

https://dspace.org/

Behavioral responses of vervet monkey Chlorocebus pygerythrus infants in a novel fostering program

Charne Van Niekerk; Neville Pillay

ROUTLEDGE JOURNALS, TAYLOR & FRANCIS LTD
https://hdl.handle.net/10539/41136
WOS

Downloaded from a DSpace repository. https://dspace.org/

Routledge
Taylor & Francis Group

Journal of Applied Animal Welfare Science

ISSN: (Print) (Online) Journal homepage: www.tandfonline.com/journals/haaw20

Behavioral responses of vervet monkey *Chlorocebus pygerythrus* infants in a novel fostering program

Charnè van Niekerk & Neville Pillay

To cite this article: Charnè van Niekerk & Neville Pillay (2024) Behavioral responses of vervet monkey *Chlorocebus pygerythrus* infants in a novel fostering program, Journal of Applied Animal Welfare Science, 27:2, 330-342, DOI: 10.1080/10888705.2023.2186786

To link to this article: https://doi.org/10.1080/10888705.2023.2186786

View supplementary material

Published online: 08 Mar 2023.

Submit your article to this journal

Article views: 78

View related articles

View Crossmark data

Full Terms & Conditions of access and use can be found at
https://www.tandfonline.com/action/journalInformation?journalCode=haaw20

JOURNAL OF APPLIED ANIMAL WELFARE SCIENCE
2024, VOL. 27, NO. 2, 330–342
https://doi.org/10.1080/10888705.2023.2186786

Routledge
Taylor & Francis Group

RESEARCH ARTICLE

Check for updates

Behavioral responses of vervet monkey *Chlorocebus pygerythrus* infants in a novel fostering program

Charnè van Niekerk and Neville Pillay

School of Animal, Plant & Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa

ABSTRACT

Vervet monkeys (*Chlorocebus pygerythrus*) are considered pests by farmers and homeowners. Consequent attempts to exterminate problem adult vervet monkeys often result in orphaned young offspring, which are sometimes taken to wildlife rehabilitation centers. We assessed the success of a novel fostering program at the Vervet Monkey Foundation, South Africa. Nine orphaned vervet monkeys were fostered to adult conspecific females of existing troops at the Foundation. The fostering protocol focused on reducing the time orphans spent in human rearing and involved a stepwise process of integration. We recorded the behaviors of orphans, including their interactions with their foster mother, to assess the process of fostering. Fostering success was high (89%). Orphans maintained close association with the foster mother and had little or no socio-negative and abnormal behavior. Comparison with literature showed a similar high fostering success in another vervet monkey study, regardless of the period and level of human-caregiving, and it is apparent that the duration of human care is less important than the protocol used for fostering. Nonetheless, our study has conservation relevance for vervet monkey rehabilitation.

KEYWORDS

Association with foster mother; behavioral responses; fostering; infants; Vervet monkey

Introduction

Humans often hand rear rejected or orphaned young individuals (Barham et al., 2008). The methods of rearing such as stimulation, feeding, play, comfort (Bashaw, Gullott, & Gill, 2010) and the reasons of rearing, depend on the caregiver and their motives for rearing (Seddon, Armstrong, & Maloney, 2007). The disadvantage of hand rearing includes the risk of young developing abnormal behaviors, such as increased aggression (Latham & Mason, 2008) and imprinting on humans. Many of these problems arise due to offspring being reared in isolation from conspecifics (Harlow & Suomi, 1971), loss of contact with a mother during the critical developmental phase (Meyer, Novak, Bowman, & Harlow, 1975) and attachment to caregivers.

The development of abnormal behaviors in hand-reared offspring can arise from a lack of stimulation (Sánchez, Hearn, Do, Rilling, & Herndon, 1998), incompetent hand rearing methods (Portin & Niebruegge, 2006), lack of contact between caregiver and offspring (Winslow, 2005) and no social interaction with playmates, often leading to self-play, resulting in a lack of appropriate social behaviors at adulthood (Harlow, Dodsworth, & Harlow, 1965), and possible increased aggression toward conspecific group members at an older age (McDougall, Réale, Sol, & Reader, 2006). Often the problem is that young individuals are not accustomed to adult conspecifics in the group (Meder, 1985). Lack of appropriate social skills by offspring can affect their acceptance and hence survival in a new group (Brightsmith et al., 2004) or their future reproduction (Ryan, Thompson, Roth, & Gold, 2002).

CONTACT Charnè van Niekerk charne123@icloud.com University of the Witwatersrand, School of Animal, Plant & Environmental Sciences, Johannesburg WITS 2050, South Africa

Supplemental data for this article can be accessed online at https://doi.org/10.1080/10888705.2023.2186786

© 2023 Informa UK Limited, trading as Taylor & Francis Group

Fostering orphan animal offspring to conspecifics can reduce their developing abnormal behavior and their attachment on human-caregivers (i.e., orphans becoming imprinted on humans). According to McCann and Rothman (1999), a successful fostering technique/requirement in primates should involve several of the following: introducing young orphans into groups in which adult/older conspecifics have already shown allo-parental care toward orphans (e.g., carrying the orphan); conspecifics are not aggressive toward introduced individuals; introduced orphans should display appropriate group social behavior (McCann & Rothman, 1999), and hand-reared offspring should be taught to drink milk from bottles when the foster female is not lactating (Emanuelson, 2006). Foster parents and/or groups should be carefully selected. It is suggested that human caregivers should cautiously introduce the individual to a conspecific individual (often to a female) (Thunström, Persson, & Björklund, 2013). An important first step is to record the behavior of all conspecific individuals initially to identify suitable foster parent/s (Jendry, 1996) that should demonstrate protective behavior toward the offspring (Chavatte, 1991). Fostering to conspecifics capitalizes on the natural ability of some primate species to foster unrelated conspecific offspring (Agoramoorthy & Rudran, 1992; Riedman, 1982).

Our study concerns fostering of orphans in captive vervet monkeys (*Chlorocebus pygerythrus*). Vervet monkeys are considered pests because of their crop-raiding behavior (Saj, Sicotte, & Paterson, 2001). They are persecuted consequently, leaving behind orphaned individuals. Orphans also result from their mothers being run over on roads. Every year, during and after the birthing season, there is an influx of orphaned vervet offspring at rehabilitation centers. A survey by Wimberger, Downs, and Boyes (2010) of 41 wildlife rehabilitation centers in South Africa showed that 26% accepted primate species, mainly Galagidae and Cercopithecidae, for rehabilitation and release. However, no reports were available of the number of centers that accepted orphaned offspring for rehabilitation or those that aided the injured for rehabilitation.

One sanctuary, the Vervet Monkey Foundation (hereafter the Foundation), however, accepts orphaned infant vervet monkeys and has a program to foster these infants into established captive troops. The aim of our study was to investigate the success of a novel fostering program used by the Foundation, whereby orphaned vervet monkey infants were hand-reared for a short duration of between 3 days and 2 months before being released into a foster female's troop. We hypothesized that a short duration of hand-rearing orphaned infants would lead to foster offspring displaying appropriate social behaviors. We also investigated which behaviors contributed to a successful fostering during their initial introduction to a foster mother in an integration cage and later with the foster mother released into the troop. We expected that successful fostering would be accompanied by greater mother-foster offspring bonding and whether orphaned vervet monkeys could be released into the same troop enclosure as the foster mother. As another measure of success, we also compared the impacts of human caregiving on fostering by comparing our findings with those of human caregiving in literature and methods of fostering in our study with another vervet monkey study that focused on integration of orphaned infants into established troops. Comparisons were made of the different methods used, such as how long it took to introduce orphans to troops, level of human involvement, behaviors observed, and the success of the foster method.

Materials and methods

Study area

The study was conducted at the Vervet Monkey Foundation located in Limpopo Province, South Africa (23.8525°S, 30.3378°E). During our study, the Foundation housed 14 vervet monkey troops. Our study occurred from December 2016 to June 2017.

We studied fostering method into two different established troops at the Foundation: the Goliath troop (established in 2005), comprising 43 adult and juvenile monkeys (16 males and 27 females), and occupying an area of about 20 000 m^2; and the Dino and Daniel (hereafter D and D) troop

(established in 2011), comprising 34 adult and juvenile monkeys (18 males and 16 females) and occupying an area of about 10 000 m^2. These troops were selected depending on the date orphans arrived at the Foundation, age of the orphans and previous experience of the troops in the fostering of orphans (information from the Foundation). Males in the troop were vasectomized, as per the Foundation's policy. Therefore, none of the females bred but they did display estrus. The Goliath troop received two male and two female orphans; one male being removed later. The D&D received five female orphans (Table 1). When orphans arrived at the Foundation, only one female (Kiki in D and D troop) had an injury sustained to the tail and was slightly dehydrated.

Integration of orphans

Integration into a troop followed a set protocol in four stages (below), developed by management at the Foundation.

Quarantine (Days 1–3)

Orphaned vervet monkeys were either dropped off by the public or collected by staff of the Foundation. New arrivals were placed into quarantine for 72 hours to receive veterinary care and received 24 h care from staff and trained volunteers. Quarantine took place in cages away from the troop enclosures. These cages had overhead netting and zinc sheets and electric fencing. The area contained cages of about 3 m × 3 m × 3 m and tree branches and pipes for climbing. Quarantine cages also contained 1 m × 1 m wire mesh feeding cages, which were used to train orphans to drink formulated milk from bottles (see supplementary image 1). Feeding cages had two entrance holes in the front to allow orphans access. Orphans were hand fed formulated milk by caregivers with baby bottles until they learnt to drink from holstered bottles in the feeding cages. If orphans did not learn to drink from the bottles by themselves, caregivers continued to train orphans in the next stage

Table 1. Description of orphans including sex, starting age, reason for being brought to the foundation, time spent in each phase, and if the integration was considered successful.

Troop	Sex	Starting age	Reason for being brought to the foundation	Time spent in phase - *Quarantine*	Time spent in phase - *Disneyland*	Time spent in phase – *Integration cage with human-caregiver*	Time spent in phase – *Integration cage with foster mother*	Considered successful integration into foster mother troop?
Goliath Troop								
Zoro	Male	3 weeks old	Unknown	3 days	16 days	4 days	41 days	Yes
Dana	Female	3 weeks old	Unknown	3 days	28 days	3 days	67 days	Yes
Maggie	Female	3 weeks old	Unknown	3 days	31 days	3 days	67 days	Yes
Neville	Male	3 weeks old	Unknown	3 days	38 days	2 days	67 days	No
D and D Troop								
Fiona	Female	4 weeks old	Mother was shot	3 days	22 days	1 day	14 days	Yes
Tammy	Female	3 weeks old	Unknown	3 days	4 days	3 days	31 days	Yes
Chica	Female	3 weeks old	Mother was shot	3 days	24 days	3 days	31 days	Yes
Cheyenne	Female	8 weeks old	Found alone alongside the road, mother assumed to have been hit by a car	3 days	0 days	0 days	15 days	Yes
Kiki	Female	3 weeks old	Unknown	3 days	27 days	3 days	55 days	Yes

(called Disneyland). Orphans were placed in carry cages and transferred into log cabins and cared for by human-caregivers at night and then returned to the quarantine cage in the morning. The staff caring for the orphans at night kept them in the carry cages and fed them as required; depending on the situation and need, such as feeding the orphan, staff removed the orphan from the carry cage. Each orphan was cared for by two to three primary staff/volunteers in the quarantine phase. If the orphan learnt to drink from the bottles while in quarantine, they would skip the Disneyland phase.

Disneyland (Days 4–42)

Following the 3-day quarantine, orphans were introduced into a section of the Foundation called Disneyland. This was a single 7 m × 7 m × 3 m building constructed of chain-link fence with a zinc roof, and branches and PVC piping for climbing. The time spent by orphans in Disneyland depended on how long it took them to become accustomed to drink from holstered bottles in the feeding cages. There were 1–2 feeding cages (see above) depending on the number of orphans in Disneyland, with two orphans per a feeding cage. Orphans were coaxed into the feeding cage using a mix of chopped fruit and vegetables. Orphans were also often encouraged to drink from the bottles by caregivers tapping on the end of the bottles once they were in the cage. Orphans were placed in carry cages and transferred into log cabins and cared for by human-caregivers at night and then returned to Disneyland in the morning. The staff/volunteers caring for the orphans at night kept them in the carry cages and fed them as required but if the staff felt the need to remove the orphan from the carry cage they were allowed to do so. Each orphan was cared for by two to four staff/volunteers during Disneyland phase. The human-caregivers were kept the same if possible, during this phase.

Integration cage with human-caregiver (Days 43–47)

Orphans that could drink independently from the bottles in the feeding cage were placed into an integration cage of a selected troop's enclosure for 1–4 days. Each troop enclosure had a 3 m × 3 m × 3 m integration cage made of chain link steel, attached to the outside. These cages were used to introduce orphans to adult female monkeys in a troop. Each integration cage housed up to two orphans and two adults and had an entrance for staff to provide food and for daily cleaning. A small gate between the integration cage and the troop enclosure allowed potential foster mothers into the integration cage and for the release of the foster mother and orphan into the enclosure. The caregiver remained with the orphan, while it explored the integration cage during the day. At night, the caregiver took the orphan to the log cabin (see above).

Host troops were selected based on the number of troop members (i.e., total number of vervets that an enclosure could accommodate without causing overcrowding), a greater female-to-male ratio, the age structure favoring more adults and juveniles, and history of the troop (e.g., ex-pets were often placed in the same troop).

Integration with foster mother (Days 48–115)

On the day orphans were introduced to the foster mothers, orphans were left alone in the integration cage. The caregivers vacated the surrounding area so as not to hinder these introductions since many orphans became attached to their caregiver (Foundation information), this was often seen by the orphan becoming dependent on the human-caregiver (i.e., for food and security). Volunteer staff members, with whom the orphan was not familiar, opened the gate between the cage and enclosure to allow access by adult female vervet monkeys, usually allowing two adult females at a time into the integration cage. If the alpha female of the troop showed interest in the individual, she was allowed into the cage first. The alpha female was allowed to remain for as long as she was interested in the orphan. If the alpha female and other high-ranking females had been in the integration on a rotational basis and none showed interest in the offspring, lower ranking females that approached the cage door were allowed into the cage.

To establish whether a female was interested in the orphan, Foundation staff monitored the interactions between the female and orphan. An interested female would approach the orphan, lip-smacked, attempted to groom or grabbed the orphan and/or pulled the offspring toward her, encouraging it to cling. Females that displayed nervous behavior, such as pacing and pulling on the gate, were let out of the cage. An adult female interested in the orphan was kept in the integration cage with the orphan from this time onwards. The orphan and foster female received a bowl of chopped fruit and vegetables in the integration cage every morning and evening. Females that became foster mothers did not leave the cage, but other females were periodically allowed into the integration cage.

Closer to the release date into the troop, other females of the troop were allowed into the integration cage as often as possible to spend time foster mother and orphan, spending 30 minutes to 12 hours. This process enabled the orphan (while with the foster female) to become familiar with different adult females before being released into the troop. The process of integration with the foster mother ranged from 14 to 67 days, and the number of days spent in the integration cage depended on the age of the orphan. Orphans were released into the troop only when they were at least 3-month old and only if they clung to the foster mother.

Release into troop (Days 116+)

Volunteers were positioned around the enclosure when orphans and foster mothers were released from the integration cage into the troop. Volunteers engaged in this activity for 1 to 2 weeks from before sunrise to after sunset to confirm whether the orphans were drinking milk from the holstered bottles in the feeding cage. Feeding cages had a similar construction as those used in the integration cage and were placed inside the troop enclosures. If the orphans did not drink, volunteers held a bottle of milk close to the fence of the integration cage to let the orphan drink or they slowly walked to the feeding cages and placed the bottle into the holster of the feeding cage.

Behavioral observations

Behavioral observations were conducted by CvN on the nine orphans from the time each orphan was placed in the troops' integration cages, where orphans could drink milk from the feeding bottles placed in the feeding cages and released into the troops' enclosures. Continuous focal observations were conducted from 07h00 to 17h00, by recording the interactions of the orphaned infants in the integration cage and the troop enclosure. Sampling was opportunistic, depending on whether the orphan was visible. Observations started when orphans were placed into the integration cage with a potential foster mother. We scored the behavior of the orphan using focal sampling. The duration of these observations ranged from 60 to 90 minutes in total per orphan in the integration cage ranged and for 10–150 minutes per orphan in the troop enclosure.

Behaviors recorded are described in Table 2 generated from the literature on primate behavior. We used the information from studies by Brown and Dixson (2000) for socio-positive behavior and mother-infant behavior, Sashaw (2012) for allo-grooming behavior and feeding and drinking behavior, Bassett, Buchanan-Smith, McKinley, and Smith (2003) for inactivity, Fedigan (1972) for behaviors associated with socio-positive behavior, Struhsaker (1967) for socio-negative behavior, and Manson *et al.* (2007) for abnormal behavior.

Data analysis

During the observation of the behavior for the orphaned infants, the duration of time (in minutes) of each behavior for the orphans was recorded for each troop for each day. The duration of sampling differed due to varying introduction dates of the orphans, release dates, and different sampling durations due to weather conditions. Data for each behavior were pooled by week by troop. Pooling the data accounted for differences in sampling days since orphans arrived at different ages and were

Table 2. Descriptions of 10 behaviors scored in orphan vervet monkeys in the integration cage with foster mother and after their release into a troop.

Type	Description
Inactive	Offspring remained in one location, alert (Bassett, Buchanan-Smith, McKinley, & Smith, 2003) or asleep but not clinging onto the foster mother. It was either seated or lying down.
Active	Travel from ground to branches, branches to branches or on the cage fence walls or roof (Bassett, Buchanan-Smith, McKinley, & Smith, 2003).
Association with foster mother	Direct contact with the foster mother. Clung onto the foster mother's abdominal area or back; suckling; sleeping while clinging to the foster mother, and grooming (Brown & Dixson, 2000).
Feed and Drink	Drank milk from bottles in the feeding cages, ate fruit and vegetables supplied by the sanctuary, and grass, leaves or seeds in the enclosure (Sashaw, 2012).
Allo-grooming	Groomed by/grooming another troop member excluding the foster mother (Sashaw, 2012).
Socio-positive	Play such as chasing and wrestling (face relaxed with the mouth slightly open and unclenched teeth), "hugging"/embracing, generally silent and non-aggressive (Brown & Dixson, 2000; Fedigan, 1972).
Socio-negative	Aggressive chasing, fighting, biting and open and closed mouthed grins (clenched teeth in an exposed grin), eyelids displayed and often accompanied with motion of the head or body moving up and down (Struhsaker 1967).
Interactions with people	Hand feeding from human, reaching for human in integration cage or once released into the troop.
Self-grooming	Grooming any reachable part of the body.
Abnormal	Digit manipulation, suckling digits, pacing, self-harm (i.e., self-biting, that causes bodily harm to self; Mason *et al*. 2007).

introduced to females at different times. The frequency of behaviors per minute was obtained by dividing the total counts of behaviors by the total observed time per individual orphan for data analysis.

Data were analyzed using Statistica 12 (www.statsoft.com). The datasets were checked for normality of variances and heteroscedasticity. The dataset was transformed using squared root transformation to approximate normality. General linear models (GLMs) with Gaussian error structure were used to analyze weekly changes in behaviors in each troop separately. In the analyses, the frequency per minute of behaviors recorded was the dependent variable, the week of sampling was the repeated measure variable, individual was included as a random variable, and Goliath troop orphans were 3-week old when we started behavioral observations and starting age was not included as a continuous predictor in the analysis. In contrast, for the D and D troop, starting ages at the time of observations for the orphans varied in the integration, but there was no significant correlation between starting age (continuous variable) and common behaviors, whilst orphans were in the integration cage ($p > 0.05$). Starting age was therefore also not considered for the GLM analyses. The behaviors recorded were the dependent variable. We analyzed behaviors that did not have a zero value or close to zero value, after being square root transformed to approximate normality. The week of sampling was the repeated measures variable, individual was included as a random variable. Significant fixed predictors were assessed using the Fisher LSD post hoc test. Alpha was set at 0.05, and tests were two-tailed.

Comparisons with other studies

Without a control study to validate the fostering procedure used by the Foundation, we compared our findings with published literature. We used Google Scholar and the Web of Science to search for studies that used different hand rearing or nursery rearing methods on vervet monkeys; we are mindful that not all these methods of rearing can result in successful integration into social groups. We initially searched for vervet monkey fostering, and vervet monkey hand-rearing. The level of human-care was weighted from zero to four based on the amount of time orphans spent with human-caregivers. Level zero was no human-care, level one was 1 to 3 months of human-care, level two was 4 to 6 months of human-care, level three was 7 to 9 months of human-care, and level four was 10 months and more of human-care. Success was based on the number of orphans released into

the troop and remained in the troop. The success of the other study was determined from reports provided by the authors.

Results

Integration cage

The full data set collected in this study is available in Supplementary tables. Behavioral observations were made as soon as the nine orphans were placed in integration cages and introduced to female vervet monkeys.

For the Goliath troop, week was a significant predictor of all behaviors in the integration cage and the individual was significant predictor of active, association with foster mother and socio-positive behavior (Table 3). Inactive behavior decreased over the 3 weeks of study (Figure 1 a). Active behavior was highest in week 2 (Figure 1 a). Association with the foster mother was lower in week 3 compared to weeks 1 and 2 which did not differ from each other (Figure 1 a). Feeding and drinking were highest in week 2 and lowest in week 3. Socio-positive behavior was highest in week 2 and lowest in week 3, overlapping with week 1 (Figure 1a). For D and D troop, week 1 was a significant predictor of active, feeding and drinking behavior and socio-positive behavior, whereas individual was a significant predictor of socio-positive behavior (Table 3). These behaviors were greater in week 1 than week 2 (Table 3). Inactive and association with the mother did not differ between the 2 weeks of sampling (Figure 1 b).

Table 3. Output of the GLM for predominant behaviors for individual and week for Goliath and D and D troop in the integration cage. Values in bold are statistically significant.

Goliath troop behavior	Individual	Week	Comparisons between weeks
Inactive	$F_{3,6} = 2{,}85$; $p = 0.127$	**$F_{2,6} = 15.24$; $p = 0.004$**	**3 < 2 < 1**
Active	**$F_{3.6} = 5.14$; $p = 0.043$**	**$F_{2.6} = 20.14$; $p = 0.002$**	**3 < 2 > 1**
Association with foster mother	**$F_{3.6} = 13.45$; $p = 0.005$**	**$F_{2.6} = 6.96$; $p = 0.027$**	**3 < 2 = 1**
Feed and drink	$F_{3,6} = 2.79$; $p = 0.132$	**$F_{2.6} = 34.84$; $p < 0.001$**	**3 < 2 > 1**
Socio-positive	**$F_{3.6} = 14.60$; $p = 0.004$**	**$F_{2.6} = 6.90$; $p = 0.028$**	**3 < 2 > 1**
D and D troop behavior	**Individual**	**Week**	**Comparisons between weeks**
Inactive	$F_{3.3} = 0.77$; $p = 0.584$	$F_{1.3} = 6.06$; $p = 0.091$	**2 < 1**
Active	$F_{3.3} = 3.99$; $p = 0.143$	**$F_{1.3} = 11.34$; $p = 0.043$**	**2 < 1**
Association with foster mother	$F_{3.3} = 1.54$; $p = 0.366$	$F_{1.3} = 10.74$; $p = 0.336$	**2 < 1**
Feed and drink	$F_{3.3} = 0.56$; $p = 0.679$	**$F_{1.3} = 10.74$; $p = 0.047$**	**2 < 1**
Socio-positive	**$F_{3.3} = 52.28$; $p = 0.004$**	**$F_{1.3} = 96.23$; $p = 0.002$**	**2 < 1**

Note: Values in bold are statistically significant

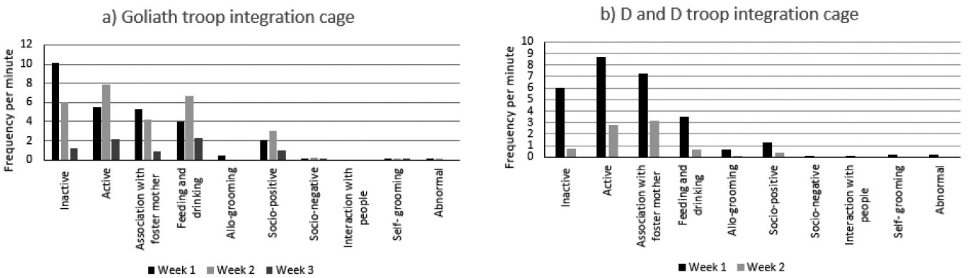


Figure 1. The frequency per minute for ten behaviors for all individuals in the a) Goliath troop for 3 weeks in the integration cage and the b) D and D troop for 2 weeks in the integration cage.

Enclosure

Behaviors of the three orphans were recorded as soon as they were released into the Goliath troop with their foster mother. The data from one orphan were excluded as it escaped from the enclosure after only being in the enclosure for a few days; it was moved to another troop after a failed attempt to reintroduce him to protentional foster mothers in the troop.

For Goliath troop, week was a significant predictor of only association with foster mother and individual was a significant predictor of association with foster mother (Table 4). Association with foster mother behaviors occurred more frequently in week 1 than week 2. Association with the foster mother was greater in week 1 compared to week 2 (Figure 2 a). Week was a significant predictor of active behavior, association with foster mother and feeding and drinking (Table 4). These behaviors were greater in week 1 than week 2 (Figure 2). For D and D troop, week was a significant predictor of active behavior, association with foster mother, and feeding and drinking; all behaviors occurred more frequently in week 1 than week 2 (Figure 2).

Comparisons with the literature

We found one study on fostering in vervet monkeys in the literature (Anonymous, 2018) for comparison with our study. The success rate of fostering of our study was 89% (eight of the nine of orphans were successfully released into their respective troops). In another vervet monkey study, behavior was compared between offspring reared by the biological mother and orphans reared by humans. Behaviors observed included aggression, drink, feed, forage, groom, locomotion, play, rest, social interaction, vigilance, and vocalization. The phases that were used for fostering were

Table 4. Output of the GLM for predominant behaviors for individual and week for Goliath and D and D troop released into the troop. Values in bold are statistically significant.

Goliath troop behavior	Individual	Week	Comparison between weeks
Inactive	$F_{2,2} = 1.22$; $p = 0.451$	$F_{1,2} = 16.36$; $p = 0,056$	2 < 1
Active	$F_{2,2} = 1.86$; $p = 0.350$	$F_{1,2} = 2.92$; $p = 0.229$	2 < 1
Association with foster mother	**$F_{2,2} = 55.70$; $p = 0.018$**	**$F_{1,2} = 43.088$; $p = 0.022$**	**2 < 1**
Feed and drink	$F_{2,2} = 1.12$; $p = 0.472$	$F_{1,2} = 1.63$; $p = 0.329$	2 < 1
Socio-positive	$F_{2,2} = 1.24$; $p = 0.446$	$F_{1,2} = 0.02$; $p = 0.891$	2 < 1
D and D troop behavior	**Individual**	**Week**	**Comparison between weeks**
Inactive	$F_{4,4} = 0.29$; $p = 0.874$	$F_{1,4} = 6.87$; $p = 0.059$	2 < 1
Active	$F_{4,4} = 0.52$; $p = 0.727$	**$F_{1,4} = 12.72$; $p = 0.023$**	**2 < 1**
Association with foster mother	$F_{4,4} = 0.29$; $p = 0.873$	**$F_{1,4} = 12.74$; $p = 0.023$**	**2 < 1**
Feed and drink	$F_{4,4} = 0.56$; $p = 0.704$	**$F_{1,4} = 11.76$; $p = 0.027$**	**2 < 1**
Socio-positive	$F_{4,4} = 1.59$; $p = 0.333$	$F_{1,4} = 2.82$; $p = 0.169$	2 < 1

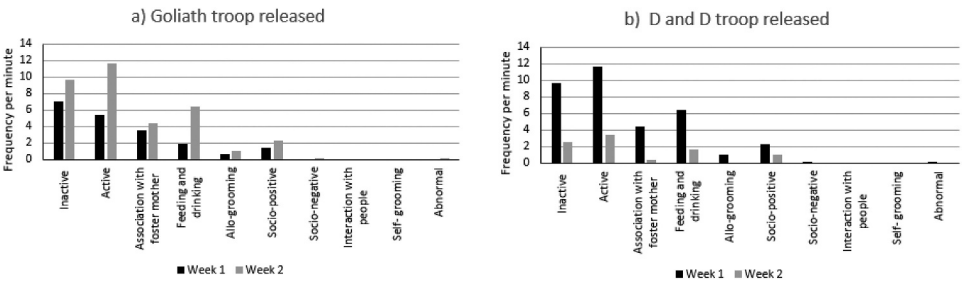


Figure 2. The frequency per minute per week for ten behaviors for all individuals in the a) Goliath troop for 2 weeks after release and b) D and D troop for 2 weeks after were released into the troop.

"Kindergarten" where human contact was considered high and "Surrogate cage" where human interaction was minimal. The ages of orphans were not provided in the study. Behavior of hand-reared offspring was normal compared to mother-reared offspring. The study was deemed successful by comparing the observed behavior of non-fostered offspring to fostered offspring and assessing whether human rearing was a viable option for orphaned individuals (Anonymous, 2018).

Discussion

Orphaned young primates are considered easier to integrate into an established troop than adults (Fontenot, Galentine, & Cummings, 2004), often because adults are attracted to infants, allowing easier integration into troops (Thierry & Anderson, 1986). We studied the success of the fostering protocol implemented by the Vervet Monkey Foundation, South Africa, to foster orphaned vervet monkeys to conspecific females in established troops. The Foundation adopted a stepwise process, comprising a quarantine phase, to a Disneyland phase to develop independent bottle feeding, an integration phase to assist in the fostering of an orphan, and finally release into the troop of the foster mother.

Nine orphans were observed from their integration to release into one of the two troops: Goliath and D and D. The Goliath troop was presented with four orphans in the integration cage. Only three orphans were released into the Goliath troop. The D and D troop received five orphans. Our fostering success was 89%.

In both troops, the inactivity of orphans decreased from 1 week to the next in both the integration cages and troop enclosure. The reasons for the decrease in inactivity during the sampling period are not known. The literature suggests that inactivity can change due to changes in the weather (Danzy, Grobler, Freimer, & Turner, 2012; Satinoff, 2011) and possibly diet (Cancelliere, Chapman, Twinomugisha, & Rothman, 2018; Menbere & Balakrishnan, 2016). Environmental conditions and feeding did not vary to a large degree in our study, and other unknown factors could explain the changes in inactivity in the vervet monkeys in our study. In the Goliath troop, orphans' activity increased over time in the integration cages but decreased over time when released in the troop. In the D and D troop, orphans' activity decreased over time in the integration troop and in the troop enclosure. It is possible that ambient temperatures influenced activity. Menbere and Balakrishnan (2016) found that vervet monkeys were more active in the morning and late afternoon when the temperatures were cooler than temperatures in comparison to the hotter midday. We collected data during the summer between 8 am and 4 pm when daytime temperatures ranged from 26°C-35°C, which possibly could explain the low activity behaviors of the vervet monkeys.

The orphans' association with the foster mother in both troops decreased over time in the integration cage and in the troop enclosure. Foster mothers had previous fostering experience, so the decrease was not due to the lack of experience of foster mothers. The reduction in association did not seem to influence the successful fostering of orphans, supporting the findings of free-living vervet monkeys (Hauser & Fairbanks, 1988). Instead, the reduced association resembles the situation of offspring becoming independent in free-living vervet monkeys (Struhsaker, 1971). Our results suggest that offspring reduced their association with the foster mother because of their growing independence (Stovall–McClough & Dozier, 2004), and a reduction in their initiation of contact with the mother, as demonstrated in chimpanzees (Yamamoto, Humle, Tanaka, & Plaistow, 2009) and in other vervet monkeys (i.e., reduced grooming in older infants; Struhsaker, 1971). The orphans were up to 5-month old at the end of the study, which matches the growth phase and emerging independence of young vervet monkeys (Struhsaker, 1971). Moreover, primate mothers reduce their contact with their offspring as they age, such as when infants seek comfort and suckling (Barrett, Dunbar, & Dunbar, 1995). Moreover, the foster mother was not lactating, and orphan fed on provisioned food, which would have reduced the contact between offspring and the foster mother (Rosenblum & Andrews, 1994).

The orphans' feeding and drinking varied over time in the Goliath troop in the integration cage but decreased over time when released into the troop. In D and D troop, feeding and drinking behavior decreased over time in both integration cage and enclosure. The reasons for the changes in feeding and drinking were not apparent.

Allo-grooming involving orphans in both troops decreased over time in the integration cages and in the enclosure. The possible reason for this could be that grooming patterns are not stable in vervet monkeys (Jarrett, Bonnell, Young, Barrett, & Henzi, 2018). There is also a possibility that interest in grooming the orphan will differ with the sex and age of the orphan (Van de Waal, Spinelli, Bshary, Ros, & Noë, 2013). In addition, socio-positive behavior in both troops varied in the integration cage and decreased over time in the enclosure. The initial high levels of socio-positive behavior of the orphan could be a coping mechanism to stress of the novel experiences of orphans in a troop, as suggested by Cheney and Seyfarth (2009). Wittig et al. (2016) suggest that chimpanzees use social behavior to buffer stressful situations, and as the conditions become less stressful, social behavior decreases. Struhsaker (1971) also observed a decrease in socio-positive behavior as individuals as they aged in free-living vervet monkey offspring.

Orphans in both troops showed low levels of socio-negative behavior. Some troop members did show socio-negative behaviors (e.g., displaying teeth in a "grin") toward orphans in the integration cages, which would be expected when unfamiliar individuals are introduced (Isbell, 1991). Foster mothers and troop members did not direct negative behaviors to orphans in the enclosures.

In both troops, self-grooming by orphans was minimal in the integration cage and the troop enclosure. Isbell and Young (1993) observed increased self-grooming in larger groups of free-living vervet monkeys, possibly due to greater parasite load. Higham, MacLarnon, Heistermann, Ross, and Semple (2009) suggest that self-grooming could be linked to greater stress, as seen in olive baboons (*Papio hamadryas anubis*). Whether one or both factors (parasite load or stress) are potential causes of reduced self-grooming requires further investigation.

In both troops, orphans rarely showed abnormal behavior (i.e., sucking of digits) in the integration cage and in the troop enclosures. Hosey (2005) suggested that abnormal behavior was related to stress in unfamiliar housing environments, so the absence of abnormal behaviors could be an indication of lack of stress during the sampling period. Whether this is the case or that the vervets were physiologically stressed without showing abnormal behavior requires further study in the orphaned infants.

Overall, there appeared to be a general decrease in socio-negative behaviors in the sampling period. This could be a consequence of the high ambient temperatures reducing general activity (Young et al., 2019). In addition, the decrease could indicate developing social stability in the groups following introduction of the orphans (Olsson & Westlund, 2007). Often when there is an increase in stress or social instability, there could be a decrease in social behavior and an increase in socio-negative or abnormal behavior (DeVries, Glasper, & Detillion, 2003) and vice versa (Panksepp, Herman, Vilberg, Bishop, & DeEskinazi, 1980). The social buffering hypothesis states that individuals with stronger social ties can have a lower stress level (and hence lower socio-negative and abnormal behavior) (Dazey, Kuyk, Oswald, Marenson, & Erwin, 1977; Young, Majolo, Heistermann, Schülke, & Ostner, 2014), particularly during high stress. Thus, it is possible that either the social buffering between orphans and foster mothers was strong enough to mitigate any stress behavior in the orphans (Gunnar & Sullivan, 2017; Kikusui, Winslow, & Mori, 2006) or that the level of stress was not sufficient to elicit a stress response in orphans, regardless of the level of bonding (Sanchez, McCormack, & Howell, 2015). The possibility that the duration an orphan spent with the foster mother could influence behaviors would require further study as well as the aspect of sex as this could influence behavior.

A comparison of the fostering protocol of the Foundation to that of the literature showed that the outcome of our study compared favorably with another study on vervet monkeys in terms of the success of fostering. The study for comparison stated that behavior observed in orphaned and non-orphaned individuals had no abnormal behavior; however, the author saw differences that orphans played and groomed more than non-orphaned infants with very little difference between those with

high human interaction and those with a low amount of human interaction. Overall, it appears that the duration of human care was less important when fostering orphans to adult females.

Conclusion

The fostering protocol for orphan vervet infants at the Vervet Monkey Foundation was considered successful because of the high success rate of fostering. Moreover, the low levels of socio-negative behavior and a virtual absence of abnormal behavior suggest successful integration was successful, at least in the short duration of the study. It is difficult to know whether the protocol used by the Foundation was instrumental in this regard, since the literature suggests that different approaches also generate reported or assumed high success of fostering. Nonetheless, the protocol reported in our study has conservation salience for primates and vervet monkeys particularly.

Acknowledgments

We thank Dave du Toit and Josie du Toit, founder, and director of the Vervet Monkey Foundation, respectively, for allowing us to conduct this study. Financial support was provided by the National Research Foundation and Jan van der Schyff. The study was approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (clearance number: 2017/06/39/B).

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

The author(s) reported that there is no funding associated with the work featured in this article.

ORCID

Charnè van Niekerk http://orcid.org/0000-0003-4845-1604
Neville Pillay http://orcid.org/0000-0002-0778-726X

References

Agoramoorthy, G., & Rudran, R. (1992). Adoption in free-ranging red howler monkeys, Alouatta seniculus of Venezuela. *Primates*, *33*(4), 551–555. doi:10.1007/BF02381155

Anonymous. (2018, August 18). Semi-wild (captive and free-roaming) infant Vervet monkey behaviour: Do orphans behave differently? Retrieved from http://undergraduatelibrary.org/system/files/1632.pdf

Barham, P. J., Underhill, L. G., Crawford, R. J., Altwegg, R., Leshoro, T. M., Bolton, D. A., & Upfold, L. (2008). The efficacy of hand-rearing penguin chicks: Evidence from African penguins (Spheniscus demersus) orphaned in the treasure oil spill in 2000. *Bird Conservation International*, *18*(2), 144–152. doi:10.1017/S0959270908000142

Barrett, L., Dunbar, R. I. M., & Dunbar, P. (1995). Mother-infant contact as contingent behaviour in gelada baboons. *Animal Behaviour*, *49*(3), 805–810. doi:10.1016/0003-3472(95)80211-8

Bashaw, M. J., Gullott, R. L., & Gill, E. C. (2010). What defines successful integration into a social group for hand-reared chimpanzee infants? *Primates*, *51*(2), 139–147. doi:10.1007/s10329-009-0176-8

Bassett, L., Buchanan-Smith, H. M., McKinley, J., & Smith, T. E. (2003). Effects of training on stress-related behavior of the common marmoset (Callithrix jacchus) in relation to coping with routine husbandry procedures. *Journal of Applied Animal Welfare Science*, *6*(3), 221–233. doi:10.1207/S15327604JAWS0603_07

Brightsmith, D., Hilburn, J., Del Campo, A., Boyd, J., Frisius, M., Frisius, R, Janik D, & Guillen, F. (2004). The use of hand-raised psittacines for reintroduction: A case study F3 of scarlet macaws (Ara macao) in Peru and Costa Rica. *Biological Conservation*, *121*(3), 465–472. doi:10.1016/j.biocon.2004.05.016

Brown, G. R., & Dixson, A. F. (2000). The development of behavioural sex differences in infant rhesus macaques (Macaca mulatta). *Primates*, *41*(1), 63–77. doi:10.1007/BF02557462

Cancelliere, E. C., Chapman, C. A., Twinomugisha, D., & Rothman, J. M. (2018). The nutritional value of feeding on crops: Diets of vervet monkeys in a humanized landscape. *African Journal of Ecology*, *56*(2), 160–167. doi:10.1111/aje.12496

Chavatte, P. (1991). Maternal behaviour in the horse; theory and practical applications to foal rejection and fostering. *Equine Veterinary Education*, *3*(4), 215–220. doi:10.1111/j.2042-3292.1991.tb01525.x

Cheney, D. L., & Seyfarth, R. M. (2009). Stress and coping mechanisms in female primates. *Advances in the Study of Behavior*, *39*, 1–44. doi:10.1016/S0065-3454(09)39001-4

Danzy, J., Grobler, J. P., Freimer, N., & Turner, T. R. (2012). Sunbathing: A behavioral response to seasonal climatic change among South African vervet monkeys (Chlorocebus aethiops). *African Primates*, *7*, 230–237.

Dazey, J., Kuyk, K., Oswald, M., Marenson, J., & Erwin, J. (1977). Effects of group composition on agonistic behaviour of captive pigtailed macaques (Macaca nemestrina). *Journal of Physical Anthropology*, *46*(1), 73–76. doi:10.1002/ajpa.1330460110

DeVries, A. C., Glasper, E. R., & Detillion, C. E. (2003). Social modulation of stress responses. *Physiology & Behavior*, *79*(3), 399–407. doi:10.1016/s0031-9384(03)00152-5

Emanuelson, K. (2006). *Neonatal care and hand rearing. Biology, medicine, and surgery of elephants* (pp. 233–241). Ames, Iowa: Blackwell Publishing. doi:10.1002/9780470344484.ch16

Fedigan, L. (1972). Social and solitary play in a colony of vervet monkeys (Cercopithecus aethiops). *Primates*, *13*(4), 347–364. doi:10.1007/BF01793655

Fontenot, M. B., Galentine, D. M., & Cummings, L. J. (2004). Fostering procedures for orphaned infants in a breeding colony of African green monkeys. *Contemporary Topics in Laboratory Animal Science*, *43*(5), 41–43. https://pubmed.ncbi.nlm.nih.gov/15461440/

Gunnar, M. R., & Sullivan, R. M. (2017). *The neurodevelopment of social buffering and fear learning: Integration and crosstalk* (pp. 1–7). Taylor and Frances Online. doi:10.1080/17470919.2016.1151824

Harlow, H. F., Dodsworth, R. O., & Harlow, M. K. (1965). *Total social isolation in monkeys. Proceedings of the National Academy of Sciences*, 54, 90–97. 10.1073/pnas.54.1.90

Harlow, H. F., & Suomi, S. J. (1971). *Social recovery by isolation-reared monkeys. Proceedings of the National Academy of Sciences*, 68, 1534–1538. 10.1073/pnas.68.7.1534

Hauser, M. D., & Fairbanks, L. A. (1988). Mother-offspring conflict in vervet monkeys: Variation in response to ecological conditions. *Animal Behaviour*, *36*(3), 802–813. doi:10.1016/S0003-3472(88)80163-5

Higham, J. P., MacLarnon, A. M., Heistermann, M., Ross, C., & Semple, S. (2009). Rates of self-directed behaviour and faecal glucocorticoid levels are not correlated in female wild olive baboons (Papio hamadryas anubis). *Stress*, *12*(6), 526–532. doi:10.3109/10253890902756565

Hosey, G. R. (2005). How does the zoo environment affect the behaviour of captive primates? *Applied Animal Behaviour Science*, *90*(2), 107–129. doi:10.1016/j.applanim.2004.08.015

Isbell, L. A. (1991). Contest and scramble competition: Patterns of female aggression and ranging behavior among primates. *Behavioral Ecology*, *2*(2), 143–155. doi:10.1093/beheco/2.2.143

Isbell, L. A., & Young, T. P. (1993). Social and ecological influences on activity budgets of vervet monkeys, and their implications for group living. *Behavioral Ecology and Sociobiology*, *32*(6), 377–385. doi:10.1007/BF00168821

Jarrett, J. D., Bonnell, T. R., Young, C., Barrett, L., & Henzi, S. P. (2018). *Network integration and limits to social inheritance in vervet monkeys. Proceedings of the Royal Society B: Biological Sciences*, 285, 1876. 10.1098/rspb.2017.2668

Jendry, C. (1996). Utilization of surrogates to integrate hand-reared infant gorillas into an age/sex diversified group of conspecifics. *Applied Animal Behaviour Science*, *4*(3–4), 173–186. doi:10.1016/0168-1591(96)01037-4

Kikusui, T., Winslow, J. T., & Mori, Y. (2006). Social buffering: Relief from stress and anxiety. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *361*(1476), 2215–2228. doi:10.1098/rstb.2006.1941

Latham, N. R., & Mason, G. J. (2008). Maternal deprivation and the development of stereotypic behaviour. *Applied Animal Behaviour Science*, *110*(1–2), 84–108. doi:10.1016/j.applanim.2007.03.026

Mason G, Clubb R, Latham N and Vickery S. (2007). Why and how should we use environmental enrichment to tackle stereotypic behaviour?. Applied Animal Behaviour Science, *102*(3–4), 163–188. https://doi.org/10.1016/j.applanim.2006.05.041

McCann, C. M., & Rothman, J. M. (1999). Changes in nearest-neighbor associations in a captive group of western lowland gorillas after the introduction of five hand-reared infants. *Zoo Biology*, *18*(4), 261–278. doi:10.1002/(SICI)1098-2361(1999)18:4<261:AID-ZOO2>3.0.CO;2-Q

McDougall, P. T., Réale, D., Sol, D., & Reader, S. M. (2006). Wildlife conservation and animal temperament: Causes and consequences of evolutionary change for captive, reintroduced, and wild populations. *Animal Conservation*, *9*(1), 39–48. doi:10.1111/j.1469-1795.2005.00004.x

Meder, A. (1985). Integration of hand-reared gorilla infants in a group. *Zoology Biology*, *4*(1), 1–12. doi:10.1002/zoo.1430040102

Menbere, I. P., & Balakrishnan, M. (2016). The effect of habitat on density, feeding behaviour and activity of heller's vervet monkey (*chlorocebus pygerythrus arenarius*): A case study in arba minch forest, Ethiopia. *International Journal of Natural Resource Ecology and Management*, *1*, 71. doi:10.11648/j.ijnrem.20160103.12

Meyer, J. S., Novak, M. A., Bowman, R. E., & Harlow, H. F. (1975). Behavioral and hormonal effects of attachment object separation in surrogate-peer-reared and mother-reared infant rhesus monkeys. *Developmental Psychobiology*, *8*(5), 425–435. doi:10.1002/dev.420080507

Olsson, I. A. S., & Westlund, K. (2007). More than numbers matter: The effect of social factors on behaviour and welfare of laboratory rodents and non-human primates. *Applied Animal Behaviour Science*, *103*(3–4), 229–254. doi:10.1016/j.applanim.2006.05.022

Panksepp, J., Herman, B. H., Vilberg, T., Bishop, P., & DeEskinazi, F. G. (1980). Endogenous opioids and social behavior. *Neuroscience and Biobehavioral Reviews*, *4*(4), 473–487. doi:10.1016/0149-7634(80)90036-6

Portin, I., & Niebruegge, K. (2006). *The changing role of hand rearing in zoo-based primate breeding programs. In nursery rearing of nonhuman primates in the 21st century* (pp. 21–31). Springer US. doi:10.1007/978-0-387-25640-5_2

Riedman, M. L. (1982). The evolution of alloparental care and adoption in mammals and birds. *The Quarterly Review of Biology*, *57*(4), 405–435. doi:10.1086/412936

Rosenblum, L. A., & Andrews, M. W. (1994). Influences of environmental demand on maternal behavior and infant development. *Acta paediatrica*, *83*(s397), 57–63. doi:10.1111/j.1651-2227.1994.tb13266.x

Ryan, S., Thompson, S. D., Roth, A. M., & Gold, K. C. (2002). Effects of hand-rearing on the reproductive success of western lowland gorillas in north America. *Zoo Biology*, *21*(4), 389–401. doi:10.1002/zoo.10045

Saj, T. L., Sicotte, P., & Paterson, J. D. (2001). The conflict between vervet monkeys and farmers at the forest edge in Entebbe, Uganda. *African Journal of Ecology*, *39*(2), 195–199. doi:10.1046/j.0141-6707.2000.00299.x

Sánchez, M. M., Hearn, E. F., Do, D., Rilling, J. K., & Herndon, J. G. (1998). Differential rearing affects corpus callosum size and cognitive function of Rhesus monkeys. *Brain Research*, *812*(1–2), 38–49. doi:10.1016/s0006-8993(98)00857-9

Sanchez, M. M., McCormack, K. M., & Howell, B. R. (2015). Social buffering of stress responses in nonhuman primates: Maternal regulation of the development of emotional regulatory brain circuits. *Social Neuroscience*, *10*(5), 512–526. doi:10.1080/17470919.2015.1087426

Sashaw, J. J. H. (2012). *Maternal strategies in vervet monkeys* (*Doctoral dissertation*), Lethbridge, Alta, University of Lethbridge, Dept. of Psychology, c2012).

Satinoff, E. (2011). Behavioral thermoregulation in the cold. *Comprehensive Physiology*, *14*, 481–505. doi:10.1002/cphy.cp040121

Seddon, P. J., Armstrong, D. P., & Maloney, R. F. (2007). Developing the science of reintroduction biology. *Conservation Biology*, *21*(2), 303–312. doi:10.1111/j.1523-1739.2006.00627.x

Stovall–McClough, K. C., & Dozier, M. (2004). Forming attachments in foster care: Infant attachment behaviors during the first 2 months of placement. *Development and Psychopathology*, *16*(02), 253–271. doi:10.1017/s0954579404044505

Struhsaker T T. (1967). Behavior of Vervet Monkeys and Other Cercopithecines. Science, *156*(3779), 1197–1203. https://doi.org/10.1126/science.156.3779.1197

Struhsaker, T. T. (1971). Social behaviour of mother and infant vervet monkeys (Cercopithecus aethiops). *Animal Behaviour*, *19*(2), 233–250. doi:10.1016/s0003-3472(71)80004-0

Thierry, B., & Anderson, J. R. (1986). Adoption in anthropoid primates. *International Journal of Primatology*, *7*(2), 191–216. doi:10.1007/bf02692318

Thunström, M., Persson, T., & Björklund, M. (2013). Integration of a hand-reared chimpanzee (Pan troglodytes) infant into a social group of conspecifics. *Primates*, *54*(1), 13–19. doi:10.1007/s10329-012-0319-1

Van de Waal, E., Spinelli, M., Bshary, R., Ros, A. F. H., & Noë, R. (2013). Negotiations over grooming in wild vervet monkeys (Chlorocebus pygerythrus). *International Journal of Primatology*, *34*(6), 1153–1171. doi:10.1007/s10764-013-9729-1

Wimberger, K., Downs, C. T., & Boyes, R. S. (2010). A survey of wildlife rehabilitation in South Africa: Is there a need for improved management? *Animal Welfare*, *19*(4), 481–499. doi:10.1017/S0962728600001962

Winslow, J. T. (2005). Neuropeptides and nonhuman primate social deficits associated with pathogenic rearing experience. *International Journal of Developmental Neuroscience*, *23*(2–3), 245–251. doi:10.1016/j.ijdevneu.2004.03.003

Wittig, R. M., Crockford, C., Weltring, A., Langergraber, K. E., Desher, T., & Zuberbühler, K. (2016). Social support reduces stress hormone levels in wild chimpanzees across stressful events and everyday affiliations. *Nature Communications*, *7*(1), 13361. doi:10.1038/ncomms13361

Yamamoto, S., Humle, T., Tanaka, M., & Plaistow, S. (2009). Chimpanzees help each other upon request. *PLoS One*, *4*(10), e7416. doi:10.1371/journal.pone.0007416

Young, C., Bonnell, T. R., Brown, L. R., Dostie, M. J., Ganswindt, A., Kienzle, S., McFarland R, Henzi SP, & Barrett, L. (2019). Climate induced stress and mortality in vervet monkeys. *Royal Society Open Science*, *6*(11), 191078. doi:10.1098/rsos.191078

Young, C., Majolo, B., Heistermann, M., Schülke, O., & Ostner, J. (2014). *Responses to social and environmental stress are attenuated by strong male bonds in wild macaques*. *Proceedings of the National Academy of Sciences*, 111, 18195–18200. https://www.pnas.org/content/pnas/111/51/18195.full.pdf