanzees are significantly affected by and sensitive to the behaviors caregivers use during interactions. Whenever possible, caregivers should use chimpanzee behaviors during interactions with chimpanzees.

The benefits of interactions between caregivers and nonhuman primates also extend to monkeys. In an early study with eight singly housed adult rhesus macaques (*Macaca mulatta*), researchers examined the effects of food treat provisioning and human interaction on cage-directed behaviors, self-directed behaviors, stereotypic behaviors, repetitive locomotion behaviors, and self-grooming behaviors (Bayne, Dexter, & Strange, 1993). The researcher exhibited submissive behaviors while giving flavored treats to the macaques and spent 6 min with each monkey per week. Behavior frequencies and durations were measured pre-interaction, during the interaction, and post-interaction. Compared to pre-interaction levels, cage-directed behaviors decreased, self-directed behaviors increased, self-grooming behaviors increased, and stereotypic behavior decreased. Repetitive locomotion behaviors did not change significantly. The results of this study provide further support for the positive effects of unstructured interactions with caregivers.

In a more recent study, Manciocco, Chiarotti, and Vitale (2009) assessed the effects of unstructured interactions between caregivers and socially housed marmosets (*Callithrix jacchus*). Researchers collected data on activity, social behaviors, tension-related behaviors, and vocalizations at baseline and following a 20-min interaction with the caregiver. Following the interaction condition, there was a significant decrease in locomotion, self-scratching, and production of “phee calls,” and a significant increase in grooming and play behaviors. There was no significant difference in rest, exploration, marking behaviors, aggressive or agonistic behaviors directed at the observer, or in abnormal behaviors, which were already low at baseline. These behavioral changes indicate that human interaction with marmosets promotes a more relaxed atmosphere and an improvement in well-being.

Operant Conditioning

The use of operant conditioning, specifically positive reinforcement training (PRT), is increasing in captive settings as a means to manage behavior. PRT is the process whereby an appetitive stimulus is presented after an organism performs a target behavior. The appetitive stimulus acts as reinforcement for performing the behavior, thereby increasing the organism's performance of that particular behavior in the future.

Thorndike (1898) generated the principles of operant conditioning by developing an apparatus to study learned associations in nonhuman animals. The apparatus was a box fitted with a door, which could be opened by loosening a bolt that held the pulley in place. The cats, dogs, and chickens used in the experiments learned to open the door of the apparatus to leave, supporting the theory that nonhuman animals have the capability to form and maintain associations between their actions and the outcomes of those actions.

The training of nonhuman animals to perform behaviors relies on the principles of operant conditioning and positive reinforcement. A popular form of PRT used with nonhuman animals is called clicker training. Clicker training is the use of secondary reinforcement. Skinner (1991) identified secondary reinforcement as a stimulus that acquires reinforcing properties through classical conditioning. Secondary reinforcement is a previously unconditioned stimulus, such as a clicker or verbal praise, which becomes a reinforcer through repeated pairing with a primary reinforcer like food (Laule & Whittaker, 2001). The secondary reinforcer is also referred to as a 'bridge.' The use of a 'bridge' fills the gap between the occurrence of the desired behavior and the delivery of primary reinforcement, and signals to the trainee exactly when he or she performed the desired behavior.

Effects of Operant Conditioning on Nonhuman Primates

Management

Operant conditioning using positive reinforcement techniques has applications for managing captive populations of non-human primates. In particular, PRT can be used to increase compliance with husbandry procedures and to manage relationships between conspecifics and with caregivers. Additionally, several studies have quantified the amount of time necessary to reach reliable performance of trained behaviors for several nonhuman primate species. These qualities of PRT are discussed in the following studies.

Studies targeting the movement of a group of NHPs from one enclosure area to another show a significant increase in compliance when researchers used PRT. Bloomsmith, Stone, and Laule (1998) implemented a voluntary movement program with eight groups of chimpanzees whereby researchers opened doors to an enclosure and gave the command “inside.” After the door was closed and locked, researchers rewarded the cooperative chimpanzees with a preferred food. All chimpanzee groups reached reliable performance, and females reached reliable performance faster than males. These results indicate that PRT is an effective way to increase compliance with voluntary movement and caregivers should take into account individual differences, such as sex, when creating training programs.

Veeder, Bloomsmith, McMillan, Perlman, and Martin (2009) found similar results with sooty mangabeys (*Cerocebus atys atys*). In this study, researchers trained a group of sooty mangabeys to move to different areas of their enclosure using PRT. In training sessions, trainers gave a verbal cue “over” with a visual cue of a hand movement. Trainers rewarded compliance with the verbal praise “good over” and a preferred food. Researchers recorded training time and assessed how dominance rank influenced success rate. Although compliance was high at baseline, performance increased with training but did not reach the intended criteria for reliable performance. Additionally, lower-ranking individuals were less compliant than higher-ranking individuals. Researchers addressed this problem by moving individuals of different ranks into different sections of the enclosure and providing extra reinforcement and enrichment to previously noncompliant individuals. With these changes, compliance of the previously noncompliant individuals reached 100%. These results further support the use of PRT to increase individuals’ cooperation with voluntary movement, and indicate that dominance rank is another factor that caregivers should consider when implementing a PRT program.

In addition to using PRT to increase compliance with movement, caregivers can use PRT to manage interactions between individuals. Schapiro, Perlman, and Bourdreau (2001) examined whether or not PRT is an effective means for increasing affiliative behavior among captive macaques. In this study, researchers assessed 28 female rhesus macaques for levels of affiliation and assigned them to either high- or low-affiliator categories. Researchers randomly selected half of the low-affiliators to receive training to promote time in affiliative interactions. Researchers randomly selected half of the high-affiliators to receive training to reduce time in affiliative interactions. A control group received no training. Researchers recorded socially-directed behaviors and time spent in social proximity. Only one low-affiliator individual engaged in social grooming with a partner after 9 months of training, and other low-affiliators progressed to various preliminary stages of grooming. However, low-affiliators socialized significantly more during sessions outside of training than during training, and approached significance for spending more time affiliating than during baseline. Researchers successfully trained all high-affiliators to remain away from other group members during training, but this effect did not generalize outside of training. These findings suggest that interactions among adult, female, group-housed rhesus macaques may be susceptible to manipulation via PRT.

Minier et al. (2011) used another form of PRT, called contra-aggression training, to reduce human-directed aggression in rhesus macaques. In this study, researchers randomly assigned 15 macaques who exhibited high levels of human-directed aggression to non-training, single trainer, or multiple trainer conditions. In training sessions, caregivers used systematic desensitization, shaping, and differential reinforcement of behaviors incompatible with unwanted behaviors, to reduce caregiver-directed aggression. For example, the trainer used systematic desensitization by rewarding the macaques for calm reactions to the presence of the trainer. The trainer used shaping via clicker training to reinforce successive approximations of desired behaviors. For differential reinforcement of other behaviors, the trainer reinforced a non-aggressive behavior that the macaque exhibited following an aggressive behavior. Researchers exposed monkeys to a human-intruder test and a husbandry-response test 1 week prior to training, 1 week after 6 weeks of training, and 1 week after a 6-week non-training phase.

Researchers recorded aggressive responses. Both single-trainer and multiple-trainer groups showed a significant decrease in human-directed aggression, and this effect remained at 6 weeks post-training. These results suggest that using PRT to reward positive behaviors in interactions between macaques and caregivers can reduce aggressive human-directed behaviors during training and generalize to non-trainers outside of these sessions.

Studies assessing the feasibility of implementing PRT programs with captive nonhuman primates have positive results. For example, Coleman et al. (2008) conducted a study to demonstrate the use PRT to train rhesus macaques to present for venipuncture in a reasonable amount of time. Researchers trained eight adult male rhesus macaques and four adult chimpanzees using PRT to place an arm in a blood sleeve and remain stationary for venipuncture. As a result, six (of eight) macaques and all four chimpanzees placed their arm in a sleeve, held a peg, and remained stationary for venipuncture. The researchers had to conduct significantly more sessions with the macaques than with the chimpanzees to reach reliability. This study demonstrates that macaques, in addition to chimpanzees, can be trained to present for medical procedures such as venipuncture.

Another study examined whether or not squirrel monkeys (*Saimiri boliviensis*) can be trained to voluntarily participate in husbandry, transport, and injection procedures, and how much training time needs to be invested in this effort (Gillis, Janes, & Kaufman, 2012). Researchers trained 14 male black-capped squirrel monkeys in targeting, handling, and injection procedures using clicker training. Targeting involved touching a stationary or moving target with the hand or foot. The researchers trained the monkeys to hold the touch for up to 5 s. Monkeys successfully learned to touch stationary and moving targets and to hold touches in a mean of 23.8 trials. Subsequently, 10 monkeys mastered handling in a mean of 40 trials and 12 monkeys mastered injection in a mean of 23.6 trials. Overall, 10 mastered training criteria on all tasks. These findings suggest that clicker training is an effective method for training monkeys to cooperate with various laboratory tasks.

Rogge et al. (2013) assessed the amount of time necessary to establish a PRT program, the progress of training, and the retention of trained behaviors in 28 owl monkeys (*Aotus spp.*) and 30 squirrel monkeys (*Saimiri spp.*). Researchers used clicker training for touch target, present hand, and present foot behaviors. Researchers recorded performance and training levels of each monkey. Monkeys who reached trained status for any behavior required between 1 and 22 sessions to do so. All of the squirrel monkeys and 18% of the owl monkeys reached criteria for target touching and present hand. Only 21.4% of the owl monkeys, in contrast to 60% of the squirrel monkeys reached criteria for present foot. A total of 63.3% of the owl monkeys and 86.6% of the squirrel monkeys reached “maintained status” for targeting, 64.2% of the owl monkeys and 60% of the squirrel monkeys reached “maintained status” for present hand, and 25% of the owl monkeys and 10% of the squirrel monkeys reached “maintained status” for present foot. Squirrel monkeys learned the initial target behavior significantly faster than did owl monkeys, but there were no significant differences between the two species in present hand and present foot. This study demonstrates that PRT can be successfully implemented with these two species as a means of managing behavior.

Medical Treatment

PRT is also used in medical treatment of captive individuals. For example, Gresswell and Goodman (2011) successfully used clicker training over 89 sessions lasting no longer than 5 min each to desensitize a female chimpanzee to the use of a nebulizer to treat airsacculitis. Bourgeois, Vazquez, and Brasky (2007) successfully reduced self-injurious behaviors in a chimpanzee by using a combination of PRT, medication, and environmental enrichment. However, it is unknown if the success of this treatment plan was due to only one component of the treatment.

Priest (1991) published a case study of PRT with a diabetic drill monkey (*Mandrillus leucophaeus*) for compliance with insulin injections and venipuncture. The drill had been confined to a veterinary squeeze cage so he could receive daily insulin injections and was exhibiting abnormal behaviors. The researcher paired the insulin injection with the drill’s afternoon meal and gradually faded the use of the squeeze cage as the drill learned to associate the injection with food. The researcher successfully trained the drill to voluntarily present for injection and to present his arm for venipuncture blood sampling. The success of the training procedures allowed caregivers to move the drill to a larger enclosure with enrichment, which decreased abnormal behaviors, thereby greatly enhancing his quality of life. Together, these four studies indicate that PRT is an effective way to provide medical treatment to captive nonhuman primates. PRT may reduce the stress that would normally occur with these procedures, as evidenced by a decrease in self-directed behaviors and fear and aggression responses in PRT individuals.

Biological Research Purposes

The benefits of PRT extend to collecting biological samples for research purposes. Vertein and Reinhardt (1989) published the first study on a procedure used to train rhesus macaques to cooperate with venipuncture. Researchers systematically exposed eight females to spending time in a squeeze-back cage, having the leg touched, having the leg pulled out and caressed, and eventually tolerating venipuncture. A food reward followed training in each phase. All eight macaques successfully completed each step, with three of the macaques voluntarily presenting a leg and the other five displaying no signs of fear or resistance when the leg was pulled out for venipuncture.

In a later study, Reinhardt (1991) trained each of 10 pair-housed male rhesus macaques to present his leg for venipuncture. Training began by using a squeeze-back cage to bring the monkey to a window where the researcher reached into the cage, pulled out a leg, and performed venipuncture. The macaque was rewarded with a preferred food at the end of the procedure. Eventually, each macaque was trained to voluntarily present his leg without physical handling or the squeeze-back being brought completely to the front. The benefits of this training were that the researchers did not have to immobilize the macaques or remove them from the cage, the interactions between macaques and caregivers became safer, and the collection of blood became easier.

Using PRT to increase compliance with laboratory procedures improves behavioral indicators of well-being. Coleman and Maier (2010) assessed the effects of training for target touching and accepting venipuncture on stereotypic behavior in 11 adult female rhesus macaques. Researchers gathered baseline behavioral data of macaques exhibiting abnormal behaviors and assigned the macaques to either the training or control group. Observations of macaques in the control group occurred on days when training did not occur. Macaques who received PRT showed significantly less stereotypic behavior than macaques in the control group. However, significance did not persist beyond 1 month after training. These results suggest that PRT may reduce abnormal behaviors in captive nonhuman primates, but continued PRT is necessary to maintain this effect.

In terms of research on laboratory procedures with large bodied apes, Videan, Fritz, Murphy, Borman, Smith, and Howell (2005) studied the effectiveness of using PRT to train chimpanzees to present a body part for an anesthetic injection. Researchers used clicker training with 40 out of 64 chimpanzees to train them to hold an arm or leg in position and allow the application of pressure and a jab with a blunt needle. The goal was to train chimpanzees to eventually participate in a ‘mock anesthetization.’ The average training time to reliability, defined as consistently presenting for at least 2 injections, was 121.8 min and 35.1 sessions. Trained chimpanzees performed significantly better than those who remained untrained. Among chimpanzees who were transferred from the trainer to supervisory staff, there was a significant decrease at 1 year post-training in voluntarily presenting for injection. These findings suggest that chimpanzees can be reliably trained to present for injection, but training must be maintained so cooperation does not decrease over time.

Brown and Loskutoff (1998) also used PRT to collect semen from three captive-born, male western lowland gorillas for artificial insemination purposes. The gorillas had no previous experience with PRT. The trainer shaped behaviors using verbal and food rewards until the gorillas appropriately responded to target, hold, and presentation prompts. Eventually, the gorillas tolerated the trainer collecting a semen sample. This training program allowed for easier collection of better quality samples without putting the gorillas under general anesthesia for electroejaculation.

The aforementioned studies indicate that PRT is an effective means of increasing compliance with invasive laboratory procedures, such as venipuncture and biological sample collection. PRT also increases the reliability that laboratory technicians will be able to get a sample and in some cases eliminates the need for anesthesia and other stressful procedures. This suggests that nonhuman primates benefit from the use of PRT in captive settings.

Physiological Indicators of Stress

Research has addressed the question of whether PRT decreases physiological parameters associated with stress in chimpanzees. In one study (Lambeth, Hau, Perlman, Martino, & Schapiro, 2006), researchers gathered archival data on physiological parameters of stress of 128 chimpanzees with previous PRT experience in husbandry and research protocols. The parameters included white blood cell count (WBC), absolute segmented neutrophils (SEG), blood glucose levels (GLU), and hematocrit levels (HCT). Researchers compared physiological parameters of stress in chimpanzees who voluntary presented for anesthetic injection to those who were forcibly anesthetized in three possible ways. Forcible anesthetization was either the chimpanzee presenting for injection after seeing the dart gun, darting the chimpanzee with the dart gun, or unexpectedly injecting the chimpanzee through the caging. Chimpanzees who voluntary presented for injection exhibited significantly lower levels of WBC, SEG, and GLU than chimpanzees who were forcibly anesthetized by any of the three means. These results indicate that using PRT techniques in the management of captive chimpanzees significantly reduces stress associated with laboratory procedures.

Videan, Fritz, Murphy, Howell, and Heward (2005) conducted a study to determine the effect of anesthetic injection versus darting on captive chimpanzee stress, as indicated by blood serum cortisol, white blood cell counts, and blood glucose levels. Researchers analyzed data from semiannual health examinations for 17 captive chimpanzees at the Primate Foundation in Arizona. They correlated physiological measures of stress with how the chimpanzee was anesthetized. Eleven of the chimpanzees had prior experience with training to present an arm or leg for anesthetic injection. There was no difference in cortisol, white blood cell count, or blood glucose levels between injected and darted chimpanzees. However, individuals with easy or cooperative anesthetizations showed lower levels of cortisol and blood glucose than those with difficult anesthetizations. Additionally, trained chimpanzees showed significantly lower levels of cortisol than untrained chimpanzees. The results of this study indicate that training for medical procedures reduces physiological indicators of stress.

Early research on the effects of PRT on physiological indicators of stress in other nonhuman primates supports the previously mentioned studies. Clarke, Mason, and Moberg (1988) assessed corticosteroid levels in 21 juvenile female macaques, including rhesus, bonnet (*Macaca radiata*), and long-tailed (*M. fascicularis*). Researchers used

PRT techniques to train the macaques to enter a transport cage for a brief confinement. Researchers compared corticosteroid levels at baseline, pre-training, and post-training, and found a significant decrease in levels for all three species at post-training compared to pre-training.

In a comparison of the reactions of rhesus macaques during conventional and refined blood collection procedures, Reinhardt (2003) trained macaques to cooperate with a blood collection procedure using PRT and measured cortisol levels as an indicator of stress for both conditions. All macaques cooperated once trained, and cortisol levels were significantly lower during cooperative conditions than restraint conditions. Another study found that blood cortisol concentrations in adult female rhesus macaques were lower when venipuncture was performed in the homecage with a moveable back wall than when it was performed using a restraint device outside of the homecage (Reinhardt, Cowley, Scheffler, Vertein, & Wegner, 1990). The findings from these two studies suggest that alternative methods allowing individuals to remain in the homecage are less stressful than more forcible methods of sample collection.

Dettmer, Phillips, Bernstein, and Fragaszy (1996) conducted a study to determine how quickly capuchin monkeys (*Cebus apella*) habituate to venipuncture procedures, as indicated by behavioral and physiological measures. Researchers trained 8 capuchin monkeys for 3 days per week over the course of 6.5 weeks to enter a transfer cage for a venipuncture procedure. On training days each monkey had the opportunity to freely enter a transfer cage from the home cage. If a monkey did not cooperate, researchers used a squeeze back until the monkey entered the box. Monkeys were then released into a cage with venipuncture equipment. A squeeze back was used if monkeys did not voluntarily present their leg for venipuncture. After each procedure the squeeze back was released and the researcher gave the monkey a food reward. Throughout the procedure researchers recorded the monkeys' behavior, particularly resistance and vocalization. Researchers characterized monkeys with low resistance behaviors and vocalizations as habituated, and monkeys with high resistance behaviors and vocalizations as nonhabituated. Both groups of monkeys were retrained for 3 days, but without blood draws. Then, researchers repeated the capture procedure and collected a blood sample, returned the monkey to the homecage, then captured the monkey again and collected a second blood sample. Researchers repeated this procedure 2 days later and collected the second blood sample 1 hr after collecting the first. Researchers analyzed blood samples for cortisol levels. Cortisol levels increased significantly over the first 5 weeks of training, and then decreased significantly during the last 2 weeks. Monkeys categorized as habituated had significantly lower cortisol levels at the 1-hr blood draw than nonhabituated monkeys, and showed no difference in cortisol levels between the first and second blood draws. Additionally, none of the monkeys voluntarily presented a leg for the procedure. While only half of the monkeys showed behaviors indicative of habituation to the venipuncture procedure, those who did habituate showed no significant increase in cortisol levels as a result of the venipuncture procedure. This indicates that over the course of time, monkeys may habituate to laboratory procedures and experience reduced stress as a result.

Another study measured the effects of PRT on behavioral and physiological indicators of stress in baboons (*Papio hamadryas*) (O'Brien, Heffernan, Thomson, &

McGreevy, 2008). Researchers used clicker training with six adult male baboons who had no previous training. Researchers recorded undesirable behavioral responses incompatible with training, and saliva cortisol at baseline before implementing the training program, and before and after training sessions once the program began. Baboons exhibited individual differences in behavior frequencies over the course of the study. Over the course of the training program, frequencies of departures from the training area, number of vocalizations, and threat displays decreased from baseline frequencies. Additionally, cortisol concentrations in saliva were significantly lower during pre- and post-training once the training program began than at baseline. Higher cortisol concentrations were positively correlated with higher frequencies of departures from the training area. The decrease in behavioral and physiological indicators of stress before and after training sessions indicates that training does not have an aversive effect on well-being, and that training and its associated stimuli become less threatening over time.

The previously mentioned studies support the use of PRT as a means to reduce the stress associated with invasive laboratory procedures. Chimpanzees, macaques, and baboons exhibit decreased physiological parameters of stress, and baboons also exhibit decreased behavioral indicators of stress when researchers use PRT. PRT is a less stressful method for invasive procedures than more forceful conventional techniques.

Other Behavioral Effects of PRT

Pomerantz and Terkel (2009) analyzed the effects of PRT sessions on the behavior of 12 adult and subadult zoo-living chimpanzees. Researchers collected data on abnormal and stress-related behaviors and prosocial affiliative behaviors at baseline and during training sessions. PRT sessions significantly decreased the chimpanzees' abnormal and stress-related behaviors and decreased aggression towards the caregiver compared to baseline. PRT sessions also significantly increased prosocial affiliative behaviors compared to baseline.

Another study used a combination of PRT and social interaction with human caregivers to reduce abnormal behaviors, particularly regurgitation and reingestation, in an adult male gorilla (Pizzutto, Nichi, Correa, Ades, & Guimaraes, 2007). Researchers recorded baseline behaviors for 6 months before the program was initiated and then implemented for 5 years. Training sessions occurred three times per week and targeted the following behaviors: sit, mouth (open), feet (present), stand, lie down, and sit. After a 10-min break, the social interaction sessions began. Social interaction sessions involved the caregiver handling objects, giving the gorilla food, and playing music. There was a reduction in regurgitation and reingestation, coprophagy, self-mutilation, intimidation, and aggressiveness. This suggests that a combination of training and caregiver interaction has a positive effect on captive gorilla behavior. However, it is unclear which aspect, PRT or social interaction, had the effect.

While PRT may increase behavioral indicators of well-being, it may only be useful for certain groups of individuals. In a study of 30 male and 33 female singly housed rhesus macaques, researchers measured the effects of PRT on behavior (Baker et al., 2009). Researchers recorded behavior at baseline and in three phases of experimental conditions. The experimental conditions included 6 min of PRT per week, 20 or 40 min of PRT per week, and 6 min of unstructured interaction per week. PRT sessions focused on training macaques to perform several control behaviors, including sitting, standing, and stationing, and to present various body parts. PRT decreased the frequency of abnormal behaviors, but only for individuals who exhibited high levels of abnormal behavior, specifically stereotypic behavior.

Baker, Bloomsmith, Neu, Griffis, and Maloney (2010) assessed the interaction of rearing history on the behavioral responses of 61 singly housed rhesus macaques to PRT and unstructured interactions. Researchers collected baseline behavioral data before experimental conditions began. During experimental conditions, caregivers engaged macaques in 6 min per week of either PRT or unstructured interaction. Data were collected 4 weeks after the onset of experimental conditions in order to assess long-term effects of the implementation of increased human interaction. There was no effect of either PRT or unstructured interaction on the behavior of singly housed macaques compared to baseline, regardless of rearing history or baseline level of abnormal behavior. A limitation of this study is that there was no comparison of behavioral responses of singly housed macaques to socially housed macaques.

As stated in the introduction, interaction with conspecifics is enriching (Brent, 2001). Bourgeois and Brent (2005) compared the effectiveness of PRT, food enrichment, non-food enrichment, and social enrichment in reducing abnormal behaviors of seven individually housed male olive hybrid baboons (*Papio hamadryas anubis*). PRT sessions involved clicker training for behaviors that were incompatible with abnormal behaviors, such as sitting at the front of the cage instead of pacing. Food enrichment involved providing novel foods and food puzzles. Non-food enrichment involved providing items with various sensory properties, such as textured items, destructible and indestructible items, visual stimuli, and auditory stimuli. Social enrichment involved housing individuals in a pair or a trio. Researchers observed the baboons at baseline and in each condition and recorded all occurrences of normal and abnormal behaviors. All enrichment conditions significantly decreased abnormal behaviors, including self-directed, self-aggression, regurgitation, part-of-body stereotypies, cage-directed, and other low frequency abnormal behaviors, from baseline levels. All enrichment conditions significantly increased species-typical behaviors from baseline levels. However, only PRT and social enrichment conditions significantly decreased whole-body abnormal behaviors, including stereotypic locomotion, bouncing, spinning, rocking, pacing, and flipping. Use of enrichment significantly decreased from baseline levels in the social enrichment condition, but was not affected by any other condition. The results of this study highlight the importance of social interaction in promoting the well-being of captive nonhuman primates.

The studies discussed above indicate that, although PRT can reduce abnormal behaviors in some cases, it should not be the sole form of social interaction for captive nonhuman primates, especially those who are singly housed. It may be more effective in improving well-being when used in combination with unstructured interactions with caregivers, and it cannot act as a substitute for social housing.

Comparative Studies on Training and Non-Training Interactions

Little comparative literature exists on the use of training and non-training interactions between chimpanzees and caregivers. One study compared the effects of two types of interaction on eight captive adult chimpanzees displaying low levels of conspecific sociality. The interaction conditions included training sessions intended to increase social interaction, and unstructured play and feeding sessions with a caregiver (Bloomsmith, Lambeth, Stone, & Laule, 1997). The chimpanzees displayed significantly less solitary and inactive behaviors in both conditions. They interacted with the caregiver more in training sessions and showed increased conspecific social behavior during and after those sessions.

A later study by Bloomsmith, Baker, Ross, and Lambeth (1999) compared the behaviors of 28 chimpanzees in either PRT or non-PRT interactions involving feeding and playing with caregivers. Researchers also recorded the chimpanzees' behaviors in matched control sessions with no caregivers present. Chimpanzees in the PRT condition interacted more with the caregiver than did chimpanzees in the non-PRT condition. Solitary and inactive behavior decreased in both PRT and non-PRT conditions. Agonism increased in PRT sessions compared to baseline, but was reduced in matched control periods for chimpanzees in both PRT and non-PRT sessions compared to baseline. Matched control periods for chimpanzees in the PRT condition indicated an increase in social play compared to baseline, and for chimpanzees in the non-PRT condition indicated decreased sociality but also a decrease in stereotypic and anxiety-related behavior. The results of this study indicate a positive effect of both PRT and non-PRT interactions on chimpanzee well-being.

A more recent study looked at the effect of a combination of training and play therapy on the behavior of a group of seven zoo-living western lowland gorillas. Carrasco et al.'s (2009) study took place over two seasons. In the first season, researchers conducted the study with an established social group. In the second season, two new females were added to the social group. In the first phase of the study the researcher interacted with the gorillas to habituate them to the researcher's presence and gathered data on baseline behaviors of the gorillas following these interactions. In the second phase of the study the researcher began experimental trials. In the experimental trials the researcher conducted training sessions with individuals separated from the group. In training sessions the researcher rewarded gorillas for copying play actions. Following training sessions, the gorillas joined the social group and the researcher encouraged play among individuals and with the researcher to create a playful atmosphere. Then, the researcher released the gorillas into their outdoor area and recorded their behavior. The researcher repeated this procedure in the second season with the addition of the new individuals. There was a significant decrease in abnormal behaviors, behaviors directed towards zoo visitors, and aggression between conspecifics, and a significant increase in affiliative and play behaviors following training/play sessions compared to baseline frequencies. The combination of training and play in interaction sessions with a caregiver increased well-being as measured by increased occurrences of species-typical behaviors following these sessions.

Summary

The Current Study

The current study expands on the work of Bloomsmith et al. (1999), Jensvold (2008), and Jensvold et al. (2011) by comparing the effects of interactions of PRT versus unstructured interactions (UI) without PRT on chimpanzee behaviors. Both PRT and UI involved caregivers using chimpanzee behaviors. Although both PRT and non-PRT interactions have immediate benefits for captive species management and behavioral indicators of well-being, the after-effects of each are not well studied. Durations of each behavioral context following interactions were compared between conditions and to matched-control periods when no caregiver interaction had occurred to determine the effect the type of interaction has on the chimpanzees' behavior. Comparing the after-effects of each interaction on the proportion of time chimpanzees spend in certain behavioral contexts provides insight into how each interaction influences the well-being of captive chimpanzees. This information will enhance caregiving practices and contribute to human knowledge of nonhuman primates.

Hypothesis

This study has two hypotheses. First, we predicted that there would be differences in the proportion of time chimpanzees spend in certain behavioral contexts during interaction conditions than during matched control conditions. Second, we predicted that there would be differences in the proportion of time chimpanzees spend in certain behavioral context between interaction conditions.

CHAPTER II

CHIMPANZEE (*PAN TROGLODYTES*) RESPONSES TO POSITIVE REINFORCEMENT TRAINING AND UNSTRUCTURED INTERACTIONS

Abstract

Positive reinforcement training (PRT) is an effective method for facilitating and reducing stress associated with captive chimpanzee (*Pan troglodytes*) husbandry. The present study compared the effects of PRT and unstructured interactions (UI) on chimpanzee behavior. In the PRT condition, a caregiver interacted with a chimpanzee to condition behaviors for 10 min. In the UI condition, a caregiver interacted without PRT for 10 min. Participants were five chimpanzees in a sanctuary setting. Chimpanzee participants were also videotaped for 10 min after trials (PTP) and for 10 min in a matched control (MC) period on a different day. From these videotapes experimenters coded chimpanzee behaviors and calculated durations in behavioral contexts. Chimpanzees spent a significantly higher proportion of time in the Affinitive context during PRT and UI (0.91 ± 0.03) than during PTP (0.06 ± 0.04, $p = .001$) and MC (0.06 ± 0.02, $p < .001$). Chimpanzees interacted equally often with the caregiver in both PRT and UI conditions. While PRT is useful in husbandry applications, the caregiver's use of chimpanzee behaviors in UIs promotes well-being equally well.

Keywords: positive reinforcement training, operant training, captive chimpanzees, caregiver interaction

Introduction

Chimpanzees (*Pan troglodytes*) are an extremely social species (Goodall, 1986) and thus relationships are critical in their daily lives. For captive chimpanzees their social group includes human caregivers. These relationships can be positive or negative (Hosey, 2008). These chimpanzee-human relationships can elicit friendly behaviors (Baker, 1997; Jensvold, 2008) or aggressive behaviors (Chelluri, Ross, & Wagner, 2013; Perlman et al., 2012), or self-injurious responses (Bourgeois, Vazquez, & Brasky, 2007). Thus it is critical to understand caregiver-chimpanzee relationships and discover ways to improve them.

Positive reinforcement training (PRT) is the process whereby an appetitive stimulus is presented after an organism performs a target behavior. The appetitive stimulus acts as reinforcement for performing the behavior, thereby increasing the organism's performance of that particular behavior in the future. The training of nonhuman animals to perform behaviors relies on the principles of operant conditioning and positive reinforcement. A popular form of PRT used with nonhuman animals is called clicker training. Clicker training involves the use of secondary reinforcement. Skinner (1991) identified secondary reinforcement as a stimulus that acquires reinforcing properties through classical conditioning. Secondary reinforcement is a previously unconditioned stimulus, such as a clicker or verbal praise, which becomes a reinforcer through repeated pairing with a primary reinforcer like food (Laule & Whittaker, 2001). The secondary reinforcer is also referred to as a 'bridge.' The use of a 'bridge' fills the gap between the occurrence of the desired behavior and the delivery of primary reinforcement, and signals to the trainee exactly when he or she performed the desired behavior.

The use of operant conditioning, specifically PRT, is increasing in captive settings as a means to manage behavior in a variety of nonhuman primate species. For example, it is used to increase compliance with voluntary movement (Bloomsmith, Stone, & Laule, 1998; Veeder, Bloomsmith, McMillan, Perlman, & Martin, 2009), encourage social behavior (Schapiro, Perlman, & Bourdreau, 2001), reduce caregiver-directed aggression (Minier et al., 2011), reduce self-injurious behavior (Bourgeois, Vazquez & Brasky, 2007), and increase compliance with insulin injection, venipuncture (Priest, 1991; Reinhardt, 1991; Vertein & Reinhardt, 1989), anesthetic injection (Videan, Fritz, Murphy, Borman, Smith, & Howell, 2005), and semen collection (Brown & Loskutoff, 1998) (see Desmond & Laule, 1994; Perlman et al., 2012; Prescott & Buchanan-Smith, 2007 for review).

The National Institutes of Health Council of Councils Working Group on the Use of Chimpanzees in NIH-Supported Research (2013) report recommends the use of PRT in all interactions with chimpanzees. This is echoed by Westlund (2014) who recommends PRT as environmental enrichment and a way to stimulate well-being. Yet these recommendations miss the value of unstructured interactions, ones that are free of requesting compliance and food motivation. Natural, unstructured interactions include activities such as grooming, playing, or looking at a magazine. In Baker (2004) caregivers increased unstructured interactions with 12 laboratory chimpanzees by approximately 10 min per chimpanzee per day. The increase in unstructured interaction time led to a significant decrease in agonistic displays, inactivity, and abnormal oral behaviors such as regurgitation and reingestation as compared to baseline. The interactions also increased grooming behaviors and the chimpanzees were less reactive to the vocalizations and displays of others. This suggests that unstructured interactions have an effect at both the individual and group level, particularly in terms of social behavior. With 10 min of unstructured caregiver interaction, rhesus macaques (*Macaca mulatta*) showed a decrease in stereotypical and self-directed behaviors (Bayne, Dexter, & Strange, 1993). In Manciocco, Chiarotti, and Vitale (2009) caregivers spent an extra 20 min interacting with socially-housed marmosets (*Callithrix jacchus*). Interactions resulted in a significant decrease in locomotion, self-scratching, and production of "phee calls," and a significant increase in grooming and play behaviors.

Unstructured interactions can further be beneficial with the addition of species-typical behaviors. Jensvold (2008) compared caregivers' use of chimpanzee behaviors versus human behaviors during 10-min interactions. In the human behavior condition chimpanzees spent significantly less time interacting with caregivers than in the chimpanzee behavior condition. Generally, in the chimpanzee behavior condition they spent more time in affinitive social, grooming, play, and serving (food) contexts than in the human behavior condition. Sanctuary-living chimpanzees were also sensitive to the differences in caregivers' use of species-typical behaviors (Jensvold, Buckner, & Stadtner, 2011).

Little comparative literature exists on the use of training and non-training interactions between chimpanzees and caregivers. Bloomsmith, Lambeth, Stone, and

Laule (1997) found that both training sessions intended to increase social interaction among captive chimpanzees and unstructured interactions with a caregiver reduce solitary and inactive behaviors. Chimpanzees interact with caregivers more in training sessions and show increased conspecific social behavior during and after those sessions. In a later study, Bloomsmith, Baker, Ross, and Lambeth (1999) compared the behaviors of chimpanzees in either PRT or non-PRT interactions involving feeding and playing with caregivers. Researchers also recorded the chimpanzees' behaviors in matched control sessions with no caregivers present. Chimpanzees in the training condition interacted more with the caregiver than did chimpanzees in the non-training condition. Solitary and inactive behavior decreased in both training and non-training conditions. Agonism increased in training sessions compared to baseline, but was reduced in matched control periods for chimpanzees in both training and non-training sessions compared to baseline. Matched control periods for chimpanzees in the training condition indicated an increase in social play compared to baseline, and for chimpanzees in the non-training condition indicated decreased sociality but also a decrease in stereotypic and anxiety-related behavior. The results of this study indicate a positive effect of both PRT and unstructured interactions on chimpanzee well-being. In a more recent study, Carrasco et al. (2009) found that a combination of training and play therapy significantly decreased abnormal and visitor-directed behaviors and conspecific aggression, and increased affiliative and play behaviors in zoo-living western lowland gorillas (*Gorilla gorilla gorilla*). This indicates that training and play in interactions with caregivers increase well-being as measured by an increase in species-typical behaviors following these sessions.

The current study expands on the work of Bloomsmith et al. (1999), Jensvold (2008), and Jensvold et al. (2011) by comparing the effects of interactions of PRT versus unstructured interactions (UI) without PRT on chimpanzee behaviors. Both PRT and UI involved caregivers using chimpanzee behaviors. Although both PRT and non-PRT interactions have immediate benefits for captive species management and behavioral indicators of well-being, the after-effects of each are not well studied. Durations of each behavioral context following interactions were compared between conditions and to matched-control periods when no caregiver interaction had occurred to determine the effect the type of interaction has on the chimpanzees' behavior. Comparing the after-effects of each interaction on the proportion of time chimpanzees spend in certain behavioral contexts provides insight into how each interaction influences the well-being of captive chimpanzees. This information will enhance caregiving practices and contribute to human knowledge of nonhuman primates.

This study has two hypotheses. First, we predicted that there would be differences in the proportion of time chimpanzees spend in certain behavioral contexts during interaction conditions than during matched control conditions. Second, we predicted that there would be differences in the proportion of time chimpanzees spend in certain behavioral contexts between interaction conditions.

Method

Participants

Chimpanzee Residents

Five chimpanzees (*Pan troglodytes*), including three males and two females, participated in this study. The chimpanzees live at the Fauna Foundation in Carignan, Québec. Detailed biographical information for each chimpanzee appears in Table 1. All five chimpanzees were trained to present arms, feet and legs prior to February 2012. Since February 2013, the chimpanzees had been maintaining these behaviors and acquiring behaviors including presenting an open mouth and presenting a toe for a prick and blood sample collection to measure glucose levels. The study received approval from Central Washington University's Institutional Animal Care and Use Committee (protocol #A051404).

Table 1

Biographical Information on the Chimpanzees

Name	DOB	Sex	Birth Location	Rearing Conditions
Spock	2/9/1976	M	Institute for Primate Studies, OK	Cross-fostered/Zoo
Maya	7/8/1977	F	Institute for Primate Studies, OK	Cross-fostered/Zoo
Petra	2/24/1988	F	LEMSIP, NY	Biomedical lab
Jethro	8/23/1988	M	LEMSIP, NY	Biomedical lab
Binky	4/10/1989	M	LEMSIP, NY	Biomedical lab

Note. DOB = Date of Birth

Fauna Foundation

Fauna Foundation is a sanctuary for 12 chimpanzees located in Carignan, Québec, Canada. Indoor living space for the chimpanzees totals 1,115m^2, and consists of 6 front rooms, 2 play rooms, and 4 smaller play areas. There are 213 linear meters of outdoor skywalk, and three outdoor islands totaling 0.81ha. The chimpanzees live in subgroups, which are separated into different areas of the facility during the day. Individuals are shifted among compatible subgroups approximately twice per week.

The chimpanzees' diet consists of about 2,000 calories per day. It includes fruits, vegetables, berries, nuts and additional protein products, juice, tea, and occasionally dairy products. The chimpanzees also receive vitamin supplements and medications. Water is always available.

Procedure

Caregiver Participant

One human participant, AW, interacted with the chimpanzees during the experimental conditions of this study. AW was the Operant Conditioning Coach and a caregiver at Fauna Foundation. She had been working with the chimpanzees at Fauna since February 2012. She had approximately 6 years of experience safely working around chimpanzees and providing care for them. She had a demonstrated knowledge of chimpanzee behaviors. The study received approval from Central Washington University's Human Subjects Review Committee (#H14118).

Study Design

We used a within-subjects design and had two experimental conditions, Positive Reinforcement Training (PRT) and Unstructured Interaction (UI). The experimenter (WE) instructed AW which condition to present immediately before the trial began. AW used chimpanzee-specific behaviors when interacting with chimpanzees in both experimental conditions. For example, she head nodded upon greeting the chimpanzees. WE instructed AW to try to engage the chimpanzee for at least 5 min during PRT and UI trials. PRT and UI trials lasted for up to 10 min each. There were also Post-Trial Period (PTP) and Matched Control (MC) conditions. During PTP and MC conditions WE videotaped the focal chimpanzee. Other caregivers were instructed to continue their work routine as usual, which included interacting with the focal chimpanzee if the focal chimpanzee solicited interaction, or serving medication or food if that was part of the schedule at that time. During all conditions (PRT, UI, PTP, and MC), focal chimpanzees were typically in a subgroup with conspecifics with whom they could interact.

Positive Reinforcement Training (PRT) Condition

In the PRT condition, AW engaged the chimpanzee in operant training using chimpanzee behaviors. AW initiated training sessions by calling the focal chimpanzee’s name and making food grunts and/or food squeaks. AW carried food and/or drink and objects to be used in training, such as a clicker, a wooden backscratcher for targeting, and a blanket to sit on to the location where the training session was to occur. PRT sessions included training for the chimpanzee to perform maintenance and new behaviors such as opening mouth for inspection, presenting arm, presenting stomach, touching a target, and presenting a foot for a toe poke and blood collection. AW gave a verbal cue in English for the desired behavior. AW determined which verbal cue to use depending on what behaviors each chimpanzee typically performs for medical check-ups and procedures in exchange for positive reinforcement. AW used chimpanzee behaviors and vocalizations appropriate for the interaction, such as head nods, breathy panting, and food grunts or squeaks.

Unstructured Interaction (UI) Condition

In the UI condition, AW engaged the chimpanzee in unstructured interaction (i.e., with no training) using chimpanzee behaviors. AW initiated the interaction by calling the focal chimpanzee's name and using chimpanzee behaviors such as breathy panting and play foot stomps. AW carried enrichment objects to the location where the interaction was to occur. AW was not permitted to serve food to the focal chimpanzee during UI trials. However, the chimpanzees always had access to produce and other foods via stationed serving trolleys as they did in the PRT condition. During the trial AW used behaviors and vocalizations chimpanzees typically use in play, greeting, grooming, submission, and friendly contexts. These behaviors include facial expressions used by chimpanzees in these contexts, such as playface, relaxed face, and grins.

Post-Trial Period (PTP)

Each experimental condition was followed by a Post-Trial Period (PTP) of focal animal follow. The PTP began when AW ended the interaction with the focal chimpanzee by gathering her interaction supplies and walking away. The PTP lasted for 10 min.

Matched Control (MC) Period

This study used a modified version of a matched control methodology (deWaal & Yoshihara, 1983). MC observations corresponded with a particular PTP. The researcher identified the temporally closest sample for the same participant during the same hour of the day, on a day following the PTP. If an experimental trial occurred on a weekday, the temporally closest weekday was selected for the MC period. If an experimental trial occurred on a weekend day, the temporally closest weekend day was selected for the MC period. MC periods matched PTPs in length of observation.

Procedure for Video Recording

WE used a digital video camera to record trials. For a week before the study began, WE carried the video camera to habituate the chimpanzees to the camera and her presence. During trials, WE recorded both the focal chimpanzee and AW in the video frame. Before the trial began, WE greeted the focal chimpanzee with a head-nod but did not interact with the chimpanzees or the caregiver while videotaping.

If a chimpanzee was not available to participate in an experimental trial, the start-time was delayed for up to 20 min until the chimpanzee was available. A chimpanzee was not available, for example, if they were in a distant location or did not move toward AW for the interaction, or the chimpanzee was scheduled to be shifted between rooms at the scheduled start-time. If an experimental trial was interrupted or the chimpanzee left the interaction before 1 min elapsed, AW waited until the chimpanzee was available and attempted the trial. If the chimpanzee still did not participate, the trial was rescheduled for another day.

WE exhibited submissive behaviors while recording. However, if the focal chimpanzee became distressed by the experimenter's presence during PTP and MC trials, as evidenced by increases in rates of threat behaviors, WE exhibited submissive behaviors, stopped recording the chimpanzee, and left the area. This occurred with one chimpanzee each time WE conducted video follow for PTP and MC trials. He was removed from the study and replaced with a different chimpanzee.

If during a trial the focal chimpanzee moved out of view for more than approximately 5 s and did not return, WE turned off the camera and resumed recording when the chimpanzee came back into view. WE recorded 10 min of video follow during PTP and MC conditions.

Study Schedule

All data were collected from July 29, 2014 to August 30, 2014. Each chimpanzee participated in each experimental condition three times, for a total of six experimental trials, six PTPs, and six MC periods per chimpanzee. Trials occurred 4 times per weekday, at 9:00 a.m., 10:00 a.m., 1:30 p.m., and 2:30 p.m. These times were selected to space out trials and reduce the potential stress associated with experimenter presence. WE randomly selected one chimpanzee for each sample time. No chimpanzee participated in experimental trials more than once per day. Each chimpanzee participated in a maximum of two experimental trials (PRT or UI) per week. Trials were not scheduled on Mondays and Thursdays, which were cleaning days. If the selected chimpanzee was not available to participate in a PRT or UI trial, the trial was rescheduled to occur at the same time of day on a later date reserved for make-up trials. Corresponding MC trials were rescheduled in the same fashion.

Behavioral Context Coding

WE selected the middle 5 min from each trial to code since interactions in experimental trials often varied in length. WE and a second experimenter (KM) coded the 5-min segments of each video for the behavioral context of the focal chimpanzee who appeared in that trial. Behavioral contexts included Affinitive Social, Agonistic, Greeting, Grooming, Multiple Interactive, Nonaffinitive Social, Noninteractive, Play, Reassurance, Serving, Threat, and Not Visible. Definitions for each behavioral context appear in Table 2. WE and KM used continuous focal sampling to record the start-time of the focal chimpanzee's behavioral context. Each time the context shifted, WE and KM recorded the new context and its start time. A shift in context occurred when the focal chimpanzee displayed the new context for longer than 5 s.

Table 2

Behavioral Context Definitions

Context	Definition
Affinitive Social (Affinitive)	Interactions often accompanied by embraces, open mouth kisses, touching, or following another chimpanzee or human. Includes soliciting an object or contact from another individual; approaching another individual that results in an affinitive social interaction; when the focal is displaced by another chimpanzee or displaces another chimpanzee. Includes receiving affinitive interactions. For example, a chimpanzee allows another individual to take an object or another individual touches the focal chimpanzee. The focal chimpanzee may be either delivering or receiving these behaviors.
Greeting (Affinitive)	An interaction between individuals who meet after a separation. Behaviors in this category include panting, bobbing, head nodding, arm stretching, kissing, and wrist bending. The focal chimpanzee may be either delivering

Table 2 (Continued)

Context	Definition
	or receiving these behaviors.
Grooming (Affinitive)	A variety of skin-care patterns directed at another individual. Includes behaviors such as parting the hair with the lips, fingers, or objects, inspecting another individual's body, lip smacking, and teeth clacking. The focal chimpanzee may be either delivering or receiving these behaviors.
Multiple Interactive (Affinitive)	When two interactive contexts occur simultaneously. For example, the focal greets one individual and is groomed by another. If one context is interactive and the other is noninteractive, only the interactive category is coded.
Play (Affinitive)	Interactions are marked by specific behaviors such as play face, laugh, play walk, tickling, or chasing. May include object play, head butts, dragging, or pinching. The play face and exaggerated behaviors are key indicators of this category. The focal chimpanzee may be either delivering or receiving these behaviors.
Reassurance (Affinitive)	An interaction in which one individual calms another after a high arousal situation. Behaviors include hug, kiss, hand hold, whimpering, and crouching. The focal chimpanzee may be either delivering or receiving these behaviors.
Serving (Affinitive)	The focal chimpanzee receives food from the caregiver. Includes approaching the caging to be served or positioning self to receive food. The context must be interactive; simply eating food is not included in this category.
Agonistic (Agonistic)	Interactions that have aggressive physical contact. This includes poking, kicking, biting, spitting (with contact), throwing an object at another individual, or hitting another individual with an object. The focal chimpanzee may be either delivering or receiving these behaviors.
Nonaffinitive Social (Agonistic)	Mildly aggressive interactions including behaviors such as blocking passage or screaming in the absence of submissive gestures or postures. The focal chimpanzee may be either delivering or receiving these behaviors.
Threat (Agonistic)	An interaction with aggressive behaviors and no contact. Threat behaviors include display, bipedal swagger, back hand thump, cough bark, spitting, or poking. The focal chimpanzee may be either delivering or receiving these behaviors.
Noninteractive	The focal chimpanzee is not engaged in an interaction. Includes copraphagy, eating, lone play, masturbation, object manipulation, rest, self-groom, stereotypic behaviors, and travel. Also includes when the chimpanzee is showing signs of arousal such as piloerect hair or swaggering but is clearly not interacting with another individual.
Not Visible	No data are available because the focal chimpanzee was not visible for longer than 3 s or the observer could not discern what the chimpanzee's behaviors were for longer than 3 s.

Note. Adapted from Jensvold (2008, p. 350). Context terms in parentheses indicate whether an interactive context falls under the Affinitive or Agonistic behavioral context.

Reliability

A reliability score of 100% was required for chimpanzee identification. A reliability score of at least 85% was required for context and time identification. Times within 3 s of each other were considered agreements. WE and KM coded behaviors from the videotapes of trials. KM learned to identify the chimpanzees with 100% reliability. KM learned to identify the behavioral contexts by studying the Ethogram and coding instructions and by coding practice videos that were not used for the study. After training was completed, WE and KM independently coded a 10-min video that was not used for the study and achieved 95.2% agreement on context variables and 85.7% agreement on time variables. WE and KM independently coded 25% of the trials (108 min, 3 s of 430 min, 14 s) and achieved 87.4% agreement on context variables and 85.2% agreement on time variables.

Context Analysis

For the statistical analysis, WE combined 10 of the 12 behavioral contexts into 2 broader categories of interactive behavior, thus resulting in 4 contexts for the analysis. The new categories were Affinitive and Agonistic. The Affinitive category included Affinitive Social, Greeting, Grooming, Multiple Interactive, Play, Reassurance, and Serving. All Multiple Interactive codes in this study involved combinations of Affinitive contexts. The Agonistic category included Agonistic, Nonaffinitive Social, and Threat. Noninteractive and Not Visible remained as originally defined in Jensvold (2008, p. 350).

WE calculated the total duration of each behavioral context for each trial. Then, WE calculated the proportion of time each chimpanzee spent in each behavioral context in each trial. Then, WE calculated the mean proportion of time each chimpanzee spent in each context per condition. A research assistant (CM) performed the same calculations to ensure WE's calculations were correct. These data appear in Table 3.

Table 3

Mean Proportion of Time Each Chimpanzee Spent in Behavioral Contexts per Interaction Type and Time

	Spock		Maya		Petra		Jethro		Binky	
Context and time	PRT	UI	PRT	UI	PRT	UI	PRT	UI	PRT	UI
Affinitive										
During	0.94	0.93	0.97	0.98	0.99	0.66	0.88	0.80	0.93	0.99
PTP	0.01	0.03	0.01	0.00	0.11	0.05	0.05	0.34	0.02	0.00
MC	0.07	0.00	0.01	0.01	0.19	0.08	0.03	0.00	0.02	0.15
Agonistic										
During	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00
PTP	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
MC	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Noninteractive										
During	0.06	0.07	0.03	0.02	0.00	0.34	0.12	0.18	0.07	0.01
PTP	0.91	0.90	0.95	0.98	0.61	0.75	0.88	0.53	0.84	0.90
MC	0.92	1.00	0.99	0.97	0.69	0.86	0.91	1.00	0.94	0.81
Not Visible										
During	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00
PTP	0.05	0.06	0.04	0.02	0.28	0.20	0.06	0.13	0.15	0.10
MC	0.01	0.00	0.00	0.02	0.12	0.06	0.06	0.00	0.04	0.05

Note. The proportion is the total number of seconds in a given context divided by the total number of seconds coded per trial.
During = PRT/UI. PTP = Post-Trial Period. MC = Matched Control.

Analysis

There were 786 min and 13 s of video data. For all 5 chimpanzees the researcher coded a total of 68 min and 37 s for PRT conditions, 70 min for PRT-PTP conditions, 70 min for PRT-MC conditions, 71 min and 37 s for UI conditions, 75 min for UI-PTP conditions, and 75 min for UI-MC conditions. Ideally, 75 min of video data would have been coded for each condition. However, 1 PRT trial and 2 UI trials ended before the 5-min mark because the focal chimpanzees left the interaction. Additionally, due to a scheduling error, one trial of PRT for the chimpanzee Binky was not completed. The researcher substituted the mean duration of time all chimpanzees spent in each behavior context during PRT, PRT-PTP, and PRT-MC trials in place of Binky's missing PRT trial. Thus, the statistical analyses for PRT, PRT-PTP, and PRT-MC trials was based on a total of 73 min and 31 s, 75 min, and 75 min respectively. The researcher conducted a two-way repeated measures analysis of variance to determine the effect of interaction type (PRT versus UI) and time (during PRT/UI, PTP, and MC) on the proportion of time the chimpanzees spent in the four behavioral contexts.

Results

The mean proportion of time the chimpanzees spent in each behavior context per interaction and time condition appears in Table 4. The Affinitive context occurred significantly more often in the PRT and UI conditions than during PTP and MC conditions. This was supported by univariate tests that showed a significant main effect of time on the Affinitive behavioral context, $F(2, 8) = 170.62$, $p < .001$, partial $\eta^2 = .98$. There was a significant linear trend, $F(1, 4) = 336.31$, $p < .001$, partial $\eta^2 = .99$, indicating that proportion of time spent in this context decreased proportionally from PRT and UI conditions to PTP and MC conditions. Post hoc tests using the Bonferroni correction showed that chimpanzees spent a significantly higher proportion of time in Affinitive contexts during PRT and UI trials (0.91 ± 0.03) than during PTP trials (0.06 ± 0.04) and MC (0.06 ± 0.02) trials (PTP: $p = .001$, MC: $p < .001$). Figure 1 shows a line graph for the main effect of time on the Affinitive context.

Table 4

Total Seconds (s) and Mean Proportion of Time Spent in Behavioral Contexts per Interaction Type and Time

	PRT			UI		
Context and time	Total (s)	Mean	*SD*	Total (s)	Mean	*SD*
Affinitive						
During	3,894	0.94	0.04	3,754	0.87	0.14
PTP	173	0.04	0.04	384	0.09	0.15
MC	269	0.06	0.08	208	0.05	0.06
Agonistic						
During	5	0.00	0.00	0	0.00	0.00
PTP	19	0.00	0.01	5	0.00	0.00
MC	0	0.00	0.00	0	0.00	0.00
Noninteractive						
During	218	0.05	0.05	529	0.13	0.14
PTP	3,516	0.84	0.13	3,654	0.81	0.18
MC	3,733	0.89	0.12	4,174	0.93	0.09
Not Visible						
During	0	0.00	0.00	14	0.00	0.01
PTP	492	0.12	0.10	457	0.10	0.07
MC	198	0.05	0.05	118	0.03	0.03

Note. The proportion is the total number of seconds in a given context divided by the total number of seconds coded per trial. Total seconds coded for: PRT During = 4,117, PRT PTP = 4,200, PRT MC = 4,200, UI During = 4,297, UI PTP 4,500, UI MC = 4,500. During = PRT/UI. PTP = Post-Trial Period. MC = Matched Control.

The Noninteractive context occurred significantly more often in the PTP and MC conditions than during the PRT and UI conditions. This was supported by univariate tests that showed a significant main effect of time on the Noninteractive behavioral context, $F(2, 8) = 95.33$, $p < .001$, partial $\eta^2 = .96$. There was a significant linear trend, $F(1, 4) = 188.00$, $p < .001$, partial $\eta^2 = .98$, indicating that proportion of time spent in this context increased proportionally from PRT and UI conditions to PTP and MC conditions. Post hoc tests using the Bonferroni correction revealed that chimpanzees spent a higher proportion of time in the Noninteractive context during PTP (0.83 ± 0.06) and MC (0.91

± 0.04) trials than during interaction (PRT and UI) trials (0.09 ± 0.03), which was statistically significant (PTP: $p = .003$, MC: $p < .001$). Figure 2 shows a line graph for the main effect of time on the Noninteractive context.

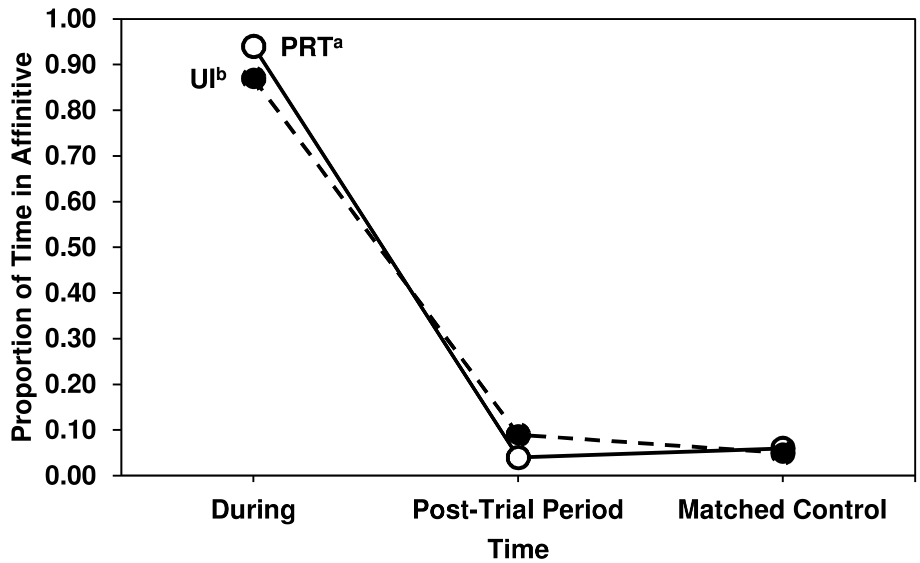

Figure 1. Mean proportion of time in the Affinitive context per interaction type and time. The proportion is the number of seconds in the Affinitive context divided by the number of seconds coded. Significance is between 'During' and 'Post-Trial Period' times ($p < .001$). Effects of interaction type (PRT versus UI) were nonsignificant ($p > .05$).
[a]PRT = Positive Reinforcement Training. [b]UI = Unstructured Interaction.

The proportion of time the chimpanzees' behavior was Not Visible was low in all conditions, as seen in Table 4. Despite this, there was a significant main effect of time on the Not Visible context, $F(2, 8) = 8.92$, $p = .009$, partial $\eta^2 = .69$. There was a significant quadratic trend for Not Visible, $F(1, 4)$, $p = .04$, partial $\eta^2 = .71$. Post hoc tests using the Bonferroni correction revealed that chimpanzees spent a higher proportion of time in the Not Visible context during PTP (0.11 ± 0.04) trials than during interaction (PRT and UI) trials (0.00 ± .00) and MC (0.04 ± 0.02) trials. Figure 3 shows a line graph for the main effect of time on the Not Visible context.

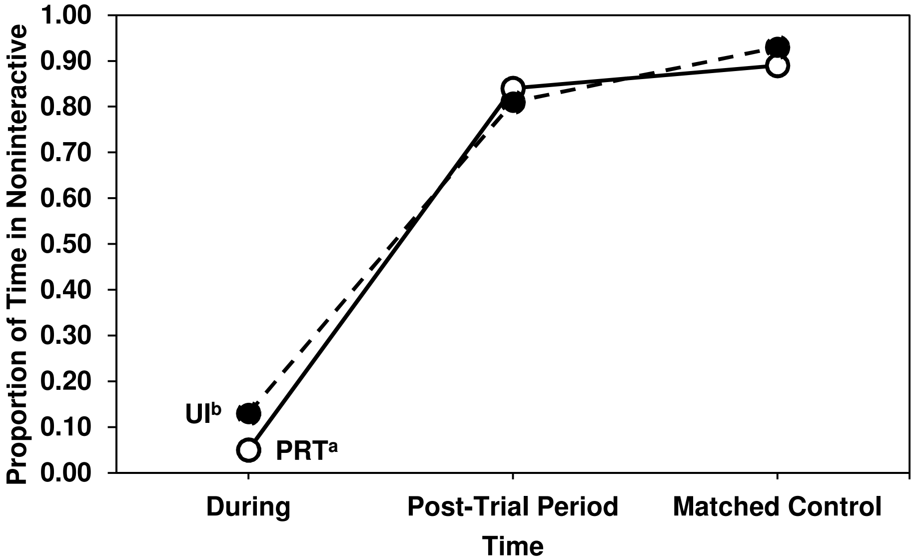

Figure 2. Mean proportion of time in the Noninteractive context per interaction type and time. The proportion is the number of seconds in the Affinitive context divided by the number of seconds coded. Significance is between ‘During’ and ‘Post-Trial Period’ times ($p < .001$). Effects of interaction type (PRT versus UI) were nonsignificant ($p > .05$).
[a]PRT = Positive Reinforcement Training. [b]UI = Unstructured Interaction.

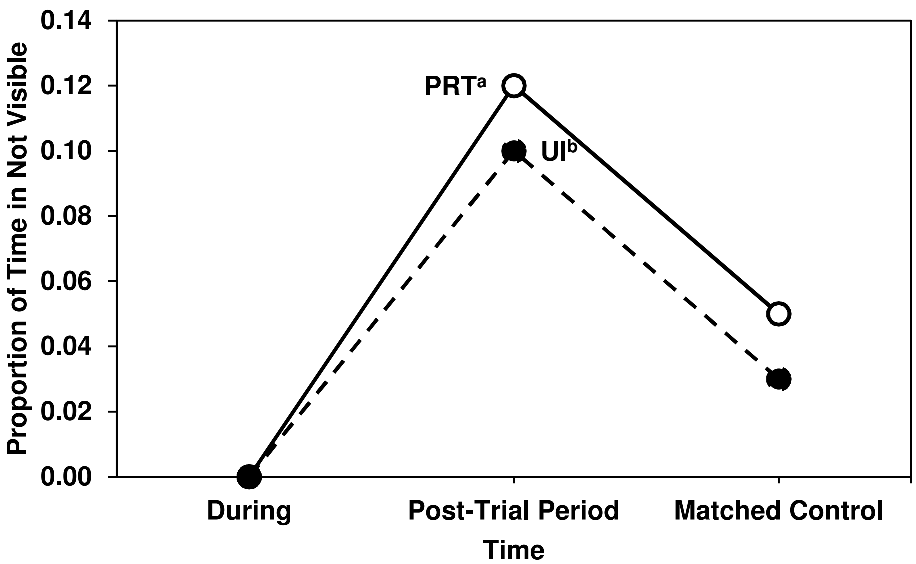

Figure 3. Mean proportion of time in the Not Visible context per interaction type and time. The proportion is the number of seconds in the Not Visible context divided by the number of seconds coded. Significance is between ‘During’ and ‘Post-Trial Period,’ and ‘Post-Trial Period’ and ‘Matched Control’ times ($p = .009$). Effects of interaction type (PRT versus UI) were nonsignificant ($p > .05$).
[a]PRT = Positive Reinforcement Training. [b]UI = Unstructured Interaction.

The proportion of time chimpanzees spent in the Agonistic behavioral context was low in all study conditions, as seen in Table 4, and univariate tests showed a nonsignificant main effect of time, $F(2, 8) = 1.33$, $p = .32$, partial $\eta^2 = .25$. The univariate test showed that the effect of interaction type (PRT versus UI) on proportion of time spent in each behavioral context was nonsignificant [Affinitive: $F(1, 4) = .15$, $p > .05$, partial $\eta^2 = .04$, Agonistic: $F(1, 4) = 1.0$, $p > .05$, partial $\eta^2 = .20$, Noninteractive: $F(1, 4) = .32$, $p > .05$, partial $\eta^2 = .07$, Not Visible: $F(1, 4) = 1.32$, $p > .05$, partial $\eta^2 = .25$]. Additionally, the statistical interaction of time (during, PTP, and MC) and interaction type (PRT versus UI) was nonsignificant [Affinitive: $F(2, 8) = 1.37$, $p > .05$, partial $\eta^2 = .26$, Agonistic: $F(2, 8) = .40$, $p > .05$, partial $\eta^2 = .09$, Noninteractive: $F(2, 8) = .70$, $p > .05$, partial $\eta^2 = .14$, Not Visible: $F(2, 8) = .52$, $p > .05$, partial $\eta^2 = .12$].

Discussion

The results of this study indicate that chimpanzees spent a significantly higher proportion of time in the Affinitive context when a caregiver engaged in either PRT or UI than during PTP or MC periods. During PTP and MC periods chimpanzees spent a significantly greater proportion of time in the Noninteractive context than during PRT and UI conditions. This indicates that inactivity significantly decreased when caregivers engaged captive chimpanzees in either type of interaction. These findings support previous research, which shows that increasing unstructured interactions with captive chimpanzees decreases inactivity (Baker, 2004) and both PRT and UI decrease inactive behaviors equally. Although the chimpanzees spent significantly more time in the Not Visible context during PTPs than during interactions and MC periods, this is likely due to the fact that the chimpanzees left the interaction area following both types of interactions with humans. The Fauna sanctuary consists of a series of tunnels connecting rooms, and chimpanzees are often difficult to see when they are traveling.

The particular chimpanzee behaviors the caregiver uses, for example, grins versus playface, head nods versus none, affect captive chimpanzees (Jensvold, 2008). In the present study, the caregiver used species-typical chimpanzee behaviors in both PRT and UI conditions. For example, the caregiver used breathy pants and head nods as greetings. The only difference between the two conditions was the occurrence of PRT. Jensvold (2008) showed the positive effect of caregiver use of chimpanzee behaviors. Bayne et al. (1993) found that caregivers' use of species-specific behaviors decreased abnormal behaviors in monkeys. The present study also showed that interactions with caregivers are attractive to chimpanzees; the use of chimpanzee behaviors is likely a reason for this. Interactions in which caregivers use species-specific behaviors promote positive relationships, which have a positive effect on well-being.

Chimpanzees in this study were significantly more interactive in both PRT and UI trials than during PTP and MC periods, with no significant difference between the two interaction conditions. It is important to note that caregivers were always available and the chimpanzees could seek them out for interaction both during and outside of the study. This indicates that engaging chimpanzees in unstructured interactions promotes well-being as indicated by an equal increase in prosocial behavior during both interactive conditions. Furthermore, the PRT condition in this study included food while the UI condition did not have food. This indicates that unstructured interactions are just as attractive for chimpanzees to participate in as food-based PRT interactions. Chimpanzees are a highly social species, so they are attracted to social situations and interactions.

Chelluri et al. (2013) found that both chimpanzees and gorillas exhibited more agonistic behavior toward caregivers during unstructured interactions than during a matched control period, which is different than the results of the present study. Relationships between captive animals and caregivers can at times be negative or nonexistent (Hosey, 2008). For example, laboratory chimpanzees had increased incidents of conspecific wounding when caregivers were engaged in routine husbandry tasks compared to when caregivers were not engaged in these tasks (Lambeth, Bloomsmith, & Alford, 1997). Rhesus macaques experienced increased heart rates during routine husbandry tasks compared to when these tasks were not occurring (Line, Markowitz, Morgan, & Strong, 1991). In some cases the mere presence of caregivers, without any interaction, can be stressful to primates. It is possible that the caregiver-directed agonism in Chelluri et al.'s (2013) study is indicative of a stressful relationship. The Chelluri et al. (2013) findings were very different than the current study, in which the Agonistic context almost never occurred in any condition. Fauna Foundation emphasizes positive relationships between caregivers and chimpanzees, and as such, caregiver discipline, harassment, or antagonism of the chimpanzee is strictly prohibited. Instead, the use of chimpanzee behaviors is emphasized. The caregiver, AW, had extensive training in the meaning of chimpanzee behaviors and years of experience using reciprocal friendly ones. The findings of this study likely reflect this institutional policy. It is important for caregivers to build positive relationships with captive chimpanzees by engaging chimpanzees in interactions that build rapport, as the present study demonstrates.

The National Institutes of Health Council of Councils Working Group on the Use of Chimpanzees in NIH-Supported Research (2013) report states, “Positive reinforcement training is the only acceptable method of modifying behaviors to facilitate animal care and fulfillment of animal needs” (p. 4). Indeed, PRT is an effective method for facilitating captive nonhuman primate population management (Bloomsmith et al., 1998; Schapiro et al., 2001; Coleman et al., 2008; Gillis et al., 2012; Minier et al., 2011; Rogge et al., 2013; Veeder et al., 2009), medical treatment (Bourgeois et al., 2007; Coleman & Maier, 2010; Gresswell & Goodman, 2011; Priest, 1991), research procedures (Brown & Loskutoff, 1998; Reinhardt, 1991; Vertein & Reinhardt, 1989; Videan et al., 2005), and behavior modification (Baker et al., 2010; Baker et al., 2009; Bourgeois & Brent, 2005; Pizzutto et al., 2007; Pomerantz & Terkel, 2009), and reduces physiological indicators of stress associated with laboratory procedures (Clarke et al., 1988; Dettmer et al., 1996; Lambeth et al., 2006; O’Brien et al., 2008; Reinhardt, 2003; Reinhardt et al., 1990; Videan et al., 2005). However, the present study’s findings suggest that UI encourages interactions just as well as PRT. Time spent in any positive interaction between caregivers and residence promotes well-being. Therefore, PRT is not the only way to encourage interaction, and the Institute of Medicine could broaden its recommendations to include the use of species-typical behaviors.

Captive environments housing nonhuman primates must have management programs that include environmental enhancement to promote psychological well-being

(Animal Plant Health Inspection Service of the U.S. Department of Agriculture, 2013). Both PRT and conventional enrichment are important in promoting the well-being of captive animals (Melfi & Hosey, 2011). Yet Westlund (2014) argues that PRT fulfills all criteria of conventional enrichment, because it "(a) give[s] the animal more control over its environment; (b) add[s] behavioral choices; (c) promote[s] species-appropriate repertoires; and (d) empower[s] the animal to deal adequately with challenges" (p. 1). Melfi (2013) argues that PRT could be considered enriching if the animal is in the process of learning new behaviors, as learning is enriching. PRT may also improve relationships between caregivers and captive animals that demonstrate a fearful personality (Ward & Melfi, 2013). However, there is presently a lack of evidence to support the argument that PRT and conventional enrichment "are comparable in terms of process, outcome or function" (Melfi, 2014, p. 104). Our findings support Melfi in that while PRT is useful for husbandry procedures, caregivers of nonhuman primates should not rely on PRT as the sole form of social enrichment.

Zoo-living Sumatran orangutans (*Pongo abelii*) and bonobos (*Pan paniscus*) with extensive experience with medical PRT showed no significant difference in salivary cortisol levels during medical PRT compared to baseline (Behringer et al., 2014). The chimpanzees that participated in our study had previous experience with PRT procedures. Future research could address stress during the acquisition phase of target behaviors in PRT sessions in order to determine if the implementation of PRT programs has any stressful effects.

Chimpanzees have unique personalities that are influenced by genetic and environmental factors (Goodall, 1986). Caregivers of zoo-living chimpanzees can reliably evaluate chimpanzee happiness (King & Landau, 2003) and personality traits (Pederson, King, & Landau, 2005). Zoo-living gorillas show individual differences in behavioral responses to crowd size based on traits such as sex, personality, and group composition (Stoinski, Jaicks, & Drayton, 2012), and zoo-living orangutans and gorillas show differences in human-directed affiliative behaviors based on age and familiarity with caregivers (Smith, 2012). There are three issues regarding individual differences that are relevant to the results of the present study. First, individual differences may influence an individual's willingness to participate in a study. One chimpanzee was removed from the present study because he exhibited behaviors indicative of stress, including avoidance of the videographer and threat displays during PTP and MC trials. What is particularly interesting is that he was the most highly trained chimpanzee at the sanctuary, as he is diabetic and reliably participates in toe pokes for blood samples and insulin injections. Therefore, it was likely not the PRT that he avoided but rather it was either the videotaping or the videographer. Thus it is important that experimenters allow chimpanzees to "withdraw" from a study, just as voluntary participation is a requirement for human subjects protections.

Individual differences may also influence an individual's responses to study conditions. In the present study three UI trials were rescheduled due to a chimpanzee's lack of interest in participating. Baker et al. (2003) exposed rhesus monkeys to different amounts of caregiver interaction and training. Monkeys who often engaged in self-injurious behaviors were more sensitive to varying levels of treatment than non-self-injurious monkeys. Waitt, Buchanan-Smith, and Morris (2002) found that monkeys reacted differently to the same caregiver treatment; monkeys who were rated as unfriendly reacted aggressively to caregivers, whereas monkeys who were rated as friendly had more affinitive interactions with caregivers. Suomi (1991) found differences in how "uptight" versus "laidback" monkeys responded to social changes. For example, young "uptight" monkeys became withdrawn after a separation from the mother, whereas "laidback" monkeys adjusted quickly. Table 3 shows the proportion of time individual chimpanzees spent in behavior contexts during the different conditions of the study. Two of the trials were with Maya and one was with Petra. The rest of the chimpanzees willingly participated in all scheduled PRT and UI trials, even though they had the option to interact with conspecifics. Although two of Maya's UI trials were rescheduled due to lack of interest in participating at the scheduled time, she spent the second highest proportion of time in the Affinitive context during UI trials (0.98) compared to the other four chimpanzees. Contrastingly, one of Petra's UI trials was rescheduled due to lack of interest in participating at the scheduled time, and she spent the lowest proportion of time in the Affinitive context during UI trials (0.66) compared to the other four chimpanzees.

Finally, individual differences may influence an individual's performance during training procedures. For example, in the use of PRT to facilitate the movement of chimpanzees from one location to another, the number of training sessions necessary to reach reliability was influenced by sex (Bloomsmith et al., 1998). Rhesus macaques categorized as having "exploratory" and "moderate" temperaments trained more easily to touch a target than individuals categorized as “inhibited” (Coleman, Tully, and McMillan, 2005). Thus it is important to account for individual differences in caregiving practices to meet individuals’ needs. While the Institutes of Medicine suggests the use of PRT to ensure cooperation, it is not effective with all individuals.

Self-directed behaviors, particularly self-grooming, scratching, and yawning, are indicators of arousal, as chimpanzees showed more of these behaviors in response to neighbor displays and vocalizations (Baker & Aureli, 1996). While the exhibition of particular behaviors is an indicator of stress levels, the inclusion of physiological measures of stress during particular points in time allows researchers to make stronger conclusions about the effects of different interaction types. A multivariate approach would also allow researchers to further understand chimpanzee stress levels during periods when they are noninteractive. Salivary cortisol is a good measure of stress because sample collection is relatively noninvasive and salivary cortisol levels fluctuate within minutes of stressors (Kirschbaum & Hellhammer, 1994). Researchers have used this technique with nonhuman primates, including chimpanzees (Kutsukake et al., 2009), bonobos (Behringer et al., 2009; Behringer, Deschner, Möstl, Selzer, & Hohmann, 2012; Behringer et al., 2013), gorillas (Kuhar, Bettinger, & Laudenslage, 2005), and orangutans (Elder & Menzel, 2001). It would be interesting to correlate these physiological measures with behavioral measures such as those used in the current study.

Results of our study suggest that caregivers can use both PRT and UI to promote positive relationships in interactions with captive chimpanzees. In addition, caregivers should include the use of species-specific behaviors in these interactions to increase rapport (Jensvold, 2008). Relationships are a critical aspect of life in captivity (Jensvold, 2008; Poole, 1996; Reinhardt, 1992) and there is physiological as well as behavioral evidence that friendly interactions are beneficial (Baker, 1997; Hemsworth & Barnett, 1987; Nerem, Levesque, & Cornhill, 1980; Pizzutto et al., 2007; Seabrook, 1984). Indeed humans with more friends have reduced stress (Taylor et al., 2000), more health benefits (Costanzo et al., 2005), and live longer (Giles, Glonek, Luszcz, & Andrews, 2005) than those with fewer friends. Zookeepers report that establishing bonds with the animals in their care makes working with the animals easier and more enjoyable, and the animals with which caregivers have established bonds respond to interactions in a calmer manner (Hosey & Melfi, 2012). PRT promotes cooperation and affinitive interactions as well. Thus, friendly relationships can improve quality of life and this study demonstrates that both PRT and UI promote this. By engaging captive chimpanzees in interactions with caregivers using species-specific behaviors, caregivers build important relationships. Estep and Hetts (1992) argue that these relationships provide research opportunities and improve animal welfare. The present study supports their point and demonstrates that engaging chimpanzees in both training and unstructured interactions promotes prosocial behavior between captive chimpanzees and caregivers, and thus improves welfare.

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