ENVIRONMENTAL ENRICHMENT AS A MEANS OF INCREASING MALE-FEMALE SOCIAL INTERACTIONS IN A CRITICALLY ENDANGERED SPECIES, *Macaca nigra*

By

Danielle Renee Smith

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Department of Biology

State University of New York at Fredonia

Fredonia, NY 14063

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[redacted]

Dr. Karry Kazial
Advisor
Department of Biology

[redacted]

Patricia S. Astry
Department Chair
Department of Biology

[redacted]

Dr. Kevin P. Kearns
Interim Provost and Vice President for Academic Affairs

Table of Contents

Table of Tables

Table of Figures

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Abstract

Environmental enrichment refers to any modification of the physical and social environment of an exhibit in an attempt to improve the animal's quality of life in captivity. While prolonged levels of both high and low stress tend to result in a suppression of reproductive physiology, acute, yet moderate stress can potentially promote reproductive activity. Sulawesi Crested Macaques are critically endangered. The species exhibits a polygynandrous (multi-male/multi-female) mating system. The captive *Macaca nigra* population at the Buffalo Zoo was observed for 14 weeks, alternating between an enrichment item and lack of enrichment, and interactions between males and females were recorded. Analysis indicates a significant increase in the frequency of friendly behaviors in the presence of enrichment, accounting for 90.43% of behaviors compared to 71.24% of behaviors without enrichment. A decrease in frequency of unfriendly behaviors was also observed with enrichment, in which 9.57% of behaviors were unfriendly compared to 28.76% of behaviors without enrichment. An increase in duration of grooming behavior from a mean of 154.2 seconds to 279.8 seconds with enrichment was observed. If enrichment can be used to increase social interactions between males and females, then this research has the potential to improve captive breeding programs, particularly for threatened, endangered and/or slowly reproducing species.

Introduction

Environmental Enrichment

In Darwin's time, animals kept in captivity failed to reproduce as they had so successfully done in the wild. Due to this, it was thought that captivity was associated with a "sterility factor" which prevented reproduction (Carlstead and Shepherdson, 1994). Prior to the 1950's, the majority of exotic animals had yet to successfully reproduce in captivity. However, during the 1950's, zoos became more aware of the reproductive needs of their animals. In order to promote reproduction, needs for nutrition, space, climate, social groups, and nesting material, as well as an overall increase in environmental complexity must be satisfied (Carlstead and Shepherdson, 1994). Subsequent to providing a more complex atmosphere, many more species were capable of breeding in captivity. This demonstrated the role environmental enrichment may play in success of captive breeding programs.

The term "environmental enrichment" originally referred to the addition of food items or toys into an otherwise empty animal exhibit. However, modern use of the term refers to any modification of the physical and social environment of an exhibit in an attempt to improve the animal's quality of life in captivity (Carlstead and Shepherdson, 1994). This includes exhibit design such as size and foliage, introducing hiding places to increase privacy, adding climbing apparatuses or hunting/foraging apparatuses, as well as the traditional inclusion of treats and toys. Environmental enrichment creates a more complex atmosphere for captive animals, which may better mimic their natural environment. This complexity can reduce stress, decrease abnormal behavior, improve overall animal health, and promote reproductive behavior (Carlstead and Shepherdson, 1994). Thus, promoting and

maintaining responsiveness to stimuli via an animal's interactions with its physical environment is the ultimate goal of environmental enrichment.

In a study providing giant pandas with enrichment, five enrichment items were alternated between manipulable plastic items, a burlap sack of straw, apples frozen in blocks of ice, a puzzle feeder, and spruce branches (Swaisgood et al., 2001). Fourteen pandas were used in the experiment in which each subject experienced a 45 minute control session at the beginning, then experienced each of the enrichment items separately for 45 minutes. Each panda spent substantially more time being active and displaying both object-directed and non-object directed behaviors in the presence of enrichment. The subjects also spent substantially less time performing indicative feeding behaviors such as pacing near the keeper entrance. No habituation to enrichment items was detected (Swaisgood et al., 2001).

Providing environmental enrichment during an individual's development can have far reaching consequences. In small mammal and other primate studies, these effects have been demonstrated to include higher cerebral cortex weight and an increase in the number of glial cells, as well as motoric activity and exploratory behavior in individuals provided with enrichment since birth compared with individuals who were never provided enrichment (Carlstead and Shepherdson, 1994). While many of these studies cannot be performed on endangered species such as the Sulawesi macaque, these studies provide evidence for a role of enrichment in caring for endangered species, including mating success and promoting natural behaviors desired in individuals which may be part of reintroduction programs (Swaisgood et al., 2001).

The Role of Stress

Studies suggest the duration of stress may also play an important role in reproduction. A prolonged level of high stress, such as a lack of privacy in their exhibit, overcrowding, or frequent relocation, is generally associated with abnormal behavior, aggression, poor nutrition, and very early death. These consequences are potentially due to the prolonged increase in sympathetic adrenal-medullary activation and the subsequent increase in cardiac output (Carlstead and Shepherdson, 1994). In fact, prior to 1977, two out of every three wild caught primates died soon after entering captivity (Boere, 2001). Additionally, a correlation was supported between elevated corticoids (stress hormones) and poor health outcomes for zoo animals. For instance, both reproductive failure in white rhinoceroses and mortality in black rhinoceroses were associated with high inconsistency of secretion of glucocorticoids from the adrenal cortex (Carlstead and Brown, 2005).

Factors such as high public displaying with little privacy, proximity of predators, and inconsistency in keepers were also associated with high fecal corticoid concentrations and deviant behavior in a multi-institutional study of clouded leopards (McPhee and Carlstead, 2010). Prolonged levels of high stress in the form of social tension caused by harassment and overcrowding have been proposed as the potential cause of hormone suppression in marmosets, leading to infertility (Carlstead and Shepherdson, 1994). Similarly, high levels of aggression created by high population density in an enclosure may have negative impacts on group social interactions, potentially preventing reproduction. Elevated levels of stress are suggested to have exacerbated effects on pregnant animals, such as those frequently transported, and may affect the development of the offspring in utero as well (Carlstead et al., 1996).

Conversely, prolonged levels of low stress are generally associated with lethargy, slower habituation to new surroundings, poor health, and a lack of search capabilities to seek out new stimuli (Boere, 2001). This may be due to the increase in adrenocortical activation associated with lack of stimulation. Long bouts of minimal stress have also been documented to result in decreased motor skills, and the introduction of intense stimuli may lead to death (Carlstead et al., 1996). Other abnormal behaviors are observed in a state of prolonged absence of stress such as self-mutilation, abnormal copulation postures, and inappropriate sexual behavior including attempts to copulate with inanimate objects (Boere, 2001). Prolonged levels of both high and low stress tend to lead to a reduction of steroid hormone levels due to changes in stress hormones of the hypothalamic-pituitary-adrenal axis such as an increase in adrenocortical activation (Carlstead and Shepherdson, 1994). This results in suppression of reproductive physiological function and reduction of sexual activity.

While lengthy durations of high or low stress tend to suppress reproduction, acute, yet moderate levels of stress, have been suggested to increase arousal to stimuli and lead to sexual activation, potentially due to the release of norepinephrine and epinephrine from the sympathetic adrenomedullary system (Carlstead and Shepherdson, 1994). Release of norepinephrine is associated with sexual activation in several mammals, including estrus induction in prairie voles and rabbits, and the pre-ovulatory surge of luteinizing hormone in rats in response to novel stimulation (Vincent and Feder, 1988). Novel stimulation provided to create intermediate levels of stress are associated with steeper learning curves, increased awareness, peaked curiosity, and even improvements in immune function in mammals (Carlstead and Shepherdson, 1994). The introduction of acute stress early in development

may allow for better coping mechanisms for future stress. These studies suggest that the increased arousal brought about by acute stress could be elicited by the introduction of a novel enrichment item.

Acute stress created by the introduction of new items may also play a role in reduction of abnormal behaviors, as well as establishing stable social interactions such as increased friendly behaviors (Carlstead and Shepherdson, 1994). In a 1990 experiment by Chamove and Moodie, the introduction of a predator (in the form of a wooden hawk passing over a skylight) to a group of captive cotton-top tamarins was used to simulate a brief, intermediate novel event. Following the introduction of predation, infants and the adults who were holding each infant were removed from the rest of the group for approximately ten hours. Data were collected on the group members five hours after the individuals were returned to the group. This brief, but moderate stress from a threat of predation, as well as the additionally level of stress from the suggested loss of an infant, resulted in an increase in friendly interactions between group members for the remainder of each trial day when compared to control trials (Chamove and Moodie, 1990).

While numerous studies have been conducted on the effects of enrichment on individuals or social group cohesion, to date no research has been conducted with regard to utilizing environmental enrichment to increase male-female social interactions in an effort to increase reproductive success. This ability to increase friendly behavior between individuals

of the opposite sex may prove invaluable when attempting to breed slowly reproducing species, and species which are rapidly declining to threatened or endangered levels.

Sulawesi Macaques

The Sulawesi Crested Macaque is critically endangered and one of seven macaque species endemic to the northern peninsula of Sulawesi, Indonesia (Reed et al., 1997). Habitat loss and poaching are the most significant reasons for their declining populations. Sulawesi macaques are largely frugivorous and semi-terrestrial. A typical group is comprised of twenty to one hundred individuals, composed largely of females (Kinnard and O'Brian, 2000). The home ranges of several groups may overlap, causing increased intergroup competition for resources. Male *Macaca nigra* are readily discernible from females due to sexual dimorphism, with males being nearly twice as large as females and possessing larger canines as well. Their canines are larger than expected proportionate to body size, and are used in competing with other males for access to females, in addition to defending food resources against rival groups (Kinnard and O'Brian, 2000).

Macaca nigra social structure consists of a linear dominance hierarchy in which males are dominant over females and some males have a higher ranking than others (Kinnard and O'Brian, 2000). Female philopatry is observed in the wild, in which females stay in their natal group and males transfer to a new group upon reaching sexual maturity. Because of this dispersal pattern, females generally have high levels of friendly behavior, resulting in a relaxed dominance hierarchy and egalitarian social relationships (Reed et al., 1997). On the other hand, males rarely engage in friendly behavior with each other, and most male/male interactions are aggressive, reinforcing their linear dominance hierarchy. Lower ranking

males are often aggressive towards females, and females frequently direct more attention towards the dominant male. This preference may be due to both protection from harassment from lower ranking males and because the higher ranking males are better mates, providing better quality genes for offspring (Reed et al., 1997).

Grooming is an excellent measure of friendly behavior among this species. Females are four times more likely to groom males than the reverse situation. Grooming of the most dominant males is most frequently observed, as remaining close to high ranking males provides females with protection from lower ranking males. The female may also benefit from having better access to foraging resources by being more attentive to dominant males (Reed et al., 1997).

Macaca nigra engage in a multi-male/multi-female mating system, in which both males and females mate with multiple partners (Thomson et al., 1992). Mating and birth occurs throughout the year. Females reach sexual maturity at approximately 49 months (Rowe, 1996). The female reproductive cycle lasts approximately 40 days, and "advertisement" in the form of swelling in the anogenital region usually occurs to indicate that females are receptive to mating (Thomson et al., 1992). However, the period of maximum swelling of this region does not coincide with the timing of ovulation. This may occur to confuse males regarding the actual paternity of the offspring after the female mates with multiple males. Obscured paternity may, in turn, reduce the risk of infanticide (Thomson et al., 1992).

Purpose

The main objective of this study was to gather data on the effectiveness of introducing environmental enrichment items to increase social interactions between males and females. This increase in interactions may lead to an increase in friendly behavior which could result in increased reproductive success. Successful captive breeding programs are vital to establish as population numbers of countless species dwindle to endangered levels, largely as a result of human activities.

If the introduction of brief, yet moderate stress (to increase arousal) can be achieved through the introduction of a novel enrichment item, then the question arises of whether environmental enrichment can be utilized to increase intersex social interactions.

Hypothesis and Predictions

It was hypothesized that the Sulawesi macaques will experience acute stress from the introduction of novel enrichment which mimics more closely what they experience in their natural environment in Indonesia, and therefore they will respond with more frequent male-female behaviors compared with the low level of prolonged stress and fewer interactive behaviors they currently exhibit in their captive environment. If this were the case, one would predict the introduction of novel enrichment items as acute stressors to be associated with an increase in duration and frequency of friendly behaviors between males and females, as well as a decrease in the duration and frequency of unfriendly intersex behaviors compared with the no enrichment condition.

Methods

Group Composition

The captive *Macaca nigra* population housed at the Buffalo Zoo currently consists of seven adults including one male and six females, as well as a juvenile male. This group size is similar to those found at other zoos. Similarly, the number of males and females within the group is relatively comparable to the sex ratio observed at other zoos. Several of the adults in the Sulawesi macaque group at the Buffalo Zoo are related. The older male (Cedric) is, therefore, chemically suppressed to prevent him from mating with his three half-sisters (Stella, Marie, and Lyla) as well as his maternal grandmother (Joan). Chemical suppression to prevent inbreeding is a common practice for this species at other institutions as well. The younger male (Lindberg) was recently introduced to the group after being transferred from the Omaha Zoo, and will be allowed to breed with all females upon reaching sexual maturity.

Sampling Procedure and Ethogram

Social behaviors between males and females were observed for two weeks, without making any alterations to the exhibit, by conducting a focal sample of all group members simultaneously. Data was always collected on Mondays, Wednesdays, and Sundays. Each observation was conducted for two and a half hours (nine thousand seconds), from 2:00pm to 4:30pm, and the occurrence and duration of each behavior observed was recorded. Week 1 consisted of initial observation to look for physical characteristics to assign individual identification and build a list of behavior descriptions and terms. Week 2 of observations was

conducted to develop an ethogram of commonly exhibited behaviors during male-female interactions (Table 1). Each behavior was then categorized as either friendly or unfriendly behavior.

Table 1. Ethogram of male-female interactions, including those which were friendly and those which were unfriendly

Ethogram of Male-female Interactions	
Behavior Name	**Description**
Friendly	
Grooming	An individual cleans/licks/picks through an individual of the opposite sex's fur which does not result in biting, teeth baring or vocalizations
Play Chase	An individual chases a member of the opposite sex, which is not followed by teeth baring, or vocalizations
Friendly climbing	Climbing of an individual onto an individual of the opposite sex which does not result in retreat of the other individual or teeth baring or vocalizations
Food Sharing	An individual approaches a member of the opposite sex which is already in possession of food and either takes the food from the individual, or consumes it while it is still in the possession of the original individual and does not result in teeth baring, vocalizations, biting, or retreat of one of the individuals
Attempted Copulation	A male individual mounts and attempts to copulate with a female individual. The act does not result in teeth baring, biting, vocalizations, or retreat or chasing of one of the individuals
Unfriendly	
Biting	An individual nipping or biting another which leads to teeth baring, vocalizations, or retreat of one of the individuals
Unfriendly Chasing	An individual chasing a member of the opposite sex which is preceded by teeth baring, biting, or vocalizations
Displacement	An individual approaches another while baring teeth, or vocalizing, resulting in the retreat of the second individual, but is not followed by chasing activity
Aggressive Posturing	Gestures such as teeth baring and vocalizations made by an individual toward other individuals which is preceded or followed by chasing activity or biting

Following this observation, alternating week long sessions of enrichment and no enrichment were conducted. A novel enrichment item was introduced in alternating weeks by the usual keeper of the exhibit to promote natural foraging behavior and social interactions. A new enrichment device was used, rather than using a device the zoo had previously used in

order to avoid biases already existing with a former device and to introduce truly novel enrichment devices. Behavior over the entire time period from August, 2012 to November, 2012 was compared to account for seasonal differences in behavior which were not the result of the introduction of an enrichment item. This allowed for twelve comparison weeks.

Enrichment Devices

At the request of the zoo, out of concern for the Sulawesi macaques being an endangered species, and not wanting to significantly alter the group social dynamic, only enrichment devices which the Sulawesi keeper believed would not provide extreme levels of acute stress were used in this experiment. Two novel enrichment items were utilized, one at a time, for the duration of the experiment: a six inch diameter Bio-Serv^{TM} stainless steel monkey shine mirror, and a five inch triangular Bio-Serv^{TM} stainless steel rattle (Figure 1). The edges of the mirror and washers on the rattle were rounded to prevent injury, and both devices are autoclavable.

Device Installation and Removal

During the enrichment trials, the enrichment item was left within the outdoor macaque exhibit for the entire week. Enrichment items were always added on Monday morning to the same general area in the exhibit, and removed the following Monday morning before the macaques were allowed access to their outdoor exhibit. The macaques were restricted to their indoor exhibit at night and, therefore, did not have contact with the enrichment item during the evening hours. The device was removed by the same zoo keeper who initially installed it to reduce the possibility of biases towards a certain staff member. Both enrichment devices remained at the zoo in the keeper's possession, and the devices

were washed between trials to limit contamination and exchange of pathogens. The same enrichment device was used for each day of an enrichment week, alternating with no enrichment every other week. Use of the mirror and rattle devices were rotated, always in the same order: one week with the mirror, followed by a week of no enrichment, then a week of the rattle, followed by no enrichment (Table 2).

Figure 1: Enrichment Devices

The enrichment devices provided to the macaques during the experiment, including the monkey shine mirror (left) and the rattle (right). Both items were purchased from Bio-Serv. Both devices are autoclavable.

Table 2: Enrichment condition for each week of observation during the experiment, including the two weeks of observations without enrichment to identify individuals and create an ethogram, and the twelve weeks of enrichment trials.

Week Number	**Enrichment Condition**
1	No Enrichment (Ethogram)
2	No Enrichment (Ethogram)
3	Mirror
4	No Enrichment
5	Rattle
6	No Enrichment
7	Mirror
8	No Enrichment
9	Rattle
10	No Enrichment
11	Mirror
12	No Enrichment
13	Rattle
14	No Enrichment

Statistical Analyses

All statistical analyses were conducted using SPSS examining duration and frequency of interactive behaviors. Since duration and frequency data were taken on few individuals exhibiting these behaviors many times, we adjusted for individual in our analyses. This way, if data is most attributable to certain individuals this will be taken into account in the analysis. A Linear Mixed Model was conducted for duration of grooming behavior, as the other eight behaviors did not occur for long durations, and analyses of behaviors occurring with such short duration may not yield reliable results. In the Linear Mixed Model duration of grooming was used as the dependent variable and presence of enrichment, sex of the actor, and order of enrichment (mirror, no enrichment, rattle, no enrichment) were factors. Identity of the actor was included as a subject variable.

Contingency Chi-square tests were used to test whether the frequency of all interactive behaviors was contingent on enrichment and whether the frequency of friendly and unfriendly behaviors was contingent on enrichment. Contingency Chi-squares were also used to examine whether certain individuals contributed more to the frequency of behaviors.

Results

The duration of friendly behaviors increased from an average of 95.14 seconds without enrichment to 150.79 seconds with the presence of a novel enrichment item (Figure 2). Attempted copulations were only observed in the presence of a novel enrichment item (Figure 3). Specifically, attempted copulations occurred in the presence of enrichment only within approximately 40 minutes of their feeding time. The duration of friendly behaviors

and unfriendly behaviors were similar for each enrichment device (Figure 4). While all friendly behaviors had a greater duration with enrichment, grooming behavior had the most significant increase, with a mean of 279.8 seconds with enrichment vs. a mean of 154.2 seconds without enrichment (Figure 5). Due to grooming duration having the most significant change, and all other behaviors being of such short duration, only grooming duration was statistically analyzed. The duration of grooming was similar for each enrichment device (Figure 6). Multiple unfriendly behaviors, specifically biting and displacement behavior were not observed during trials with an enrichment item in place, as they had been without enrichment (Figure 3).

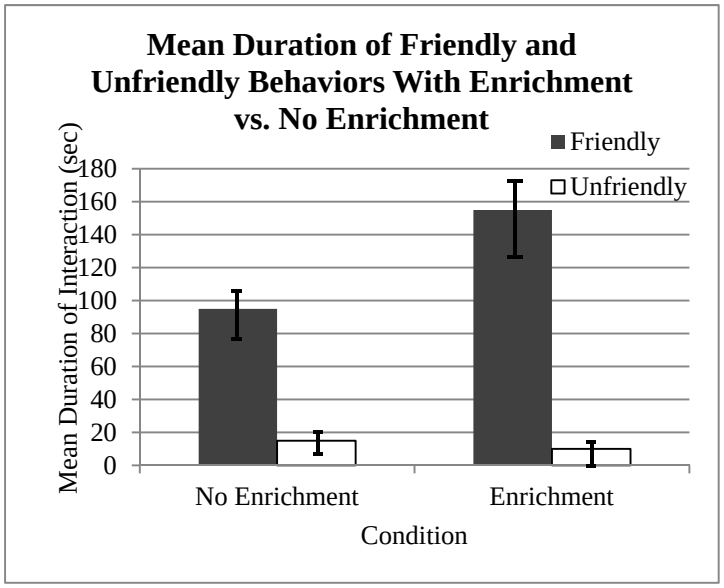

Figure 2: Mean duration of friendly and unfriendly behaviors (in seconds) between males and females per 9,000 second observation period for no enrichment and with enrichment. Error bars demonstrating two standard errors are included.

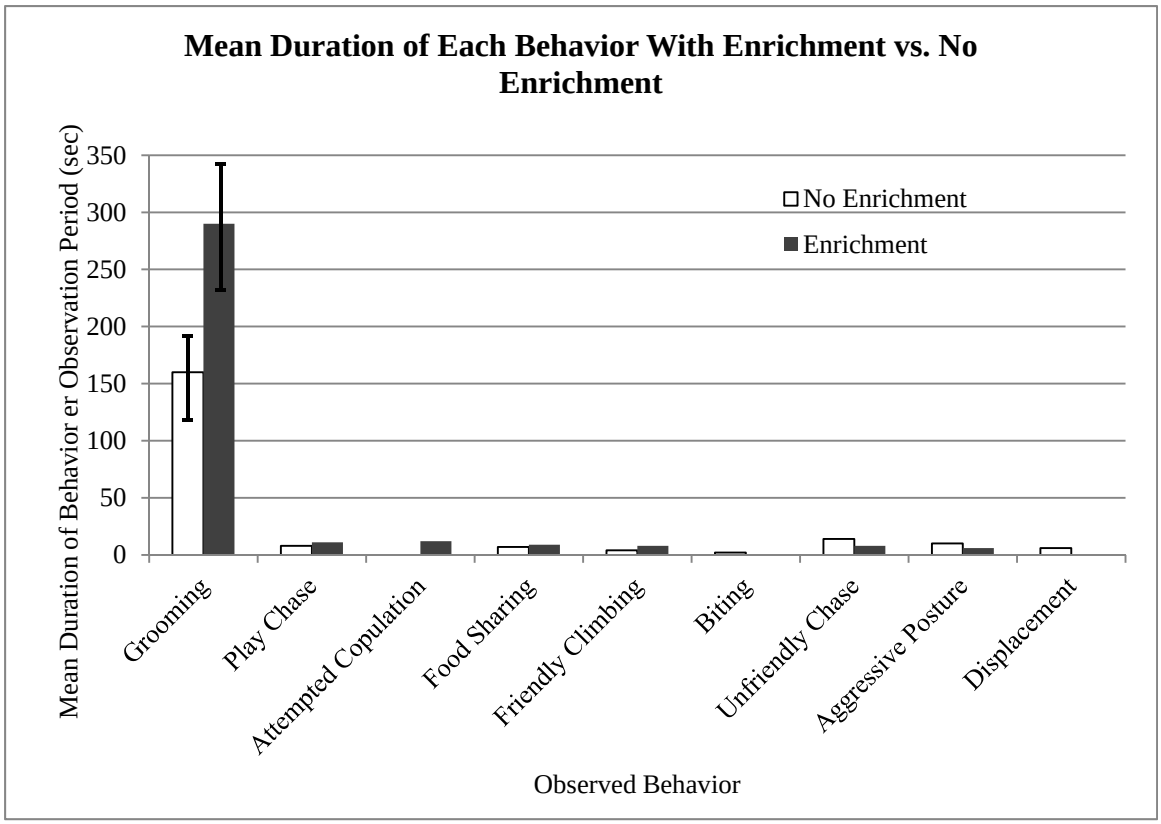

Figure 3: Mean duration of each behavior in seconds between males and females per observation period for no enrichment and with enrichment, including bars for 2 standard errors. Observation periods were 9,000 seconds long.

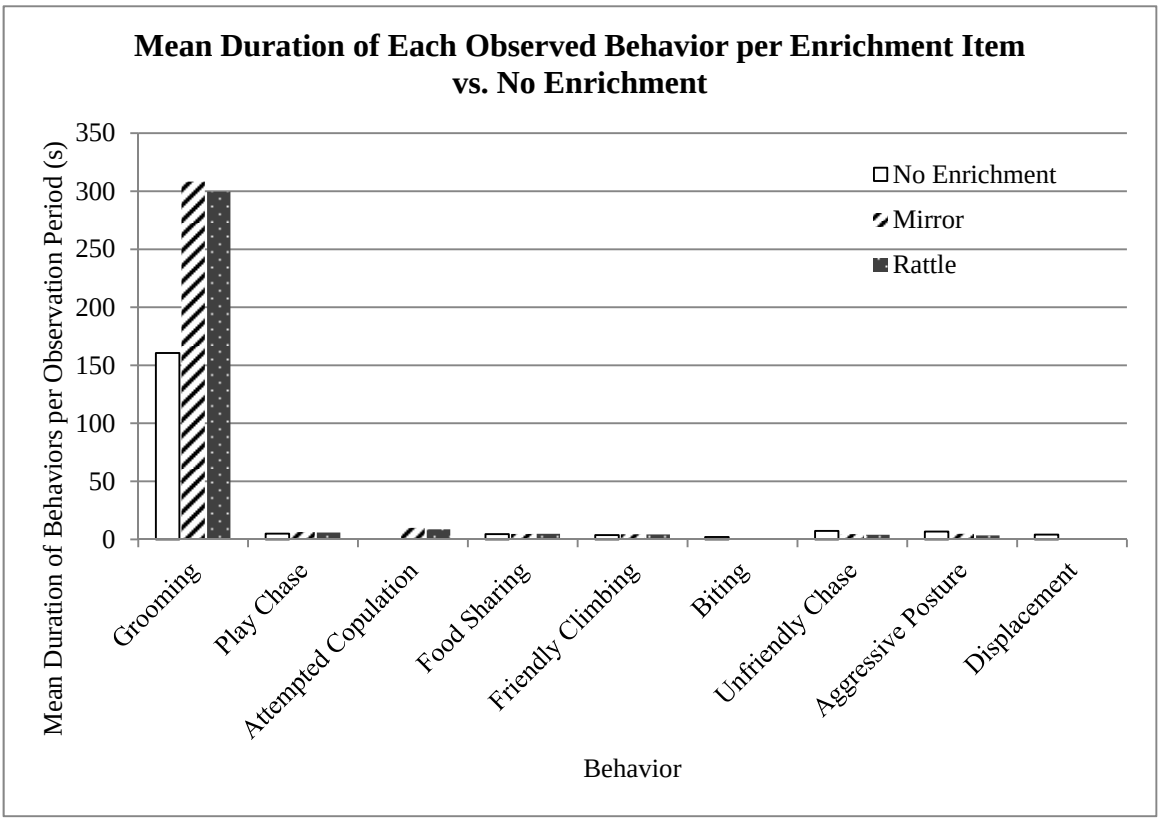

Figure 4: Mean duration of each behavior in seconds between males and females per 9,000 second observation period for both the mirror and the rattle vs. without enrichment.

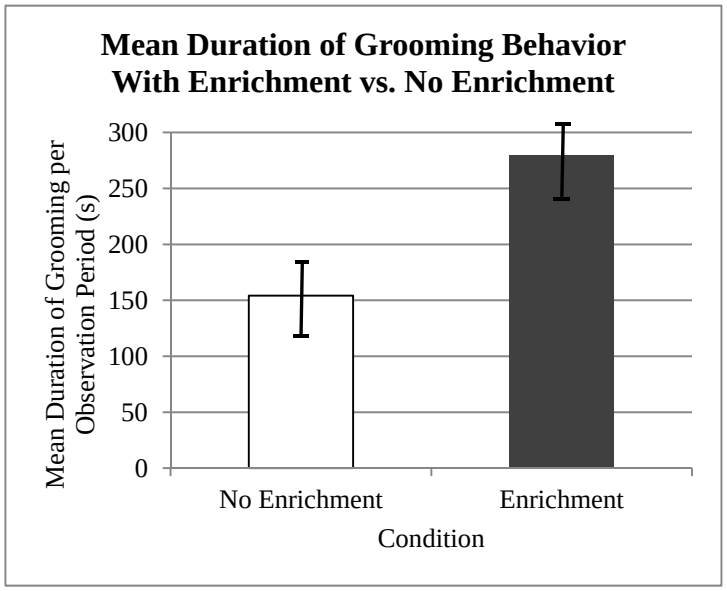

Figure 5: Mean duration of grooming behavior (in seconds) between males and females per 9,000 second observation period for no enrichment and with enrichment. Error bars demonstrating two standard errors are included.

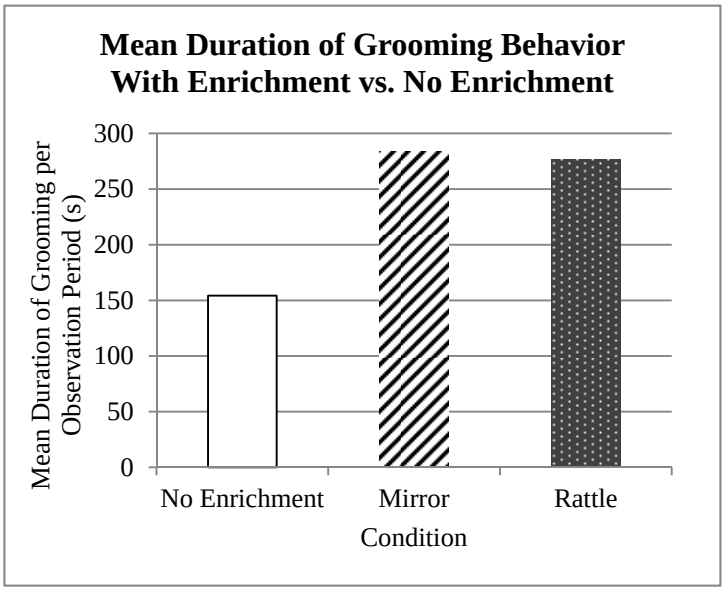

Figure 6: Mean duration of grooming behavior (in seconds) between males and females per 9,000 second observation period for both the mirror and rattle vs. no enrichment. Error bars demonstrating two standard errors are included.

The Linear Mixed Model of duration of grooming behavior yielded a statistically significant difference between enrichment conditions ($F = 84.80$, $df = 1,140$, $p < 0.0005$). Sex of the actor ($F = 0.849$, $df = 1,42$, $p = 0.362$) and the order of enrichment condition (mirror, no enrichment, rattle, no enrichment) ($F = 0.850$, $df = 2,139$, $p = 0.430$) did not yield signification differences for duration of grooming.

The frequency of interactive behavior types is contingent on enrichment (Contingency Chi-square, Chi-square = 34.55, $df = 9$, $p < 0.0005$). All individuals show increased initiation of interactive behaviors with enrichment. The frequency of friendly and unfriendly behaviors is contingent on enrichment (Contingency Chi-square, Chi-square = 22.35, $df = 1$, $p < 0.0005$) (Figure 7). The identity of the individual initiating an interactive behavior is not contingent on enrichment (Contingency Chi-square, Chi-square = 5.17, $df = 7$, $p = 0.640$). The identity of the individual initiating an interactive behavior is contingent on the type of behavior (Contingency Chi-square, Chi-square = 490.47, $df = 63$, $p < 0.0005$). This indicates certain individuals performed certain types of behavior more than other individuals. The

identity of the individual initiating an interactive behavior is contingent on the whether the behavior was friendly or unfriendly (Contingency Chi-square, Chi-square = 91.95, df = 7, $p < 0.0005$). This indicates certain individuals were more likely to perform friendly or unfriendly behaviors compared with other individuals.

An increase in frequency was observed for all friendly behaviors with enrichment, accounting for 90.43% of all behaviors compared to 71.24% of all behaviors without enrichment (Figure 7). Grooming, play chasing and food sharing behaviors had the largest increase (Figure 8). Attempted copulations were only observed in the presence of enrichment and within 40 minutes of feeding time. The lowest increase in frequency occurred in friendly climbing. Conversely, a decrease in frequency was noted for all unfriendly behaviors. Aggressive posture behavior had the most substantial decrease. Displacement and biting were only observed without enrichment. The slightest decrease in frequency occurred in unfriendly chasing behavior. Frequency of interactive behavior increased for both males and females in the presence of enrichment (Figure 9).

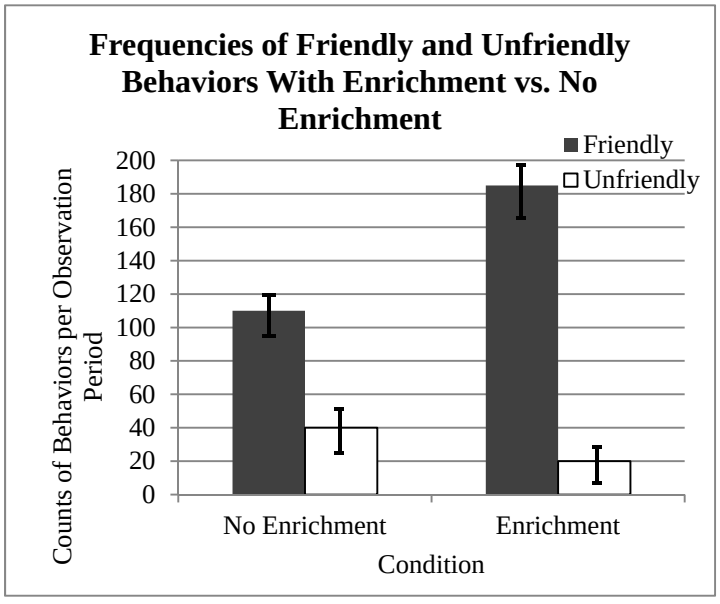

Figure 7: Frequencies of friendly and unfriendly behaviors for males and females per 9,000 second observation period for no enrichment and with enrichment. Error bars demonstrating two standard errors are included.

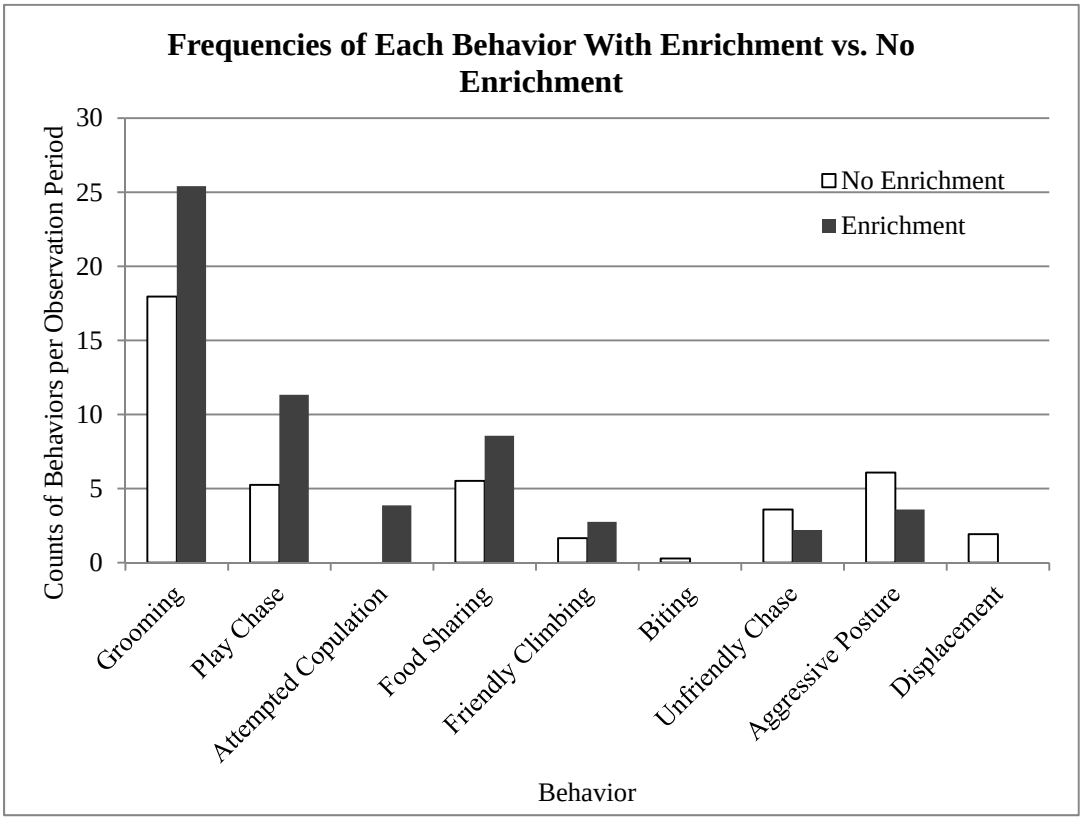

Figure 8: Frequencies of each behavior for males and females per observation period for no enrichment and with enrichment. Observation periods were 9,000 seconds long.

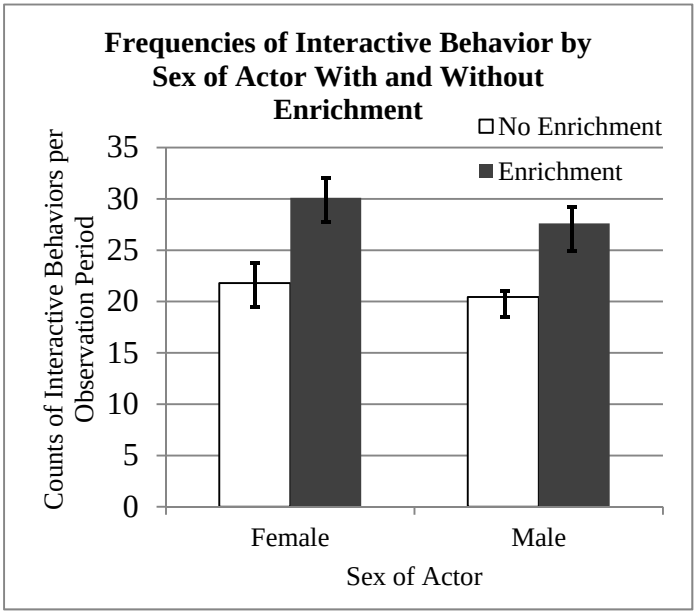

Figure 9: Frequencies of interactive behavior per gender of the actor initiating the behavior per 9,000 second observation period for enrichment vs. without enrichment.

Discussion

This is the first known study to examine the effects of environmental enrichment on the duration and frequency of intersex social interactions in a primate species. Fourteen weeks of observation yielded the observation that males and females seldom interact with each other compared to the frequency at which females interact with members of their own sex. This is consistent with studies of wild populations (Reed et al., 1997). However, the males in the captive population studied at the Buffalo Zoo interacted far more frequently than males are reported to interact in the wild. Furthermore, while most male/male interactions within wild groups are observed to be aggressive, interactions between the males at the Buffalo Zoo were seldom unfriendly behaviors.

Statistical analyses indicate a substantial increase in both frequency and duration of male-female friendly behavior when a novel enrichment item was present in the exhibit and interactive time nearly doubled, with the most notable increase occurring with grooming behavior. Conversely, a significant decrease in frequency and duration of unfriendly behaviors resulted with enrichment. These findings support the hypothesis that environmental enrichment may be used to increase friendly intersex social interactions. Both an increase in the frequency of friendly behaviors and a decrease in unfriendly behaviors were observed for both males and females in the presence of enrichment. Upon comparison of the duration of behaviors acted out by males and females, a clear difference between the sexes was observed with enrichment. Females engaged in interactive behaviors with a greatly increased duration with enrichment than was observed in males. These results suggest that while the duration and frequency of interactive behavior increase for females when a novel

enrichment item is introduced, males interact more frequently, but not with a greater duration than without enrichment.

There may be several possible explanations for the mechanism of this shift in social interactions between males and females when a novel enrichment item was added. In exhibits in which enrichment is absent, the stress from being in captivity may cause the equilibrium of friendly and unfriendly behaviors observed in the wild to be shifted toward unfriendly behaviors in captive groups. Due to being in an enclosure of a finite area, males and females within the group cannot distance themselves from each other, and therefore, such extended existence in close proximity may foster an increase in unfriendly behaviors. The intermediate stress associated with providing a novel enrichment item may provide relief from the stresses of the captive group social dynamic.

On the other hand, the stress associated with the introduction of a novel enrichment item may affect intersex social interactions by providing a means of distraction. Enrichment, by creating a more complex environment within the exhibit, may divert attention away from other stresses encountered within the group. This distraction may lead to a decrease in unfriendly behaviors.

The size of the enclosure in captivity is also substantially smaller than the home range of Sulawesi macaque groups in the wild, which ranges from 0.47 to 3.48 km^2. As a result of this space constraint, the normal balance of friendly and unfriendly behaviors could be further skewed towards increased in unfriendly behavior in captivity. Another possible source of chronic addition of stress could arise from the tendency of males to transfer out of their natal group in the

wild. Since this cannot be done in captive populations, unfriendly behaviors may become more frequent.

This research has potential applications for not only strengthening group cohesion among captive species, but also for improving reproductive efforts. If the intermediate, brief stress associated with introducing novel enrichment has the potential to increase friendly behaviors between males and females as well as decrease unfriendly behaviors, then this effect may extend to mating behaviors as well. Numerous species currently experience low reproductive rates in captivity, a fact which further increases the odds of extinction for these species. Zoos, therefore, must incorporate new ways to encourage threatened and endangered species to breed. The potential additive effect of providing enrichment in conjunction with food may further aid in success of captive breeding programs. This could be investigated with further research.

This study is not without its limitations. While the frequency of female interactions coincided with data from wild populations, the males in the group interacted more frequently than observed in wild populations, and such interactions were rarely aggressive as they are in the wild. There are numerous potential explanations for this anomaly. Firstly, the older of the two males, Cedric, is chemically suppressed to prevent reproduction with members of the group to which he is related. This may potentially result in a lesser degree of aggression toward other males than would be observed under normal conditions. Additionally, being in captivity eliminates the potential to compete with rival groups of the same species, which often occurs in the wild for territory and resources, which may affect the level of aggression between males. The younger male having not yet reached sexual maturity may also be a

factor. Repeating the experiment with a group of Sulawesi macaques in which members are not chemically suppressed and obtaining similar results would further support the hypothesis.

While chemical suppression is commonly done on this species in several zoos, the chemical suppression of the older male within the Sulawesi macaque population housed at the Buffalo Zoo leads the application of this data to other macaques at different institutions to be somewhat restricted. Upon repeating the experiment at another zoo, one would expect to see similar results in macaque populations which do not have chemically suppressed individuals. However, less friendly interaction between males in other institutions would also be expected. Repeating these procedures to a species outside the order Primates could further test the capacity for enrichment to affect social interactions between males and females.

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