Behavioural responses of vervet monkey *Chlorocebus pygerythrus* infants in a novel fostering programme

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A dissertation submitted to the Faculty of Science, University of the Witwatersrand, in fulfilment of the requirements for the degree of Master of Science.

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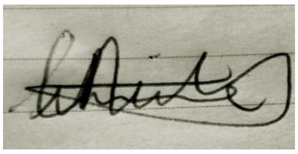
Declaration

I declare that this dissertation is my own unaided work. It is being submitted for the Degree of Master of Science at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University.



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Abstract

Vervet monkeys *Chlorocebus pygerythrus* are viewed as pests by farmers and home owners. Consequent attempts to exterminate problem vervet monkey individuals often results in orphaned young whose mothers are killed. I studied the rehabilitation of orphans at The Vervet Monkey Foundation, South Africa. My aim was to assess the success of the fostering program at the Foundation. Orphaned vervet monkeys are fostered by adult vervet monkey females at the Foundation using a specific protocol focused on reducing human rearing. The protocol involves a step-wise process of integration, comprising of a quarantine phase to the next phase of Disneyland to develop independent bottle feeding, an integration phase to assist in the adoption by a foster female and finally release into the troop of the foster mother. I evaluated the success of fostering of eight orphans into two troops, and compared this protocol to published literature. I also evaluated the behaviours of the orphans and their interactions with their foster mother to assess the process of fostering at a finer scale. Following release into the troops, I also investigated the responses of the fostered offspring to vervet alarm calls to provide another measure of the integration of orphans into the troops. Calls were played alone or accompanied with a dummy predator model stimulus, and I assessed whether the orphans sought the protection of foster mother or another troop member. During the fostering process, 89% of the orphans were successfully fostered to their designated troops. A similar high success rate was reported in other primate studies. These studies suggested that the protocol followed for rearing had more impact on success and behaviour than the period of human-caregiving. Orphans altered some of their behaviours during alarm call playbacks, particularly when accompanied with the visual aid. However, they ran for the cover of the trees rather than sought out the foster mother or another individual. My study demonstrated a high fostering success of orphaned vervet monkeys with little or no socio-negative and abnormal behaviour and close association with the foster mother. The alarm call playback experiments showed that the orphans did recognise conspecific alarm signals but did not rely on the foster mother for protection, possibly related to their growing independence of the foster mother.

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Introduction

Rationale

Vervet monkeys *Chlorocebus pygerythrus* are often shot by farmers for causing crop damage when they opportunistically raid farms for food. Mothers are often killed, resulting in orphaned young (Healy and Nijman 2014). Orphaned offspring are either kept as pets or taken to a local wildlife sanctuary (Wimberger *et al*. 2010a). Those kept as pets are often abandoned later when they become troublesome or unwanted (Grobler *et al.* 2006). Orphaned and ex- pet vervet monkeys are often brought to the Vervet Monkey Foundation in Tzaneen, Limpopo Province, South Africa to be rehabilitated and then integrated into an established troop within the sanctuary. During my study there were 14 troops on the foundation and over 600 vervet monkeys in total. The Vervet Monkey Foundation rehabilitation programme was started in 1998 in hopes of providing a sanctuary for orphaned infants and injured vervet monkeys (as per Vervet Monkey Foundation information).

Free roaming vervet monkeys give birth during the rainy season (September – February; Rowell and Richards 1979). Every year during and after the birthing season, there is an influx of orphaned vervet offspring at the foundation (as per Vervet Monkey Foundation information). Orphaned offspring (hereafter referred to as orphans) arrive in various states of health (e.g. some injured, suffering from malnutrition or ill) and range in age from a few weeks old to six months old. The offspring are then rehabilitated to be released into a troop on the foundation premises. Orphans are considered easier to integrate into an established troop than are adults (Fontenot *et al.* 2004), often because foster adults are attracted to infants, allowing easier integration into troops (Thierry and Anderson 1986). Infant integration takes priority in the Vervet Monkey Foundation information. Breeding at the foundation is prevented by vasectomising males when they reached two and half years old.

My intention in this study was to document a novel fostering programme at the Vervet Monkey Foundation. This programme uses a hand rearing method where orphans are introduced to a potential foster mother as young as three months of age. Wimberger *et al.* (2010b) conducted survey on the number of wildlife rehabilitation centres in South Africa. At the time, of the 41 wildlife centres surveyed, 26% accepted primate species, mainly *Galagidae* and *Cercopithecidae*, for rehabilitation and release of vervets brought into rehabilitation centres or sanctuaries but excluded orphaned young rehabilitation. There seems to be a gap in research on conservation of vervet monkeys focusing on infant rehabilitation and the effect on behaviour on infants that are placed in these centres. In addition, methods sanctuaries use to ensure development of abnormal behaviour is minimised is unknown.

Natural Fostering

Fostering is found in many mammals and bird species that have a cooperative breeding system (Riedman 1982). Fostering is sometimes synonymous with adoption in the literature or the two may be considered different in humans, where fostering is regarded as short term care and adoption as long term care of offspring (Barratt 2002). In my study, I make no distinction between the terms since the process of fostering and adoption in non-human animals are both usually defined as an individual caring for a related or non-related young individual in the presence or the absence of the biological parents of young, which can be long or short term (Boesch *et al*. 2010). Allo-parental care, which can also be considered as fostering, occurs in the presence of biological parents (Samuk and Avilès 2013), and is usually considered to be behaviours (e.g. grooming, feeding and babysitting) directed towards unweaned offspring (König 1997). Adult or sub-adult females often foster young (Silk 1999), but, for example in Mongolian gerbil *Meriones unguiculatus*, males can also foster offspring of other group members (French 1994).

Fostering of offspring in birds can be intentional or unintentional. For example, abandoned penguin *Eudyptula minor* chicks are raised by foster parents intentionally when they are lost (Wienecke 1995), a few owl species, such as the Tengmalm's owl *Aegolius funereus*, owlets switch nest intentionally their biological nest to a different nest (Kouba *et al.* 2017) and Egyptian vultures *Neophron percnopterus* leave their nest intentionally for neighbouring nests to increase chances of being fed there (Donazar *et al.* 1990). Ring-billed gulls *Larus delawarensis* chicks are fostered unintentionally due to poor offspring recognition by the foster parents (Brown 1998). In some bird species, such as white storks *Ciconia ciconia*, chicks which are lost or have intentionally abandoned their home nest often move to a neighbouring nest to be fostered unknowingly by another brood (Redondo *et al.* 1995).

In mammals, fostering is usually intentional. The European badger *Meles meles* breeds communally (Woodroffe and Macdonald 2000) and exhibits alloparental care, in which mothers often nurse their own cubs along with those of other cubs of females in the clan (Dugdale *et al.* 2010). The harbour seal *Phoca vitulina* populations are large, and pups often become lost and are then fostered (adopted) by a lactating female which may have her own pup or lost her pup (Boness *et al.* 1992). Examples of fostering in non-human primates (hereafter referred to as primates) include the Japanese macaques *Macaca fusca* (Schino *et al.* 1993), rhesus macaques *Macaca mulatta* (Berman 1982), red howler monkeys *Alouatta seniculus* (Agoramoorthy and Rudran 1992)*,* ring tailed lemur *Lemur catta* (Gould 2000), common marmosets *Callithrix jacchus* (Mota and Sousa 2000), mantled howler monkeys *Allouatta palliata* (Clarke and Glander 1981) and vervet monkeys *Chlorocebus pygerythrus (*Hauser 1988). Often an adult female primate will adopt an orphaned or abandoned young while caring for her own offspring (Ellsworth and Andersen 1997). Pelè and Petit (2015) observed a female tufted capuchin *Sapajus* sp. which adopted a neonate after it was abandoned by its mother; the female capuchin had her own offspring and the care given to both biological and adoptive young was similar.

In primates, the level of care given to an adopted orphan or a biological offspring will depend on several factors. Younger females sometimes adopt an orphaned individual to gain maternal experience (Hamiliton *et al.* 1982). The adoption of offspring by immature female primates does not influence the reproductive activity of the foster mother (Hobaiter *et al.* 2014), but the level of care might be reduced because the females are inexperienced with raising offspring (Mann and Smuts 1998). Care provided to foster offspring might be reduced when females are raising their own young. For example, in colobus monkeys *Colobus angolensis palliates*, Dunham and Opere (2016) found that when females adopted orphans despite having her own offspring, the care given to the adoptee could be less than that given to the biological offspring possibly due to independence of the adoptee (e.g. Barbary macaques *Macaca sylvanus*, Paul and Kuester 1996).

An adult fostering orphans can increase the chances of survival for these young (Guerra *et al.* 1998), but it would represent wasted investment into unrelated (assuming non-kin or even distantly related kin) offspring by the adult (Stanford 1992). For the foster parents, the energy spent in caring for unrelated young (including suckling) is costly, which needs to be offset against caring for concurrent and future biological young (Roulin 2002; König 2006). So, how and why does fostering occur? There are several (potential) explanations for adoption, adaptive and non-adaptive, as described below.

1) *Impaired kin recognition*. Kin selection does not seem to be evident for fostering to occur in some species (Hoffman and Amos 2005). Such fostering occurs in a large populations, as in the Antarctic fur seal *Arctoceephalus gazelle*, where there are a large number of females with pups in one location and poor offspring recognition within the population (Gemmell 2003). Hawaiian monk seal *Monachus schauinislandi* pups produce distinctive vocal calls, but mothers have poor vocal recognition, possibly resulting in fostering by taking care of a pup other than her own (Job *et al.* 1995; Pitcher *et al.* 2009). Impaired kin recognition could be the result of poor maternal experience (Riedman and Le Boeuf 1982) as described in the Antarctic fur seal and Hawaiian monk seal.

2) *Brood parasitism*. This form of imposed fostering is common in many egg laying birds where foster mothers/parents care for non-biological offspring (reviewed in Lyon and Eadie 2008). The host provides parental care to non-filial eggs or chicks, (Hoover and Reetz 2006 and Frumkin 1994). Such imposed fostering occurs between species, such as cuckoos, but also within the same species, such as in the wood duck *Aix sponsa* (Semel *et al.* 1988), zebra finch *Taeniopygia guttata* (Birkhead *et al.* 1990), and brown-headed cowbird *Molothrus ater* (Robertson and Norman 1977).

3) *Adoption by kin*. In some primates, siblings or related individuals will adopt an orphaned young (Agoramoorthy and Rudran 1992). Such caring for related offspring will increase the inclusive fitness of females (Gorrell *et al.* 2010).

4) *Kidnapping*. This often occurs in primates when a female, typically a non-breeding female, “kidnaps” young from a biological parent (Jouventin *et al.* 1995). In some cases a higher ranking female kidnaps a lower ranked female’s offspring (Shopland *et al.* 1987, Silk 1980). Kidnapping young could be due to unfavourable conditions for an individual to have its own young (e.g. lack of resources for breeding; sparse food resources; Riedman and Le Boeuf 1982). Since the foster mother is often non-lactating, kidnapping could lead to the death of the kidnapped young (Maestripieri 1993).

5) *Hormonal priming*. Two hormones, oxytocin and vasopressin, are important mediators of offspring care in mammals (Pedersen and Prange 1979) and monogamous avian species (Pedersen and Tomaszycki 2012). Oxytocin is involved in mother-offspring bonding (Reyes and Mateo 2008), and vasopressin (Bester-Meredith and Marler 2003), regulates maternal behaviour and allo-parental behaviour (Olazabal *et al.* 2006). Thus, it is possible that lactating females with their own young

(Roulin 2002) or females that have recently lost their own offspring (e.g. chimpanzee *Pan troglodytes*; van Wulfften Palthe and van Hooff 1975) would be primed to foster offspring. Such hormonally primed females are attracted to cues elicited by young stimuli (sight, smell and sound of infant; Bick *et al.* 2013, Ridgway *et al.* 1995, Aguilar *et al.* 2007, Ebensperger *et al.* 2006, Job *et al.*1995).

In sum, fostering is common in group-living species or aggregations, usually by individuals of the same species, occurring either incidentally (poor recognition) or deliberately (kin recognition, kidnapping, brood parasitism), and are possibly hormonally mediated by, for example, oxytocin.

Human Imposed Fostering

Cross-fostering is the rearing of young with non-related caregivers (Noakes and Barlowy 1973, McGuire 1988, Bird *et al.* 1985). Cross-fostering often entails humans removing a member of a species at different developmental stages, and placing offspring in an artificial environment, either with the same or different species (Brown and Brown 2000). Cross-fostering has been implemented in the same and different species of domesticated animals, such as sheep, *Ovis aries* (Alexander *et al.* 1983) and pigs, *Sus* spp., (Heim *et al.* 2012). Examples of cross-fostering in free-living species by humans include birds, such as the great tit, *Parus major* (Slagsvold *et al.* 2002), zebra finch *Taeniopygia guttat* (Sonnemann and Sjölander 1977)*,* collared flycatcher*, Ficedula albicollis* (Qvarnström *et al.* 2005), greylag goose *Anser anser,* Canadian goose *Branta canadensis* (Fabricius 1991), and mammals, such as the coyote *Canis latrans* (Kitchen and Knowlton 2006), captive species such as deer mouse *Peromyscus maniculatus* (Dewsbury 1979), house mouse *Mus musculus* (Aldhous 1989), and rock-wallaby *Petrogale penicillata* (Taggart *et al.* 2005).

The reasons for using cross-fostering differs based on the intended purpose and can vary with the stage of offspring development (Tochukwu 2013). Cross-fostering has been done for several reasons, examples of which are discussed next.

1) *Developmental research studies* (Winney *et al.* 2015). The health of the neonate can be assessed when it is given to a different lactating female (Daft *et al.* 2015). For example deer mouse *Peromyscus maniculatus* were cross-fostered in attempt to remove *Helicobacter* infection via nursing (Pritchett-Corning *et al.* 2015).
2) *Development.* Here, cross-fostering can be used to assess genetic and non-genetic influences on the phenotype. Examples include genetic imprinting being

modulated by maternal environment of cross-fostered mice (Hager *et al.* 2009), and sexual ornaments being influenced by environmental conditions in house sparrows *Passer domesticus* (Griffith *et al.* 1999). Laboratory studies use cross-fostering to investigate phenotypic development, such as when individuals with different genotypes are placed in different pre- and post-natal environments, to assess whether the environment shapes the phenotype (Suriyasomboon *et al.* 2006).

3) *Kin recognition.* Kin recognition of offspring can be studied through cross-fostering by presenting offspring of different ages to foster mothers. For example, Pillay (2000) found that African striped mice *Rhabdomys* spp. accepted foster offspring that were younger than ten days of age but not older offspring that were closer to weaning.
4) *Conservation efforts* (Cade Temple 1995; Curio 1996). Cross-fostering is used in conservation, whereby orphans are introduced to captive foster parents (Smith 1986). This method can be used for endangered species to aid in population growth (Temple 1978), although this process can also be time consuming (Snyder *et al.* 1996). For example, captive bank voles *Clethrionomys glareolus* behaviours are assessed by observing free-roaming bank voles as this will aid in assessing viability of releasing species from captivity as conservation efforts (Mathews *et al.* 2005).
5) *Physiological effects*. Other studies have used cross-fostering to investigate whether a larger litter created by the addition of fostered offspring influence maternal milk delivery, such as in sows (King *et al.* 1997), laboratory mice (Falconer 1947), and rats (Champagne *et al.* 2003) and suckling behaviour (McCracken and Gustin 1991).

Hand rearing by humans, often of rejected (by the biological parents) or orphaned young (Barham *et al.* 2008) is also a form of fostering. The methods of rearing, such as stimulation, feeding, play, comfort (Meder 1989) as well as the reasons of rearing, will depend on the caregiver or researcher and their motives for rearing (Seddon *et al.* 2007; Kossak 1981).

The disadvantage of hand rearing include the risks of adoptees developing abnormal behavioural, as seen in primates (Latham and Manson 2008) and in birds (Kreger *et al.* 2004; Feenders and Bateson 2011). These behaviours can arise from a lack of stimulation (Sánchez *et al.* 1998), incompetent hand rearing methods (Porton and Niebruegge 2006), lack of contact from the human rearing the young (Winslow 2005) to soothe the neonate (Horwich and Manski 1975), and no social interaction (e.g. no playmates). The latter often leads to self-play, resulting in a lack of appropriate social behaviours at adulthood; (Harlow *et al.* 1965; Lutz *et al.* 2003; Gusset *et al.* 2006), and possible increased aggression toward group members at an older age, if they are re-introduced into conspecific groups (McDougall *et al.* 2006). Many of these problems arise due to young being reared in isolation from conspecifics (Harlow and Suomi 1971), loss of contact with a conspecific mother during the critical developmental phase (Meyer *et al.* 1975) and attachment to caregivers, all making it challenging for the fostered young to adjust to conspecifics later (Topál *et al.* 2005). Often the problem with integrating a hand reared animal into an established captive group is that young are not accustomed to adult conspecifics in the group (Meder 1985).

According to McCann et al. (1999), a successful fostering technique in primates of same species should involve several of the following: introducing young into groups in which adult/older females or males have already shown allo-parental care toward introduced young (i.e. carrying young) previously; females and males must display non-aggressive behaviour towards young; young should display more appropriate group social behaviour (McCann *et al.* 1999); and hand reared offspring should be taught to drink milk from bottles in situations when the foster female is not lactating (Emanuelson 2006 and Harlow 1958). Lack of group social skills in the young can affect their survival in a new group (Brightsmith *et al* 2004) and also their future reproduction (Ryan *et al.* 2002).

For fostering, foster parents and/or groups should be chosen with careful consideration. The groups' behaviour needs to be observed as well as the behaviour of each individual in the group (Jendry 1996). There is however no set criteria for such selection and the human caregiver/researcher would have to cautiously introduce an young to a female over a period of time (Thunström *et al.* 2013). Potential foster parents under observation should demonstrate protective behaviour towards the offspring in stressful situations as well out of stressful situations (Chavatte 1991).

Response to predator alarm calls

Alarm calls are often given as inter- and intra-group warning of a potential predator, and these will sometimes differ according to the predator type (Magrath *et al.* 2007 and Fallow *et al.* 2011). Evans *et al.* (1993) found that male chickens *Gallus gallus domesticus* have different warning calls for terrestrial predators than for avian predators. Different alarm calls will also elicit a particular response. For example, yellow- bellied marmots *Marmota flaviventris* ran back to their burrow when a raptor was a particular distance (i.e. visual cue) from them (Blumstein and Armitage 1997) and ground squirrels *Urocitellus beldingi* ran to shelter when they heard alarm calls (auditory cues) identifying avian species (Sherman 1985). Unrelated, co-existing species can respond to each other's calls. For example, redfronted lemurs *Eulemur fulvus rufus* and Verreaux's sifakas *Propithecus verreauxi verreauxi* have an understanding of each other's alarm calls for aerial and ground predators (Fichtel 2004).

Alarm calls can also differ with urgency and age, as seen in meerkats *Suricatta suricatta*. More frantic alarm calls cause the surrounding individuals to act with a higher degree of urgency (Manser *et al.* 2001). Young often seek the safety of adults, particularly the mother, when they hear alarm calls. In meerkats, offspring seek protection when they hear alarm calls but as they became older, they would scan for the source of the alarm call first (Hollèn and Manser 2006).

There are a few instances where responses to alarm calls have been observed in fostered offspring. Cross-fostered newly hatched reed warblers *Acrocephalus scirpaceus,* dunnocks *Prunella modularis*, and robins *Erithacus rubecula* only responded to their own species alarm calls and not their foster parents alarm calls (Davies *et al.* 2004). Young reared in isolation responded to alarm calls in a similar way as mother-reared young, although responses to particular alarm calls are often not as strong. For example, hand-reared squirrel monkey *Saimiri* spp. offspring reacted to alarm calls in the same way as mother reared offspring when presented with a reference objects (e.g. leopard or bird model) but were uncertain when the alarm calls were presented without reference objects (Herzog and Hopf 1984). Hand-reared budgerigars *Melopsittacus undulates* produced the same alarm call to potential predators as mother-reared budgerigars but the development of alarm calls was found to be slower in hand-reared budgerigars (Brittan-Powell *et al.* 1997).

Study species

Vervet monkeys are found throughout Africa, mostly in the southern and eastern parts of Africa (Cramer and Gallistel 1997). Their preferred habitats are woodland and savannah which provide food and safety from predators as well as water (Struhsaker 1967). Vervets are mostly herbivorous, eating flowers, seeds, fruits and vegetables, and sometimes their diet includes insects and eggs (Whitten 1983).

Vervet monkeys have grey- frizzy fur, black faces bordered with white fur, black feet and tail tip is black (Cardini *et al.* 2007). Adult males weigh about 6kg and are heavier than females, which weigh about 4kg (Turner *et al.* 1997). Mature males develop a blue scrotum and red penis (Cramer *et al.* 2013). Female vervets stay in their natal troop lifelong, while sexually mature males vervets emigrate from their natal troop (Cheney and Seyfarth 1983). Hierarchies among females is generally determined by her mother's rank (Horrocks and Hunte 1983). The ranks of adult males are determined by age, ability to fight, and allies within the troop (Fairbanks *et al.* 2004). Interactions between troop members are often between those with a similar in rank within the troop (Schuster *et al.* 1993).

Reproduction occurs from September to February. Gestation is about 165 days, and a female has one offspring per annum (Eley *et al*. 1986). Females do not breed again while looking after unweaned offspring and this can range from one to two years, however, if unweaned offspring die from lack of food or predation, the female will become receptive (Fairbanks and McGuire 1995). Interestingly, females that had lost an offspring are apparently more attentive to the next offspring (Fairbanks 1988). Offspring are attentively cared for by the mother for the first three months of life, which is often considered the pre-weaning period. Offspring are then also cared for by siblings and other females within the troop with the offspring spending less time in close proximity to the mother (Johnson *et al.* 1980). Offspring become more independent as they became older, indicated by them moving further away from the mother, less ventral contact with the mother, mother denying young suckling, and increase in play behaviour with other young (Lee 1984).

Potential predators of vervets are leopards *Panthera pardus*, raptors, such as the African crowned eagle *Stephanoaetus coronatus*, and snakes, such as python *Python sebae*, Egyptian cobra *Naja anniulifera* and puff adder *Bitis arietans arietans* (Ducheminsky 2014). Vervet monkeys respond to and produce alarm calls according to the predator type they witness or hear. For snake alarm calls, they usually respond by standing on the hind legs and looking at a nearby bush or run up a tree and look onto the ground, whereas alarm calls identifying eagles would cause them to look up and run into shrubbery or into a tree, and alarm calls to leopards caused them to take shelter in trees (Seyfarth *et al.* 1980b and Enstam and Isbell 2002). Vervet monkeys often also react to the alarm calls of other species (Seyfarth and Cheney 1990) such as starlings *Spreo superbus* (Seyfarth and Cheney 1990).

Hauser (1988) found that young vervet monkeys started to distinguish between different calls from the age of four to six months. Once older than 6 months of age, offspring were more independent and responded to alarm calls in the same manner as adults (Fichtel 2008). Alarm calls from infants or juveniles are often unpredictable (Hollèn and Radford 2009) and they often give a general call to different predator types, such that all terrestrial and avian predators types will illicit the same response (Mccowan *et al.* 2001). Consequently, infants and juveniles often look to adults for an appropriate response to alarm calls (Fischer *et al.* 2000). Seyfarth and Cheney (1980) recorded the responses of vervet monkey offspring to experimental playback of alarm calls and found that offspring reacted as adults would to alarm calls, largely because they were always in close proximity to their mothers.

Aims and Objectives

Aim 1

The first aim of my study was to assess the success of the fostering program used for orphaned vervet monkeys by the Vervet Monkey Foundation in Limpopo Province, South Africa compared to the available literature of fostering protocols of primates in other institutes.

Objective 1. I assessed whether the release of orphans into the troop was successful, and investigated which behaviours contributed to successful adoption of the orphans. Behavioural data were collected through direct observation of orphaned young by recording their interactions initially with potential foster mothers while in the integration cage used to introduce orphans to potential foster mothers, and later with the foster mother (released into the established troop of the foster mother) and the interaction between troop members and newly adopted orphans.

Objective 2. I compared methods of fostering in my study with those of published literature on primates from other studies. Comparisons were made of the different methods used, such as how long it took to introduce orphans to troops, level of human involvement, behaviours observed, and the success of the adoptions in published literature.

Aim 2

The second aim was to ascertain the responses of the newly adopted young vervets to predator alarm calls. I established whether their responses were comparable to that of the literature on previously studied vervet monkeys. Comparisons could not be made with the foster mothers' own offspring within the foundation as none of the vervets were allowed to breed in the foundation enclosures. Responses to predator alarm calls and visual models were used as another measure of successful integration into the troops at the foundation.

Objective 1. I used recordings of predator alarm calls and visual predator models as a measure to assess the fear reaction of the adopted orphans and foster mothers. I hypothesised that the adopted orphans and the foster mother would react to predator alarm calls and visual models in a similar fashion to that of vervet monkeys reported in literature. I predicted that orphans would seek protection by going to the foster mother or other females if the foster mother was not within the immediate vicinity.

Methods and Materials

Study area

The study was conducted at the Vervet Monkey Foundation (hereafter the Foundation) located in the outskirts of Tzaneen, Limpopo Province, South Africa (23.8525° S, 30.3378° E). At the time of study, the Foundation housed 14 vervet monkey *Chlorocebus pygerythrus* troops and one samango monkey *Cercopithecus mitus* troop, each in one to two ha enclosures. The enclosures were comprised of dense vegetation, such as trees (e.g. common hook thorn, *Acacia caffra,* red thorn acacia *Acacia gerrardii*, knob-thorn *Acacia nigrescens,* white-stem thorn *Acacia polyacantha,* fever tree *Acacia xanthophloea*, impala lilly *Adenium multiflorum,* agave *Agave sisalana,* sickle leaved albizia *Albizia harveyi*, sicklebush *Dichrostachys cinerea*, and camels foot *Piliostigma thonningii*), shrubs (e.g. white berry *Flueggea virosa*) and grasses (e.g. cat's tail *Perotis patens,* common finger grass *Digitaria eriantha,* creeping bristle grass *Setaria sphacelata var. torta,* curly leaf *Eragrostis rigidior*, fine thatch grass *Hyparrhenia filipendula,* foxtail buffalo grass *Cenchrus ciliaris*, guinea grass *Panicum maximum*, Berea grass *Dactyloctenium austral*, red grass *Themeda triandra*, spear grass *Heteropogon contortus,* and stinking grass *Bothriochloa radicans*).

The 14 vervet troops were used for the integration of orphans by the Foundation. Each enclosure was separated from each other by electrified fencing of roughly 5m high. Gaps of at least 5m and above were between the enclosures which allowed volunteers and staff to walk around enclosures. The electrified fences were used to deter vervet monkeys from escaping or from free-roaming vervet monkeys entering enclosures. Safety switches for the electric fence are located outside enclosures near each entrance point to switch off electric fences in case of emergencies. Each enclosure had a door for entry for staff to administer basic husbandry (e.g. clean water bowls).

Each enclosure had a 3m x 3m 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 human minders to provide food and clean the integration cage daily. Between the integration cage and the troop enclosure was a small gate whose access controlled by a staff member during integration to allow a potential foster mother into the integration cage and for the release of the foster mother and orphan into the enclosure.

My study was conducted from December 2016 to June 2017. I observed two different troops; position of enclosures shown in Figure 1: the Goliath troop, comprising of a total of 43 adult and juvenile monkeys (16 males and 27 females), and occupying an area of about 20 000 m^2; and the Dino & Daniel troop, comprising of a total of 34 adult and juvenile monkeys (18 males and 16 females) and occupying an area of about 10 000 m^2. These two troops were considered for study because the orphans were first introduced to these troops adult females by the Foundation during my study.

Figure 1. Map of the Vervet Monkey Foundation showing 14 vervet *Chlorocebus pygerythrus* and one samango *Cercopithecus mitus* monkey troops. The troops I studied (Goliath and Dino and Daniel troop) indicated in purple.

Fostering

The Goliath troop received four orphans (Zoro, Dana, Maggie, and Neville) during my study period. The details of the orphans are provided below. The number of orphans received and fostered was determined by the Foundation staff.

1) Zoro (Photograph 1). A male found on Elim Road, Tzaneen (23º49’59”S; 30º09’48”E). It was not known why he was orphaned. He was brought to the Foundation on 17 November 2016, and was about three weeks old and had no injuries. 2) Dana (Photograph 2). A female found in Levubu (23º4’60”S; 30º15’0”E). It was not known why she was orphaned. She was brought to the Foundation on 23 December 2016, and was about three weeks old with no injuries. 3) Maggie (Photograph 3). A female found in Tzaneen (23º49’59”S; 30º09’48”E). It was not known why she was orphaned. She was brought into the Foundation on 19 December 2016 and was about three weeks old with no injuries. 4) Neville (Photograph 4). A male found in Limpopo, Tzaneen (2323º49’59”S; 30º09’48”E). It was not known why he was orphaned. The date he was brought to the Foundation is not known. He was about three weeks old and had a broken arm.

Photograph 1. Zoro with sharp facial features, and mouth drawn slightly backwards.

Photograph 2. Dana with light, big ears, and yellow fur on the head.

Photograph 3. Maggie with dark, big ears, and dark fur on the head.

Photograph 4. Neville has dark ear tips, dark face, dark fur on head and white fluff.

The Dino and Daniel troop received five orphans during the study period. The details of the orphans are provided below. The number of orphans received was determined by the Foundation.

1) Fiona (Photograph 5). A female found in Maastroom (22º40’40”S; 28º13’43”E). It was reported by the people who found her that her mother was shot. She was brought to the Foundation on 7 of January 2017 and was about four weeks old with a slight head injury. 2) Tammy (Photograph 6). A female found in Tzaneen (23º49’59”S; 30º09’48”E). It is not known why she was orphaned. She was brought to the Foundation on 27 of November 2016, and was three weeks old with no injuries. 3) Chica (Photograph 7). A female found in Luvubo (23º4’60”S; 30º15’0”E). It was reported by the people who found her that her mother was shot. She was brought to the Foundation on 7 November 2016 and was about three weeks old with no injuries. 4) Cheyenne (Photograph 8). A female found in Soekmekaar (23º28’0”S; 29º58’60”E). It was reported by the people that found her that she was found alongside a road alone, and it was assumed her mother was hit by a car. She was brought to the Foundation on 19 January 2017 and was about eight weeks old with no injuries. 5) Kiki (Photograph 9). A female found in Ohrigstad (24º44’59”S; 30º33’59”E). It was not known how she was orphaned. She was brought to the Foundation on 2 December 2016 and was about two to three weeks old, slightly dehydrated and had wounds on her tail.

Integration of orphans

Integration into a troop followed a set protocol (Figure 2), developed by management at the Vervet Monkey Foundation.

Quarantine (Days 1-3)

Orphaned vervet were brought to the Foundation, either dropped off by the public or collected by staff of the foundation. New arrivals were placed into quarantine for 72 hours after arrival (Figure 2) to ensure any identifiable diseases could be detected and treatment could be administered by local veterinarians. Orphans in quarantine received 24h care from staff and trained volunteers. The quarantine area was closed

Photograph 5: Fiona with a small, light body and small puff of yellow fur on her head.

Photograph 6: Tammy with a small black colouring on face, and small body.

Photograph 7: Chica with black face and hands and fluffy head.

Photograph 8: Cheyenne with a larger and fluffy body.

Photograph 9: Kiki with a white fluff and slightly dark ears.

off within the Foundation grounds by an electric fence with four individual cages within this area. Each cage was similarly constructed to the integration cages of all the troops. Quarantine cages had netting and zinc sheets to create shelter from the sun or rain, tree branches and pipes were placed in the cage for climbing. Feeding cages were placed inside the quarantine cage to train orphans to drink from milk bottles from the feeding cages. However, if orphans did not learn to drink formulated milk from baby bottles in the feeding cages, human-caregivers would continue to train orphans in Disneyland. At night, orphans were placed in carry cages and transferred into a log cabins and then cared for by human-caregivers and returned to the quarantine area in the morning or Disneyland after their three day quarantine period.

Arrival and Quarantine (3 days maximum)	Disneyland (38 days maximum)	Integration cage - Human Care (4 days maximum)	Integration cage - Foster Mother (67 days maximum)	Release into Troop
Day 1 – 3	Day 4 - 42	Day 43 - 47	Day 48 - 115	Day 116 - onwards
Zoro- 3 weeks old (3 days) Maggie- 3 weeks old (3 days) Dana- 3 weeks old (3 days) Neville- 3 weeks old (3 days)	Zoro (16 days) Maggie (31 days) Dana (28 days) Neville (38 days)	Zoro (4 days) Maggie (3 days) Dana (3 days) Neville (2 days)	Zoro (41 days) Maggie (67 days) Dana (67 days) Neville (67 days)	Zoro Maggie Dana
Tammy- 3 weeks old (3 days) Chica- 3 weeks old (3 days) Kiki- 3 weeks old (3 days) Cheyenne- 2 months (3 days) Fiona- 1 month old (3 days)	Tammy (4 days) Chica (24 days) Kiki (27 days) Fiona (22 days)	Tammy (3 days) Chica (3 days) Kiki (3 days) Fiona (1 day)	Tammy (31 days) Chica (31 days) Kiki (55 days) Cheyenne (15 days) Fiona (14 days)	Tammy Chica Kiki Cheyenne Fiona

Figure 2. Timeline showing each individual vervet monkey orphan's care from arrival to release into troop and the days spent in each stage of care. A line divides the Goliath troop above from the D and D troop below.

Disneyland (Day 4-42)

Following the three day quarantine, offspring were introduced into a section of the foundation called Disneyland. Disneyland was a single building constructed of chain-link fence about 7m x 3m in size with a zinc roof, branches and PVC piping for climbing. All orphans that were in Disneyland were placed together and not in separate cages. The orphaned young received care from human-caregivers. The duration of time that orphans spent in Disneyland was dependant on the duration it took orphans to become accustomed to drinking formulated milk from holstered milk bottles (on the sides of the cage) in the feeding cages. The number of feeding cages was one or two depending on the number of orphans in the Disneyland.

The feeding cages were made from wire mesh with two entrance holes in the front to allow orphans access into and out of the feeding cage. The cages were approximately 1m x 1m and had netting above to provide shade while the orphans drank milk. The orphans were hand fed by the human caregivers with baby bottles until they learnt to drink from the bottles and then trained to drink milk from the holstered milk bottles in the feeding cages (as shown in Photograph 10, all feeding cages looked similar). To train orphans to drink from the bottles inside the feeding cage, they were coaxed into the feeding cages with plates of chopped fruit and vegetables, such as apple, pear, cucumber, spinach, and eggplant placed into the feeding cages. Orphans were also often encouraged to drink from the bottles by human-caregivers tapping on the end of the bottles once they were in the cage.

Photograph 10. An integration cage used at the Vervet Monkey Foundation to introduce orphan young to females and feeding cages where bottles were holstered from which orphans could feed.

<u>Integration cage with human-caregiver (Day 43 - 47)</u>

Orphans that could drink from the bottles in the feeding cage were placed into an integration cage of a selected troop for a maximum of four days, ranging from one to four days (Figure 2 timeline) by a human-caregiver. The human-caregiver remained with the orphan while it explored the cage for the duration that the orphan was in the integration cage. Host troops were selected based on the number of troop members, the sex ratio, and age structure of the troop and history of the troop, such as if they were pets or free-roaming when they were brought to the foundation. While orphan/s were in the cage, females curious about the orphans approached the cage from the enclosure side. Some vervet monkey females reached for the orphan/s, lip-smacked and/or attempted to groom them through the fence (personal observation). Male vervet monkeys in the troop mostly did not approach the integration cage.

Integration with foster mother (Day 48 - 115)

On the day orphans were to be introduced to vervet foster mothers, the human-caregiver left the orphan alone in the integration cage alone. The minders exited the cage and the surrounding area; this was done to not hinder these introduction since many of the offspring became attached to their human-caregiver (as per Foundation information). Volunteer staff members opened the entrance gate by pulling on a rope to open or close the gate allowing vervet females to enter and exit the integration cage, usually allowing two females at a time into the integration cage. If the alpha female of the troop showed interest in the young, 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 was not interested in the orphan, she was let out via the gate between the troop and integration cage. 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 with the orphan.

To establish if a female was interested in the orphan, the staff at the Foundation monitored the interactions of the potential foster mother with the orphan. Interested females would approach the orphan, lip-smacked, attempted to groom or grabbed the orphan and/or pulled the offspring toward her and made it cling onto her (information from the Foundation). Females that displayed nervous behaviour, such as paced and pulled on the door to open, were not allowed with the orphan (information from the Foundation). Adult females that showed interest in the orphan and were not nervous were 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 placed into the integration cage every evening and every morning while in the integration cage.

Closer to the release date in the troop, other females of the troop were allowed into the integration cage. This ranged from 30 minutes to 12 hours, and as often as possible. The process of changing adult females was to enable the offspring to become familiar with different adult females before they were released into the troop. The process of integration with the foster mother ranged 14 to 67 days (Figure 2), and the number of days spent in the integration cage depended on the age of the offspring. Orphans were only released into the troop when they were at least three months old.

Release into troop (Day 116+)

At the point of release into the troop, the offspring had to be clinging to the foster mother. Volunteer staff would pull on ropes that were attached to the small gate that allowed females to enter to allow foster mother and clinging offspring out of the integration cage. Human volunteers were positioned, for one to two weeks from before sunrise to after sunset around the enclosure when orphans were released from the integration cage into the troop; the vervets slept at night. The volunteers had 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 cages, and were placed inside the troop enclosures. If the offspring did not drink from the feeding cages, volunteers held the bottle close to the fence and let the orphan drink from the bottle or they slowly walked to the feeding cages while still keeping the bottle close to the fence and placed the bottle into the holster of the feeding cage.

Behavioural observations

Observations were conducted from December 2016 to April 2017. Behavioural observations were conducted on the eight orphans placed in two different troops' integration cages. Observations were conducted during the day from 7am to 5pm. In Goliath troop, Zoro was in his own integration cage, Dana, Maggie and Neville were in an integration cage together and shared the same foster mother. In the D and D troop, Tammy and Chica were in the same integration cage and shared the same foster mother, Kiki and Cheyenne were in a cage together and shared the same foster mother and Fiona was in her own integration cage. Observations started when orphans were placed into the integration cage (day 48) with a potential foster mother. I catalogued the behaviour of the orphan and their interactions with the potential foster mother, other orphans and troop members, using focal individual sampling. The duration of these observations in the integration cage were generally from 60 – 90 minutes and when released into the troop ranged from 10– 150 minutes, depending on whether the orphan was visible. Behaviours recorded are described in Table 1.

Observations started from the first day an orphan was in the integration cage until first released into the troop and then after the release into the troop. The duration of time (in minutes) of each behaviour for each orphan was recorded. As times of sampling differed due to varying introduction and release dates, data were pooled for the number of observational times in the weeks of an orphan in each troop. For example, Tammy and Chica were introduced to adult females in the integration cage on 19 December 2016. They were both released into the troop with the foster mother on 30 January 2017, resulting in 42 days from introduction to release. Cheyenne was introduced to adult females in the integration cage on 22 January 2017 and was released on 7 February 2017, resulting in 16 days from introduction to release. Pooling the data accounted for differences in sampling days since orphans arrived at different ages and were introduced to females are different times.

Data analysis

Data were analysed 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. I used a general linear model (GLM) to investigate changes in behaviours of the orphans. For the purpose of analyses, the duration (minutes) of behaviours recorded was the dependant variable, the week of sampling was the repeated measure variable, individual was included as a random variable, and the starting of three to eight weeks for D and D troop was a continuous predictor; all Goliath troop orphans were three weeks old when studied and starting age was not included as a continuous predictor in the analysis. Behaviour types were classified into common or uncommon categories, calculated by generating the percentage duration scores for the weeks in the integration cage and release into troop. Common behaviours were those occurring more than 5% of the total sampling and uncommon behaviours were below 5% of the total behaviours scores. Only common behaviours were analysed. Significant fixed predictors were assessed using the Fisher LSD post hoc test. Alpha was set at 0.05 and tests were two-tailed.

Table 1. Descriptions of ten behaviours of offspring during integration cage with foster mother and after their release into a troop.

Type	Description
Inactive	Offspring remained in one location, alert (Bassett *et al.* 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 et al. 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
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
Allo-grooming	Groomed by/ grooming another troop member excluding the foster mother.
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 (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).

Comparisons with other studies

Without a control study to validate the fostering procedure used by the Foundation, I compared the efficacy of the fostering protocol used here with those found in the literature. I used Google scholar and the Web of Science to search for studies that used different hand rearing or nursery rearing methods on vervet monkeys and other primates. I used the key words of vervet monkey fostering and vervet monkey, hand rearing. Due to the lack of studies done on vervet monkeys, I also searched for hand-reared primates. I found seven studies that matched my search criteria of testing the effects of different rearing methods. I extracted the following information: ages of orphans; phases of integration; level of human-care involvement; the behaviours observed and fostering success. The level of human- care was weighted from zero to four. Level zero was zero months of human-care, level one was one to three months of human-care, level two was four to six months of human-care, level three was seven to nine months human-care, and level four was ten months and more of human-care. In my study, success was based on the number of orphans released into the troop and remained in the troop. The success of the other studies were determined from reports of the study authors.

Alarm call production

My intention was to elicit alarm calls of a leopard and a snake threat from Goliath and D and D existing troop individuals. However, there were no leopard sightings within the study area. Although snakes, such as the Egyptian cobra *Naja anniulifera* and puff adder *Bitis arietans arietans*, were seen between the vervet enclosures by myself and the Foundation staff, they were not present during predator alarm call production. Due to there being no available real models of leopards and snakes available, I used a stuffed leopard and a toy snake to elicit predator alarm calls. The leopard model was placed close to different trees around the enclosure's fence where different individuals of the troop could see it. To simulate movement, the leopard model (Photograph 11A) was propped up by a stick or I held it and moved it while being out of view of the vervet monkeys. The snake model (Photograph 11B) was placed in various positions around the enclosure fence close to as many different vervet individuals as possible. I tied a thin rope around the snake model's head and tugged it to simulate movement.

Photograph 11A. The leopard model used as visual aid to elicit the snake alarm calls from the vervet monkeys.

Photograph 11B. The snake model used as visual aid to elicit the snake alarm calls from the vervet monkeys.

The predator models were shown to individuals in the troop at 15 minute intervals for a minimum of five repeats for each troop. Each troop was rotated with the two models daily for seven days. As a safety precaution, I did not place the leopard and snake model inside the enclosure as many of the monkeys were known to be aggressive towards people that entered the enclosures. The calls produced by the vervets were recorded using a Canon Powershot camera as soon as the model was placed and for two minutes or until the individuals stopped alarm calling. The individuals that made the alarm call and the duration of the call in minutes was noted for the playback experiment. Alarm calls that were clear and close to the camera or longer than one minute were to use as playbacks to assess the potential of fostered orphans to potential threats.

I selected five calls elicited from a leopard model and five calls elicited from the snake model of each troop at random and played it back to the troops via concealed Shox mini speaker. Playback of recorded alarm calls from the troops yielded no reaction to both predator alarm calls of both models for both troops. Since there was no reaction to the recorded alarm calls, I used recorded predator alarm calls of vervet monkeys from Youtube https://www.youtube.com/watch?v=-uCn-XGUdns&t=70s (leopard) and https://www.youtube.com/watch?v=bsWyp0aAUBc&t=17s (snake), recorded by Prosound Effects in Kenya. The leopard predator alarm call was from one male for the majority of the recording. The snake predator alarm call had some microphone bump sounds and a distant plane in the background.

Playback

Playback recordings of predator specific alarm calls of either leopard alarm call or a snake alarm call was broadcasted to the Goliath troop and the D and D troop orphans randomly in the morning between 7:00 and 11:00 or the afternoon between 13:00 and 17:00 for three weeks. Alarm calls were played back on a concealed Shox mini speaker placed 0-2m away from the enclosure.

Tests were run for four to five days per week for three weeks per troop (Tables 2.1 and 2.2). The same type of predator alarm calls were not played for the same troop consecutively (i.e. an alarm call played in the morning time slot was not repeated in the afternoon time slot) or for a different troop on the same day. Following Seyfarth and *et al.* (1980a), no alarm calls were played within a 15 minute interval between experimental calls or after naturally occurring alarm calls. Repetitions were done to include as many offspring as possible for each predator alarm call on specified time allocations.

Behavioural observations were conducted ten seconds before the alarm call was played, during the alarm call (30 seconds to about one minute), and ten seconds after the alarm call stopped playing. On random alternating days, a visual stimulus accompanied alarm calls (Table 2.1 and 2.2). On days when an alarm call to a leopard was played back, I also presented a visual stimulus of the stuffed leopard model either held up by me into the view of the vervet monkeys or propped up on a stick and moved around while the alarm call played. Similarly, a snake model accompanied snake elicited alarm call play back. The snake model was tied by the neck with a thin rope, and placed close to outside the enclosure fence hidden in grass. Once the alarm call was played back, I pulled the rope to move the snake or pulled the snake along the enclosure. Once the alarm call had stopped playing, I hid the models from view. I combined the alarm calls and visual stimulus since the response to a predator in vervet monkeys might be summative of different predator cues.

Table 2.1. The sequence and types of alarm call playbacks to elicit behavioural responses in the Goliath troop vervet monkeys. Visual aids (i.e. stuffed leopard and snake model) were included on 15 days.

	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM
week 1		Snake call	Leopard call				Snake call - visual aid			Leopard call
week 2		Snake call-visual aid		Leopard call		Snake call-visual aid	Leopard call-visual aid		Snake call-visual aid	
week 3		Snake call				Snake call	Leopard call			Leopard call-visual aid

Table 2.2. The sequence and types of alarm call playbacks to elicit behavioural responses in the Dino and Daniel troop vervet monkeys. Visual aids (i.e. leopard and snake model) were included on 15 days.

	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM
week 1	Snake calls			Leopard call-visual aid		Snake call-visual aid		Leopard call	Snake call	
week 2			Snake call - visual aid		Leopard call			Snake call - visual aid		Leopard call-visual aid
week 3	Leopard call-visual aid		Snake call					Snake call-visual aid	Leopard call-visual aid	

Data collection

The predator alarm calls were played for a minimum of 30 seconds to about one minute for each predator alarm call. Observation were made 10 seconds before the playback and the ten seconds after the playback. The length of time of the alarm call playback was determined by whether I played the alarm call alone or played the call and presented the model (which took longer). The description of five behaviours is described in Table 3.

Video recordings of all behavioural responses were made of offspring using a Canon Powershot digital camera. If more than one offspring was present, the video recordings helped to record the behaviour of each individual. This also ensured that behaviours observed before, during and after the predator alarm call playback were not elicited by another source, such as human shouts, dog barks, or vehicles, which I could sometimes detect on the recordings.

Table 3. Description of the five behaviours scored during the predator alarm call playback and the ten behaviours before and after playback.

Behaviour	**Description**
During playback	
Startled	Head jerked in a swift movement toward the source of sound (Fichtel and Kappeler 2002).
Orientation toward the source	Head or body turned toward the source of the alarm call playback (Owings and Virginia 1978).
Cover in trees	Ran for the tree cover and remained in the tree (Coss *et al.* 2007).
Observational stance	Stood on hind legs and looked towards the ground (van Schaik and van Noordwijk 1989).
None response	None of the behaviours above were observed.
Before and After alarm call play back	
Inactive	Offspring remained in one location. Alert (Bassett *et al.* 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 et al. 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.
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.
Allo-grooming	Groomed by another troop member excluding the foster mother.
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 (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).

Data analysis

A change of behaviour was tested multiple times for leopard alarm call without and with visual stimulus and for snake alarm call without and with visual stimulus. The proportion of behaviour change was calculated from before, to during, to after the alarm call played. This was calculated by counting the number of times the individual orphan changed from one behaviour to another divided by all behaviours recorded in all tests conducted for that individual for each alarm call without and with visual aid. I also calculated the proportion of occurrences that each individual spent with their respective foster mother for the leopard and snake alarm call without and with visual aid before, during and after the alarm call was played. This was calculated using the number of occurrences each individual spent with foster mother divided by the number of overall tests conducted for that individual. Finally, I calculated the proportion of occurrences each orphan spent with another vervet monkey for the leopard and snake alarm call without and with visual stimuli before, during and after the alarm call was played. This was calculated using the number of times each individual spent with another vervet monkey divided by the number of overall tests conducted for that individual.

A chi-squared test of independence was used to analyse whether the frequency of changes in behaviour occurred by chance. The observed of change in behaviour was compared to the expected change of behaviour for each individual from before, to during, to after the alarm call played for leopard alarm call without and with visual stimulus and for snake alarm call without and with visual stimulus. A chi-squared test was used to analyse whether the frequency of changes in behaviour occurred by chance. The observed number of occurrences individuals were with foster mothers compared to the expected number of occurrences individuals were with their foster mothers before, to during, to after the alarm call played for leopard alarm call without and with visual stimulus and for snake alarm call without and with visual stimulus. Finally, a chi-squared test was used to determine the number of occurrences that orphans spent with other vervet monkeys, during and after the alarm call play-back. The observed number of occurrences individuals were with vervet monkeys compared to the expected times individuals were with other vervet monkeys before, to during, to after the alarm call played for leopard alarm call without and with visual stimulus and for snake alarm call without and with visual stimulus. Model level of significance was 0.05.

Results

Fostering

Goliath troop

All four orphans studied in the integration cage in Goliath troop were approximately three weeks old when they were brought to the foundation. Staff at the Vervet Monkey Foundation mentioned that the Goliath troop foster mothers preferred to adopt younger and smaller orphans. Zoro, Maggie, Dana and Neville were the youngest orphans that were trained to drink milk from the feeding cage at the Foundation during the study period.

Zoro was introduced to adult females on 12 December 2016 and released into the enclosure (troop) on the 23 January 2017 (Figure 3). Neville was in an integration cage with Dana and Maggie, and all three were introduced to adult females on 27 January 2017, and released with a foster mother into the troop on 5 March 2017. Neville escaped from the enclosure the next morning. He was returned to the integration cage and then moved to a different troop. I did not consider his behaviour when he was released into this other troop. Two additional two orphans, Amandla and Aurhoa, were introduced to the troop females in the integration cage on 12 December 2016, but due to illness they were removed from the integration cages on 24 December 2016 and were not returned.

D&D troop

Tammy and Chica were introduced to adult females in the integration cage on 19 December 2016 (Figure 4). Chica and Tammy were both released into the troop with their foster mother on 30 January 2017. Cheyenne was not introduced into Disneyland or into the integration cage with human-caregivers due to her arriving at the Foundation at an older age (about two months old) and was taught to drink milk formula from the feeding cage while in quarantine. Cheyenne was introduced to adult females in the integration cage on 22 January 2017 and was released into the troop with a foster mother on 7 February 2017. Kiki was introduced to females in the integration cage on 6 January 2017 and released into the troop with a foster female

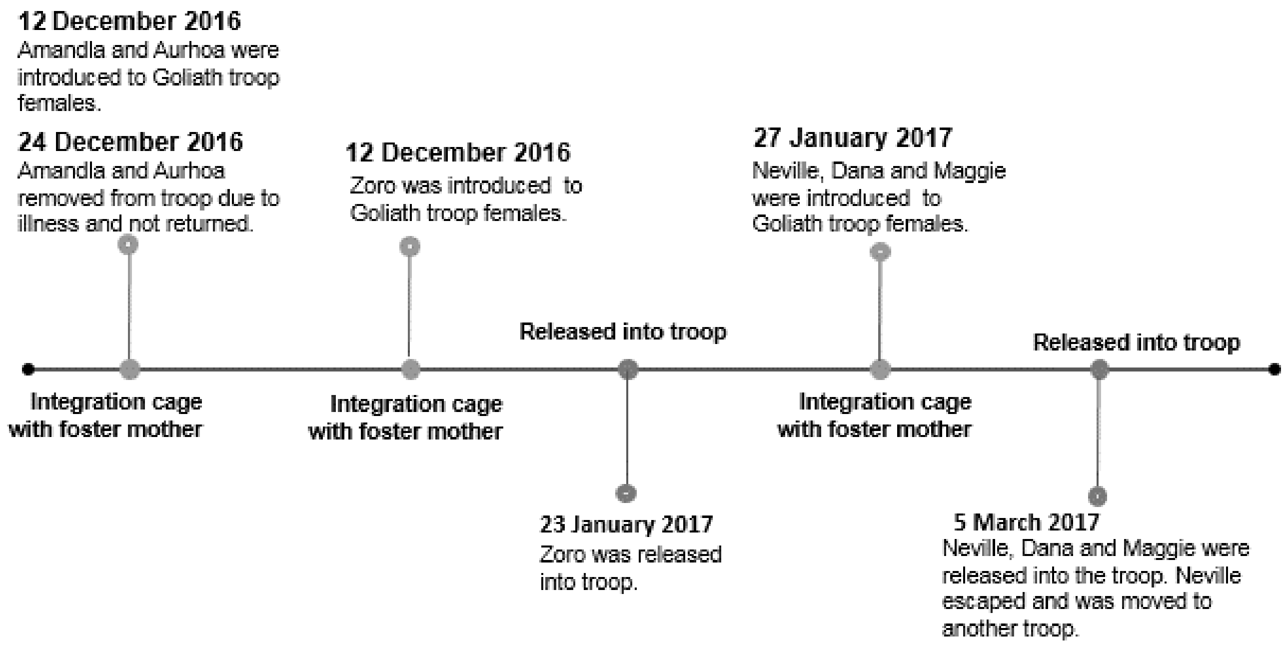


Figure 3. Timeline diagram of integration of orphans with a foster mother and release into the Goliath troop.

on 3 March 2017. An earlier release attempt was made to release the pair, although Kiki's foster mother did not leave the integration cage, possibly because she was avoiding the alpha female of the troop with which she had a fight previously (personal observation). Fiona spent one day in the integration cage with human minders, unlike the usual three or four days due to the high volume of orphans arriving at the Foundation during this time and very few volunteer staff members being available to assist. Fiona spent less than a month in human care and the directors of the Foundation expected she would adapt quicker to being with adult vervet monkeys. Fiona was introduced to adult females in the integration cage on 3 February 2017. Fiona also spent a short time in the integration cage with a foster mother before release into the troop. This was due to an accidental release on 18 February 2017. Fiona was returned four days later into the integration cage with her foster mother and released into the troop on 7 March 2017.

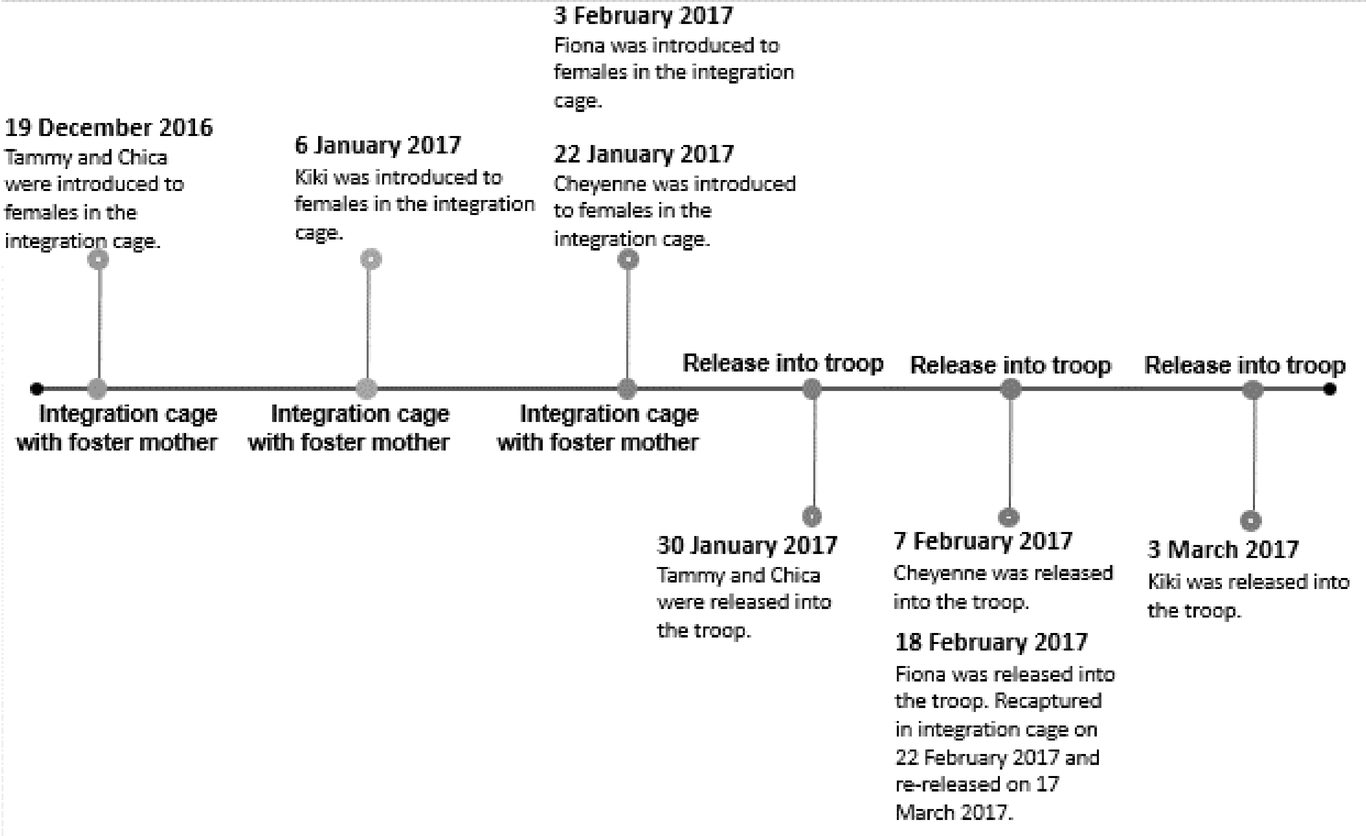


Figure 4. Timeline diagram of integration of orphans with a foster mother and release into the D and D troop.

Integration cage

I made behavioural observations as soon as orphans were placed in integration cages and introduced to female vervet monkeys. In the Goliath troop, I recorded Zoro's behaviour for a total of 17 days continuously. His foster mother was Mrs. Gold who had previous fostering experience. Dana, Maggie and Neville were in the same integration cage and I recorded their behaviour for a total of 16 days; they shared a foster mother, Shorty, who had previous fostering experience. The duration of behaviours was recorded for each orphan, and pooled by orphan per week (i.e. three weeks) because of the unbalanced sampling of individuals (see methods). In the Goliath troop, one of day of Zoro's observations was omitted (n= 3675 minutes). I calculated the frequency of duration spent on each behaviour over the total sampling time per day for each individual. These values were then pooled (i.e. frequency of observed behaviour for each individual per week of sampling) and reported as mean percentages of frequencies of duration for observed behaviours (Table 4.1).

For the Goliath troop, in the integration cage, inactive, active, association with foster mother, feed and drinking, and socio-positive occurred most often in all three

Table 4.1. Mean and SD percentage frequency of duration of observed behaviours for each orphan for three weeks in the integration cage for the Goliath troop.

	Inactive		Active		Association with foster mother		Feed and Drink		Allo- grooming		Socio-positive		Socio-negative		Interactions with people		Self-grooming		Abnormal	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Zoro	24	0.63	32	0.69	14	0.32	25	0.53	1	0.04	1	0.03	0	0	0	0	0	0	1	0.04
Maggie	38	0.86	26	0.55	3	0.08	18	0.36	0	0	14	0.30	0	0	0	0	0	0	0	0
Dana	12	0.26	13	0.26	44	1.01	22	0.48	0	0	7	0.14	0	0	0	0	0	0	0	0
Neville	35	0.86	26	0.55	3	0.08	17	0.35	1	0.04	16	0.34	1	0.04	0	0	0	0	0	0

Table 4.2. Mean and SD percentage frequency of duration of observed behaviours for each orphan for two weeks in the integration cage for the D and D troop.

	Inactive		Active		Association with foster mother		Feed and Drink		Allo- Grooming		Socio-positive		Socio-negative		Interactions with people		Self-grooming		Abnormal	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Tammy	29	0.62	8	0.14	50	0.97	6	0.1	4	0.1	3	0.06	0.4	0.01	0	0	0	0	0	0
Chica	28	0.74	38	0.84	17	0.36	9	0.2	0.2	0.07	5	0.17	0.8	0.02	0.8	0.02	1	0.03	0.2	0.07
Kiki	6	0.1	34	0.57	41	0.89	14	0.35	2	0.07	0.8	0.02	0	0	0	0	0	0	2	0.06
Cheyenne	16	0.28	48	0.98	7	0.17	17	0.37	1	0.03	10	0.17	0.4	0.01	0	0	1	0.03	0	0

weeks of sampling (Table 4.1). Allo-grooming, socio-negative, interactions with people, self-grooming, and abnormal behaviour occurred at low levels (Table 4.1). Behaviours occurring more than 5% (n=183 minues) of the total sampling time included inactive, active, association with foster mother, feeding and drinking, and socio-positive for all orphans. However, Zoro had lower socio-positive behaviour (1%; n=36 minutes), possibly due to being the only individual in the integration cage with his foster mother. Maggie and Neville had lower association with the foster mother (3%; n=110 minutes), possibly due to there being only one foster mother in the cage with three orphans. These exceptions were not excluded from the analysis because they were common in the other orphans of this troop. Behaviours below the 5% (n=183 minutes) of occurrence were allo-grooming, socio-negative, interactions with people, self-grooming, and abnormal behaviour.

In the D&D troop, Chica and Tammy were in the same cage. Both were observed for a total of 21 days. Both orphans had the same foster mother, Honeybear, who had previous fostering experience. Kiki was observed for a total of 24 days. Cheyenne was in the same integration cage as Kiki and was observed for a total of nine days due to scheduling constraints for her release. Cheyenne and Kiki's foster mother was Phyllis who had previous fostering experience. Fiona was observed for a total of seven days, her foster mother was Hazel who had previous fostering experience. Due to the different sampling days for the offspring, the data for observations were truncated to nine days (i.e. two weeks; n= 2399 minutes) and Fiona was excluded from the analysis since she was sampled for seven days. The proportion of behaviours and data pooling were done as described for the Goliath troop (above), and reported as percentages (Table 4.2).

For the D and D troop, the common behaviours (above 5% of occurrence; n= 120 minutes) were inactive, active, association with foster mother, feed and drinking, and socio-positive (Table 4.2). There were exceptions to these behaviours, such as Tammy having lower socio-positive (3%; n=72 minutes) and Kiki with lower socio-positive behaviour (0.08%). These exceptions were not excluded from the analysis because of their importance to the other orphans in this troop. The behaviours with the lowest proportion (below 5% occurrence; n=120 minues) were allo-grooming, socio-negative, interactions with people, self-grooming, and abnormal behaviour (Table 4.2).

Enclosure

I recorded the behaviours of fostered offspring under study as soon as they were released into the troop with their foster mother. In the Goliath troop, Zoro's behaviour was recorded for a total of 25 days. Dana and Maggie were observed for a total of ten days; the lower number of observation days was due to the difference in the timing of the release days. Neville was not part of the enclosure release (see above). Due to the differences between Zoro, Dana and Maggie in the number of days of observations, the data set was truncated to ten days (two weeks; n=1976 minutes). The proportion and pooling of data per week were done as described above, and reported as percentages (Table 4.3).

In the enclosure, the common behaviours (above 5% occurrence; n=99 minutes) were inactive, active, association with foster mother, feeding and drink, and socio-positive (Table 4.3). The exception to these were Maggie's low association with foster mother (1%; n=20 minutes) and Dana with low socio-positive behaviour (4%; n=79 minutes). These behaviours were not excluded from the analysis since they were important in the other individuals. Uncommon behaviours (below 5% occurrence; n=99 minutes) were allo-grooming, socio-negative, interactions with people, self-grooming, and abnormal behaviour (Table 4.3). Zoro's allo-grooming was high (6%; n=118 minutes) but his behaviour was not included in the analyses because of the generally low or absent allo-grooming in the other orphans in this troop.

In the D&D troop, Chica's and Tammy's behaviours were recorded for 22 days. Cheyenne was observed for a total of nine days. Kiki was observed for a total of nine days. Fiona was observed for a total of 13 days. Due to the different number of sampling days between the offspring, the data were truncated to nine days (i.e. two weeks; n= 2389 minutes) for analyses. The proportion and pooling of data per week were done as described above, and reported as percentages (Table 4.4).

Here, inactive, active, association with foster mother, feed and drink, and socio-positive were common (above 5% occurrence; n=120 minutes) (Table 4.4). Exceptions were Chica with low association with foster mother (4%; n=96 minutes), Tammy had socio-positive (4%; n=96 minutes), and Cheyenne with low socio-positive behaviour (3%; n=72 minutes). These behaviours were not excluded as they were important to other orphans in this troop. Uncommon behaviours (below 5% occurrence; n=120 minutes) were allo-grooming, socio-negative, interactions with people, self-grooming, and abnormal behaviour (Table 4.4). Tammy had a high (7%; n=167 minutes) allo-grooming, but her data were excluded because of its rarity in the other orphans in this troop.

Table 4.3. Mean and SD percentage frequency of duration of observed behaviours for each orphan for two weeks in the Goliath troop enclosure.

	Inactive		Active		Association with foster mother		Feed and Drink		Allo- Grooming		Socio- positive		Socio- negative		Interactions with people		Self- grooming		Abnormal	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Zoro	21	0.41	31	0.60	14	0.30	15	0.29	6	0.14	9	0.20	0	0	0	0	0	0	0	0
Maggie	38	0.84	36	0.77	1	0.04	6	0.14	1	0.02	12	0.25	0	0	0	0	0	0	0	0
Dana	33	0.74	13	0.23	31	0.66	7	0.42	0	0	4	0.09	0	0	0	0	1	0.04	0	0

Table 4.4. Mean and SD percentage frequency of duration of observed behaviours for each orphan for two weeks in the D and D troop enclosure.

	Inactive		Active		Association with foster mother		Feed and Drink		Allo- Grooming		Socio- positive		Socio- negative		Interactions with people		Self- grooming		Abnormal	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Tammy	19	0.49	40	0.79	7	0.17	18	0.46	7	0.17	4	0.1	0	0	0	0	0	0	0	0
Chica	29	0.7	28	0.49	4	0.1	22	0.49	4	0.09	13	0.2	0	0	0	0	0	0	0	0
Kiki	35	0.81	37	0.82	5	0.1	18	0.3	0.2	0.006	5	0.1	0	0	0	0	0	0	0	0
Fiona	29	0.53	29	0.75	16	0.44	13	0.35	0.2	0.006	13	0.28	0	0	0	0	0	0	0	0
Cheyenne	23	0.59	35	0.61	20	0.54	19	0.33	0.3	0.009	3	0.05	0.1	0.003	0	0	0	0	0	0

Statistical analyses

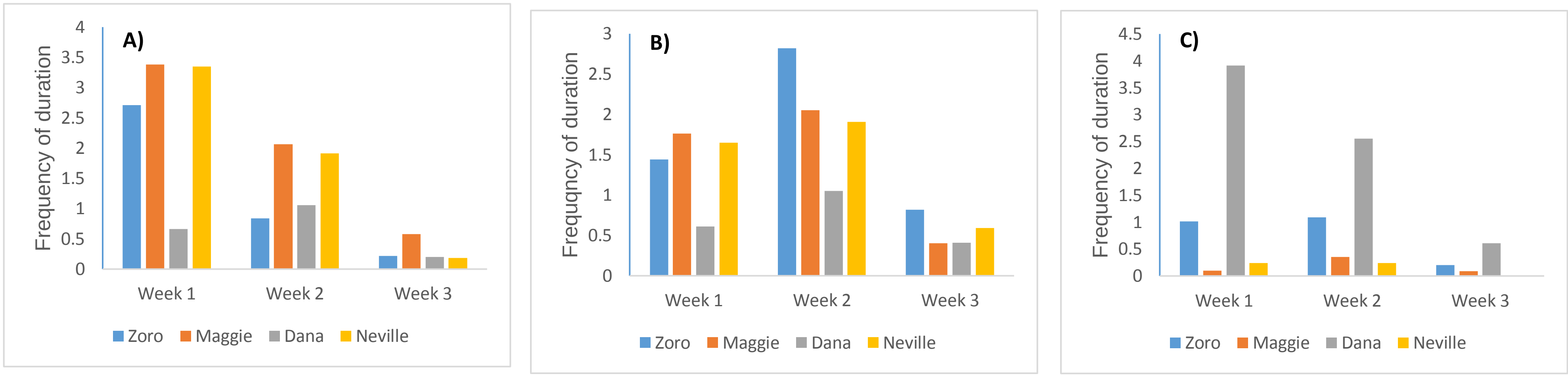
Integration cage

The results of the GLM on the common behaviours for the Goliath troop orphans in the integration cage are shown in Table 5.1. All individuals were observed at the same starting age. Individual was a significant predictor of active behaviour, association with foster mother behaviour and socio-positive behaviour. Maggie, Neville and Zoro had similar durations of active behaviour while Dana had the lowest duration of active behaviour over the observation weeks (Figure 5 B). Dana had the highest duration of association with foster mother, followed by Maggie, Zoro and then Neville (Figure 5 C). Neville had a similar duration to Maggie which was the highest duration of socio-positive behaviour, followed by Dana and Zoro had the lowest duration (Figure 5 E).

Week was a significant predictor of all common behaviours (Table 5.1). Inactive behaviour decreased over the three weeks of study (Figure 5 A). Active behaviour was highest in week two; week one was slightly lower in duration than week two while week three had the least active behaviours recorded (Figure 5 B). Association with foster mother was lower in week three compared to weeks one and two which did not differ from each other (Figure 5 C). Feeding and drinking was highest in week two and lowest in week three (Figure 5 D). Socio-positive behaviour was highest in week two and lowest duration in week three overlapping with week one (Figure 5 E).

Table 5.1. Output of the GLM for common behaviours displayed by orphans in the integration cage of the Goliath troop. Significant values are shown in bold.

Behaviour	**Individual**	**Week**
Inactive	$F_{3,6}$=2,85; p=0.127	**$F_{2,6}$=15.24; p=0.004**
Active	**$F_{3.6}$=5.14;p=0.043**	**$F_{2.6}$=20.14; p=0.002**
Association with foster mother	**$F_{3.6}$=13.45;p=0.005**	**$F_{2.6}$=6.96; p=0.027**
Feed and drink	$F_{3.6}$=2.79;p=0.132	**$F_{2.6}$=34.84; p<0.001**
Socio-positive	**$F_{3.6}$=14.60; P=0.004**	**$F_{2.6}$=6.90; p=0.028**



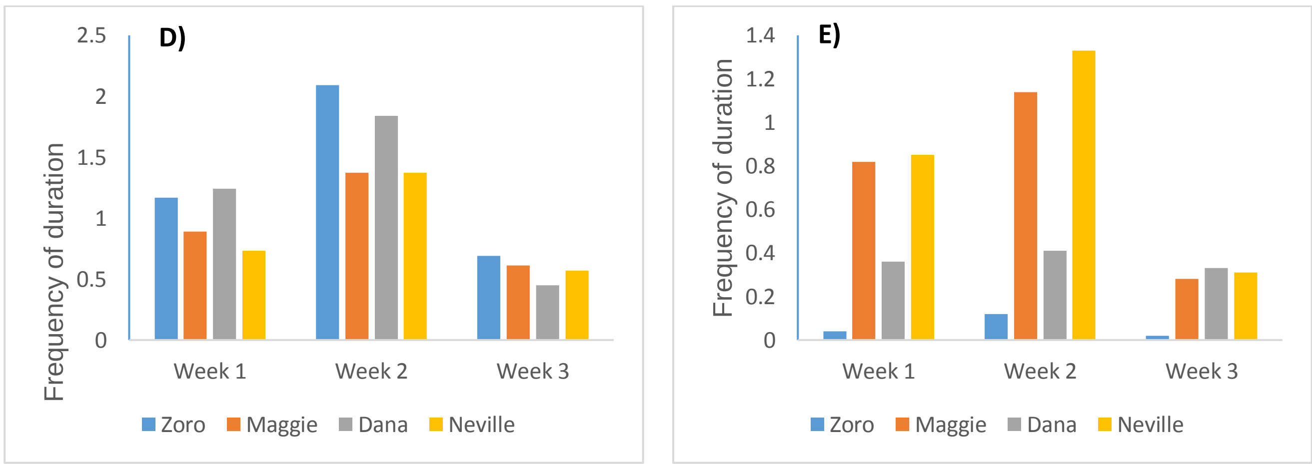


Figure 5. The frequency of duration of A) inactive behaviour, B) active behaviour, C) association with foster mother behaviour, D) feeding and drinking, and E) socio-positive behaviour in Goliath troop integration cage.

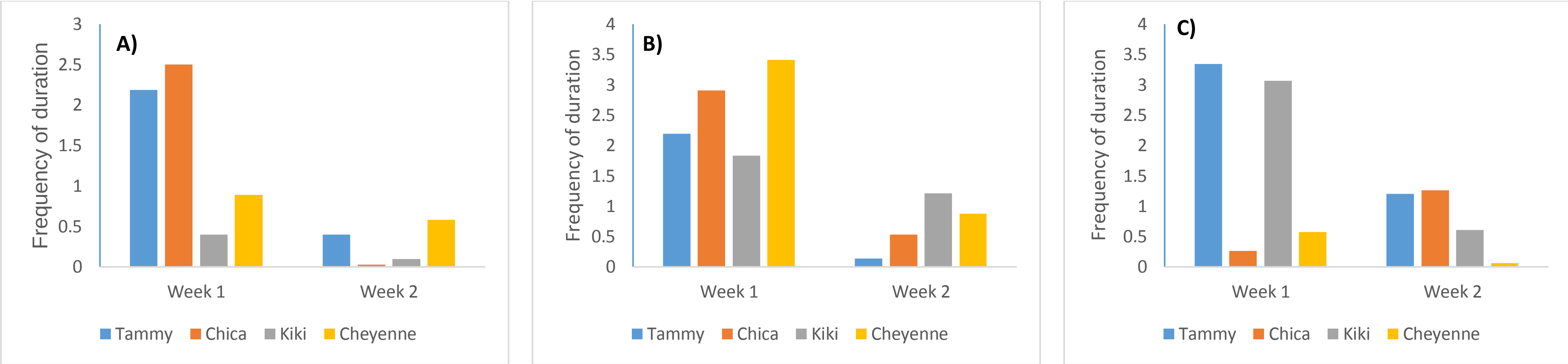
The starting ages for the orphans varied in the integration for the D and D troop. There was no significant correlation between staring age (continuous variable) and common behaviours, whilst orphans were in the integration cage ($p>0.05$). Starting age was not considered from the GLM analyses.

Individual was a significant predictor of socio-positive behaviour (Table 5.2; Figure 6 E). Week one had the highest duration in comparison to week two.

Week was a significant predictor of active (Figure 6 B), feeding and drinking behaviour (Figure 6 D), and socio-positive behaviour (Figure 6 E). for active behaviour, feeding and drinking, and socio-positive behaviour week one had the highest duration in comparison to week two (Figure 6 B, C, E).

Table 5.2. Output of the GLM for common behaviours displayed by orphans D and D troop in the integration cage. Significant values are shown in bold.

Behaviour	Individual	Week
Inactive	$F_{3.3}=0.77$; $p=0.584$	$F_{1.3}=6.06$; $p=0.091$
Active	$F_{3.3}=3.99$; $p=0.143$	**$F_{1.3}=11.34$; $p=0.043$**
Association with foster mother	$F_{3.3}=1.54$; $p=0.366$	$F_{1.3}=10.74$; $p=0.336$
Feed and drink	$F_{3.3}=0.56$; $p=0.679$	**$F_{1.3}=10.74$; $p=0.047$**
Socio-positive	**$F_{3.3}=52.28$; $p=0.004$**	**$F_{1.3}=96.23$; $p=0.002$**



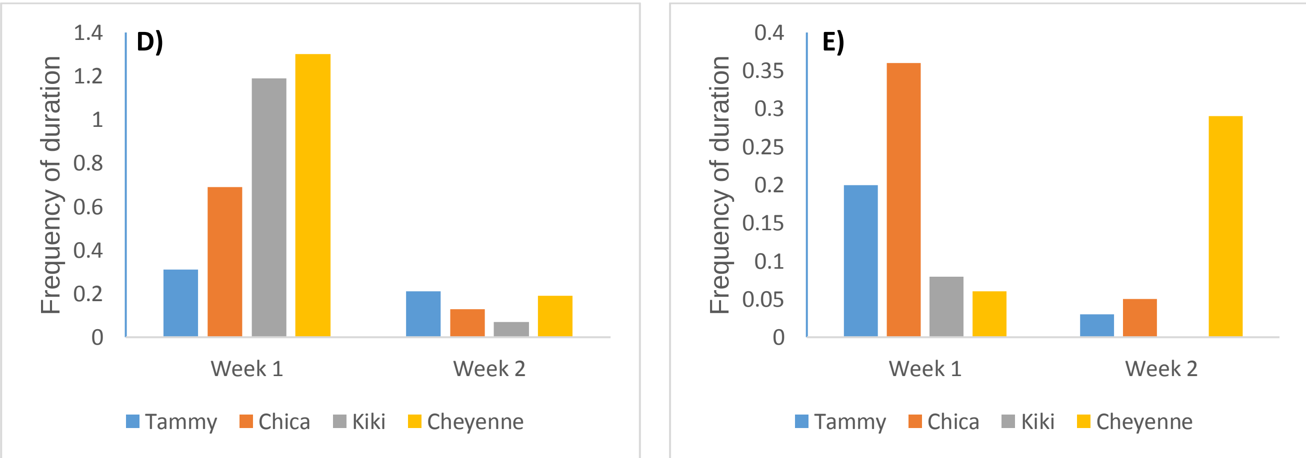


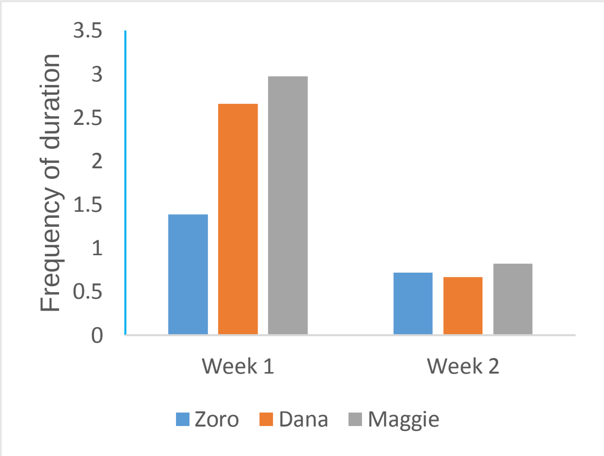
Figure 6. The frequency of duration of A) inactive behaviour, B) active behaviour, C) association with foster mother behaviour, D) feeding and drinking, and E) socio-positive behaviour in D and D troop integration

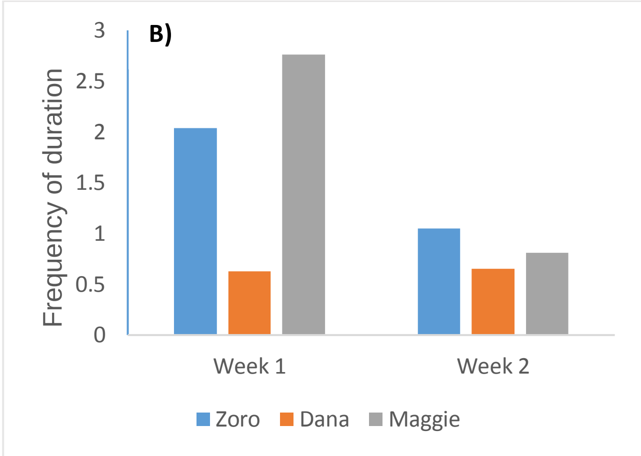
Enclosure

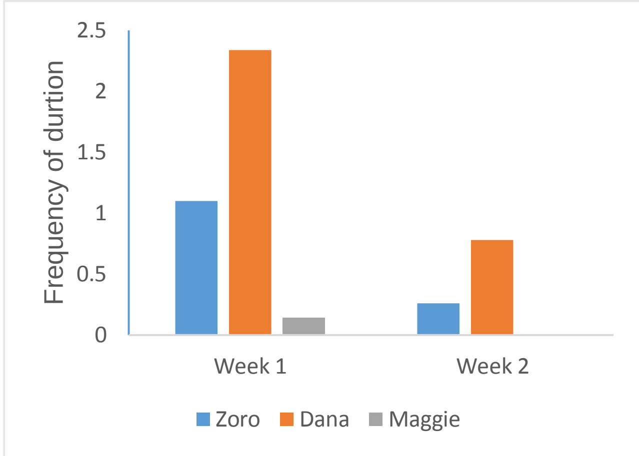
For Goliath troop the GLM (Table 5.3) was done once orphans had been released into the troop enclosure. Individual was a significant predictor of association with foster mother (Figure 7 C), Dana had the highest duration of association with foster mother behaviour followed by Zoro and Maggie had the lowest duration. Week was a significant predictor of association with foster mother (Figure 7 C), and week one had the highest duration of association with foster mother behaviour in comparison to week two.

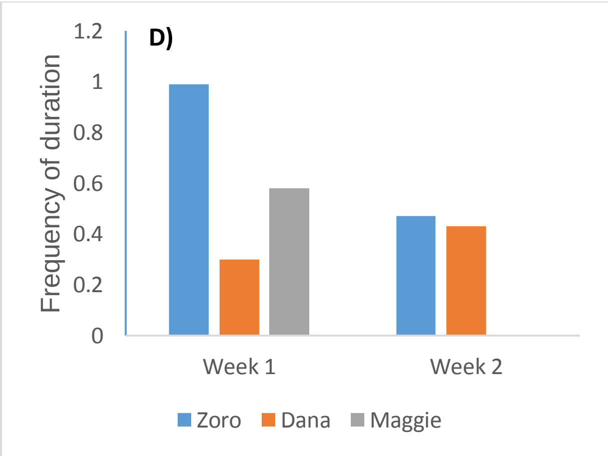
Table 5.3. Output of the GLM for common behaviours displayed in Goliath troop orphans released into the troop. Significant values are shown in bold.

Behaviour	**Individual**	**Week**
Inactive	$F_{2.2}$=1.22; p=0.451	$F_{1.2}$=16.36; p=0,056
Active	$F_{2.2}$=1.86; p=0.350	$F_{1.2}$=2.92; p=0.229
Association with foster mother	**$F_{2.2}$=55.70; p=0.018**	**$F_{1.2}$=43.088; p=0.022**
Feed and drink	$F_{2.2}$=1.12; p=0.472	$F_{1.2}$=1.63; p=0.329
Socio-positive	$F_{2.2}$=1.24; p=0.446	$F_{1.2}$=0.02; p=0.891









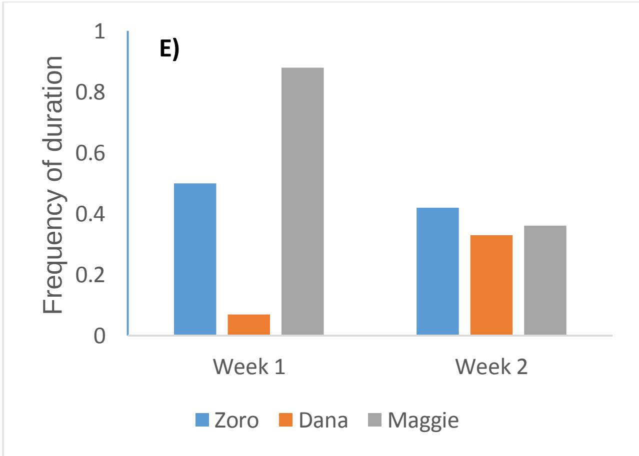


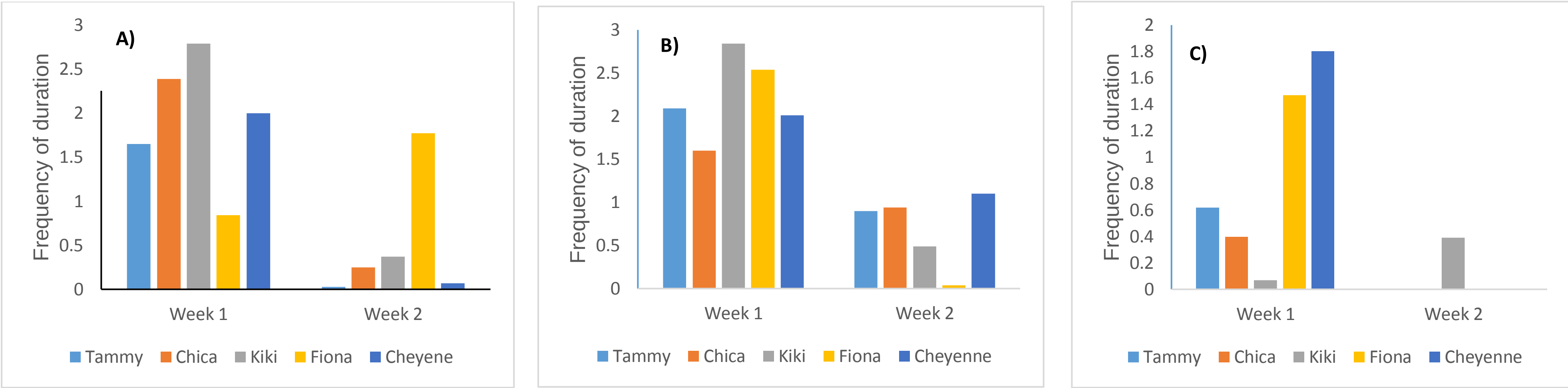
Figure 7. The frequency of duration of A) inactive behaviour, B) active behaviour, C) association with foster mother behaviour, D) feeding and drinking, and E) socio-positive behaviour in Goliath troop once released into the enclosure.

As with the D and D troop integration cage, orphans had varying starting ages. A variance correlation test was done on ages. There was no correlation between staring age (continuous variable) when released into the troop ($p>0.05$) and individual and week. A simple regression test was conducted on the data for each week to test for the relationship between starting age and duration of behaviour. The simple regression test confirmed that starting age was not a significant predictor of common behaviours observed in the D and D troop orphans released into the troop. Starting age was excluded from the GLM model (Table 5.4).

Week was a significant predictor of active behaviour (Figure 8 B), association with foster mother (Figure 8 C), and feeding and drinking (Figure 8 D). For active, association with foster mother, and feeing and drinking behaviour week one was higher than week two (Figure 8 B, C, D).

Table 5.4. Output of the GLM for common behaviours displayed in D and D troop orphans released into the troop. Significant values are shown in bold

Behaviour	**Individual**	**Week**
Inactive	$F_{4.4}$=0.29; p=0.874	$F_{1.4}$=6.87 ; p=0.059
Active	$F_{4.4}$=0.52; p=0.727	**$F_{1.4}$=12.72 ; p=0.023**
Association with foster mother	$F_{4.4}$=0.29; p=0.873	**$F_{1.4}$=12.74 ; p=0.023**
Feed and drink	$F_{4.4}$=0.56; p=0.704	**$F_{1.4}$=11.76 ; p=0.027**
Socio-positive	$F_{4.4}$=1.59; p=0.333	$F_{1.4}$=2.82 ; p=0.169



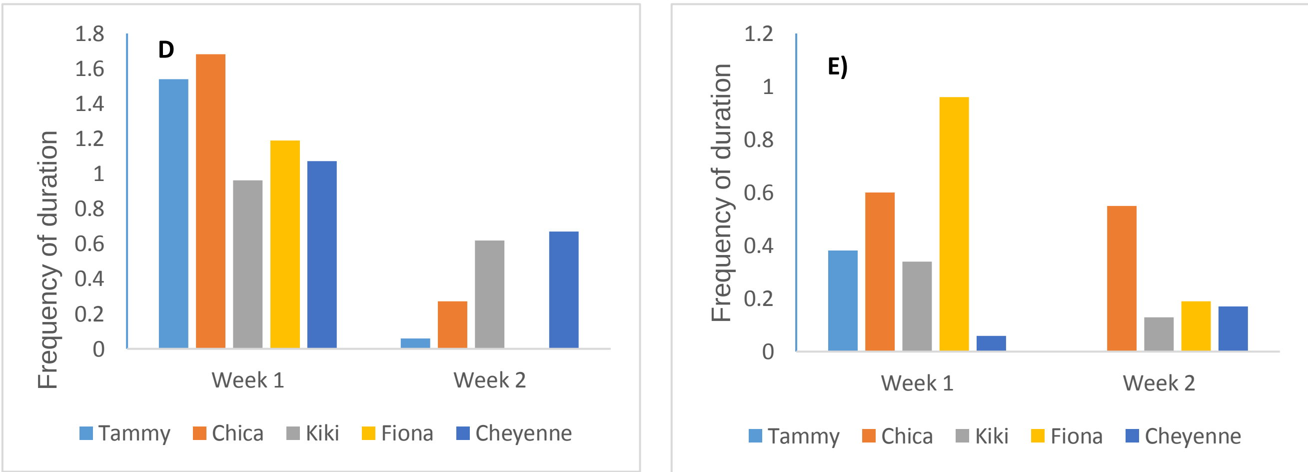


Figure 8. The frequency of duration of A) inactive behaviour, B) active behaviour, C) association with foster mother behaviour, D) feeding and drinking, and E) socio-positive behaviour in D and D troop once released into the enclosure

I found seven studies on fostering in the literature for comparison with my study on vervet monkeys (Table 6). All studies focused on different methods for hand-rearing or behaviours observed during or after hand-rearing. The success rate of my study was 89% (eight of the nine of orphans in my studied successfully released into their respective troops). I could only find one vervet study done on vervet monkey orphaned young (Anon 2018) to compare my study to. The comparison of behaviour was made between offspring reared by biological mother and orphans brought into the centre reared by humans. Orphaned young was kept in a stage called Kindergarten and surrogate cage. The study was deemed successful and human-rearing a viable option for orphaned young,

A study on baboons *Papio cynocephalus* by Coelho *et al.* (1984) on peer-rearing (i.e. young being reared with other young with little to no human or mother interaction) compared to mother-reared infants, and differences were reported in allo-grooming and hold behaviours (holding a part of another baboons body), mother-reared infants had a higher mean compared to peer-reared offspring. There was little to no human contact. The success was not described as a numeric value sincee the study focused on the behaviours of the offspring and how did observed behaviours differ between mother-reared offspring and peer-reared offspring.

Champoux *et al.* (1991) compared human-reared to mother-reared rhesus macaques *Macaca mulatta*. Human- reared infants were more active and had more self-directed behaviours in larger groups compared to being mother-reared. This study suggests that mother rearing was more successful in normal behaviour.

In another study of rhesus macaques, Rommeck *et al.* (2009) investigated rearing techniques in a nursery, focusing on different peer- rearing techniques with basic human care. The amount of human minding was a month long but human interaction was only limited to feeding and changing diapers of young. Young exhibited abnormal behaviours such as floating limb, self-biting, or motor stereotypes. The success was dependant on behaviour exhibited due to the different methods of rearing but mostly abnormal behaviour was observed.

van Ijzerndoorn *et al.* (2008) testing attachment and cognitive development in nursery reared infant chimpanzees *Pan troglodytes*. They compared two methods of care, i.e. standard care (i.e. focused on peer-rearing with human-minders providing basic care) or responsive care (i.e. extra care given to young from human- minders) up to one years old. Standard care was given to chimpanzees that were placed in the nursery after one day of birth. Responsive care was given to chimpanzees placed in the nursery at birth. Chimpanzees in responsive care showed less attachment to objects. All chimpanzees showed typical cognitive development. The success was of the study was dependant on the type of care given to the young but was not numerically reported. Responsive care was more successful for cognitive development in young.

Abello and Colell (2009) studied the integration of gorilla *Gorilla gorilla* offspring of younger than one year old with foster mothers. Younger gorillas adapted to the foster mothers quicker and adults guided young behaviourally when they displayed inappropriate gorilla behaviour often acquired from being reared by humans. The study was considered completely successful with a 100% adoption rate of young into an established captive gorilla troop.

Using a cross fostering technique, Fontenot *et al.* (2004) studied the behaviour of rejected African green monkeys *Chlorocebus sabaeus* offspring. Offspring were introduced to females (name species) with their own neonates. This fostering method eliminated human-minding and lessened the risks of abnormal behaviour during development. This method reported a 75% success rate.

Table 6. Comparison of methods of seven studies for fostering/rearing primate offspring.

	The Vervet Monkey Foundation – Vervet monkeys	Bambelela Wildlife Care and Vervet Monkey Rehabilitation – Vervet monkeys	South- west Foundation for Research and Education – Baboons	Rhesus Macaques	California National Primate Research Centre - Rhesus Macaques	Great Ape Nursery - Chimpanzees	Barcleona Zoo - Gorillas	African Green monkey
Behaviours observed	Inactive, active, association with foster mother, feed and drink, allo-grooming, socio-positive, socio-negative, interactions with people, self-grooming, and abnormal	Aggression, drink, feed, forage, groom, locomotion, play, rest, social interaction, vigilance, and vocalisation.	Allo-groom, hold, muzzle-muzzle, touch, ear flatten, follow, lip smack, and social approach.	Sleep, nurse, environmental exploration, locomotion, self-mouth, self-clasp, self-scratch, motion, spasm, and vocalization.	Floating limb (e.g. limb moving of own accord), self-bite, play, aggression, cling, gecker (high-pitched vocalization), self-stimulation, and motor stereotypes.	Age appropriate behaviour, object attachment, distress reactions.	Gorilla appropriate behaviour.	General, and mother-young- directed behaviour.
Phases of integration	Phase 1: Quarantine, Phase 2: Disneyland, Phase 3: Integration cage with human-	Kindergarten, and surrogate cage.	Phase 1: Peer pairs Phase 2: New social groups.	Phase 1: Neonate peer rearing. Phase 2: Placed in two- peer only groups.	Phase 1: Removal of infants from mothers. Phase 2: Restricted human handling.	Phase 1: Nursery care. Phase 2: Standard care or responsive care.	Phase 1: Habituation to new surroundings. Phase 2: Visual contact. Phase 3: Introduction to conspecifics.	Phase 1: Removal of rejected young. Phase 2: Introduction to foster mothers

	minder, Phase 4: Introduction to adult females Phase 5: Release into troop.			Phase 3: Social group placement.	Phase 3: Pairing young with other young. Phase 4: Permanent housing in pairs.	Phase 3: Outdoor enclosure	Phase 4: Introduction of infant and foster mother to group. Phase 5: Observation of interactions.	
Ages of infants	Staring ages range from 3 weeks – 8 weeks old	Unknown (not reported)	Starting age <1 day old	Starting age <1 day old	Starting age <1 day old	Staring age range from <1 day to 12 weeks old	Starting age ranged from 3 to 8 months	Starting age 1 to 5 days old
Level of human-minding weighting	1	Unknown (reported as high human interaction)	0	1	1	4	4	0
Outcome								
Study success	89%	Successful	Behaviour dependant	Behaviour dependant	Behaviour dependant	Behaviour dependant	100%	75%
Conducted by:		Unknown	Coelho *et al.* (1984)	Champoux *et al.* (1991)	Rommeck *et al.* (2009)	van Ijzerndoorn *et al.* (2008)	Abello and Colell (2009)	Fontenot *et al.* (2004)

Responses to alarm calls

I recorded a total of 70 minutes of behavioural responses to predator alarm calls. Of these, 30 minutes were for the Goliath troop, 40 minutes for the D and D troop. Number of tests and behaviours are described in Table 7.

Table 7. Number of tests for predator alarm call type and the behaviours observed before, during, and after alarm call playback.

Individual	**Alarm call type**	**Number of times tested**	**Behaviours exhibited before, during and after alarm call playback**
Zoro	Leopard without visual stimulus	6	Feeding and drinking, socio-positive, inactive, and active.
	Leopard with visual stimulus	1	Socio-positive, active, and inactive.
Zoro	Snake without visual stimulus	1	Active, and inactive.
	Snake with visual stimulus	3	Feeding and drinking, active, and inactive.
Dana	Leopard without visual stimulus	4	Active, feeding and drinking, socio-positive, and inactive.
	Leopard with visual stimulus	1	Inactive, and active.
Dana	Snake without visual stimulus	2	Active, and feeding and drinking.
	Snake with visual stimulus	4	Active, feeding and drinking and inactive.
Maggie	Leopard without visual stimulus	5	Inactive, active, and feeding and drinking.
	Leopard with visual stimulus	2	Active and inactive.
Maggie	Snake without visual stimulus	4	Feeding and drinking, active and inactive.
	Snake with visual stimulus	1	Feeding and drinking.
Tammy	Leopard without visual stimulus	2	Active, feeding and drinking, and inactive.
	Leopard with visual stimulus	5	Feeding and drinking, active and inactive.
Tammy	Snake without visual stimulus	4	Feeding and drinking.

	Snake with visual stimulus	2	Feeding and drinking, active and inactive.
Chica	Leopard without visual stimulus	1	Feeding and drinking, active and inactive.
	Leopard with visual stimulus	7	Feeding and drinking, socio-positive, active, and inactive.
Chica	Snake without visual stimulus	4	Inactive, feeding and drinking, and active.
	Snake with visual stimulus	7	Feeding and drinking, socio-positive, active and inactive.
Cheyenne	Leopard without visual stimulus	1	Active and feeding and drinking.
	Leopard with visual stimulus	3	Feeding and drinking, and active.
Cheyenne	Snake without visual stimulus	2	Feeding and drinking, and active.
	Snake with visual stimulus	5	Feeding and drinking, socio-positive, active and inactive.
Kiki	Leopard without visual stimulus	2	Active, socio- positive, and inactive.
	Leopard with visual stimulus	6	Feeding and drinking, active and inactive.
Kiki	Snake without visual stimulus	3	Feeding and drinking, allo-grooming, and active.
	Snake with visual stimulus	3	Feeding and drinking, and active.
Fiona	Leopard without visual stimulus	1	Socio-positive.
	Leopard with visual stimulus	4	Feeding and drinking, active and inactive.
Fiona	Snake without visual stimulus	6	Active, feeding and drinking, and inactive.
	Snake with visual stimulus	5	Active, feeding and drinking, allo-grooming and socio- positive.

Table 7 shows the responses to alarm calls produced to a leopard and snake without and with visual stimuli. The number of times each orphan was tested was used to calculate the percentage of occurrences. The percentage of occurrences each orphan changed behaviours from before to during to after playback of alarm calls varied from 50% to 100% (Table 8.1). In Goliath troop, orphans generally changed their behaviours but with visual stimulus they always changed their behaviour. Zoro changed his behaviour from before, to during, to after the alarm call played most frequent without visual stimulus, then Maggie and Dana changed behaviour the least number of occurrences. No infant spent time with their foster mother before, during or after the alarm call. Orphans spent time with other individuals in the troop either before, during, and/or after the alarm call was played; these behaviours included allo-grooming and socio-positive behaviour. In most occurrences, Zoro spent was with other troop members without visual stimulus and with visual stimulus, Dana spent fewer number of occurrences than Zoro with other individuals in the troop without visual stimulus but was not with troop members when the visual stimulus was presented, and Maggie was not with troop members without and with visual stimulus.

For D and D troop, orphans generally changes their behaviour with visual stimulus (Table 8.1) Chica changed her behaviour the most without visual aid followed by Cheyenne, Tammy and Kiki; Fiona not change her behaviour (Table 8.1). During calls with a visual stimulus, Tammy changed her behaviour the most followed by Cheyenne, Kiki and Chica; Fiona changed her behaviour the least. Fiona had the highest number of occurrences spent with troop members followed by Kiki, but Tammy and Chica. Cheyenne was not with other troop members when calls were played back without a visual stimulus. With a visual aid stimulus, Chica had some occurrences with other troop members while no other orphans had occurrences with other troop members.

Chi-square analyses for leopard alarm call on the behaviour of orphans is shown in Table 8.2. In Goliath troop, the change of behaviour from before to during to after the alarm call playback, was significant for Zoro without a visual aid stimulus. For Maggie, change of behaviour was significant with the calls only. No orphan showed significant changes in behaviour when they were with the foster mother with or without the visual stimulus. For the number of occurrences spent with another troop member, only Dana showed a significant change in behaviour when a visual stimulus was present.

In the D and D troop, there was no significant difference for changes in behaviours without a visual stimulus (Table 8.2). Tammy, Chica, Cheyenne, and Kiki showed significant changes in behaviours when a visual stimulus was present. No orphan showed significance in the time with the foster mother with or without the visual stimulus. Only Chica showed significant changes in behaviour during the time with other individuals in the troop (Table 8.2).

Table 8.1. Percentage of occurrences individual vervet monkeys changed their behaviour and was with the foster mother or another individual before, during and after the leopard call playback alone and with a visual stimulus.

		Changed behaviours from before to during to after		Spent with a foster mother before, during and after		Spent with another individual before, during and after	
Troop	Individual	Call alone	With visual stimulus	Call alone	With visual stimulus	Call alone	With visual stimulus
Goliath	Zoro	94	100	0	0	11	33
	Dana	50	100	0	0	7	0
	Maggie	73	100	0	0	0	0
D and D	Tammy	50	93	0	0	0	0
	Chica	100	76	0	0	0	5
	Cheyenne	67	89	0	0	0	0
	Kiki	50	87	0	0	50	0
	Fiona	0	75	0	0	100	0

Table 8.2. Chi-squared test for leopard alarm call without and with visual stimulus, for Goliath and D and D troop. Changes in behaviours, time spent with foster mother, and time spent with another individual before, during and after the alarm call playback. Significant values are shown in bold. NA = no statistics possible.

		Change in behaviours from before to during to after				Spent with a foster mother before, during and after				Spent with another monkey before, during and after			
		Call alone		With visual stimulus		Call alone		With visual stimulus		Call alone		With visual stimulus	
		x^2	p	x^2	p	x^2	p	x^2	p	x^2	p	x^2	p
Goliath	Zoro	**14.2**	**<0.001**	3	0.083	0	NA	0	NA	0.67	0.413	0.33	0.566
	Dana	0	NA	3	0.083	0	NA	0	NA	**8.33**	**0.004**	0	NA
	Maggie	3.27	0.071	**6**	**0.014**	0	NA	0	NA	0	NA	0	NA
D and D	Tammy	0	NA	**11.27**	**0.001**	0	NA	0	NA	0	NA	0	NA
	Chica	3	0.083	**5.76**	**0.016**	0	NA	0	NA	0	NA	**17.19**	**<0.001**
	Cheyenne	0	0.564	**5.44**	**0.020**	0	NA	0	NA	0	NA	0	NA
	Kiki	0	NA	**8.07**	**0.005**	0	NA	0	NA	0	NA	0	NA
	Fiona	0	NA	3	0.083	0	NA	0	NA	3	0.083	0	NA

Table 8.3 shows responses to the alarm calls produced to a snake. For the snake predator alarm call Goliath troop, orphan generally changed behaviour with visual stimulus. Zoro and Dana had the same number of changed behaviour while Maggie did not change her behaviour without visual stimulus (Table 8.3). With visual stimulus Zoro changed his behaviour the most followed Dana and Maggie with the same proportion of behaviour changed. No orphan spent time with their foster mother before, during or after the alarm call payback. None of the Goliath troop infants spent time with other individuals and Dana was the only infant to spend some time with troop members with visual stimulus.

In D and D troop, orphans generally changed their behaviour with visual stimulus present. Cheyenne change her behaviour from before, during to after the alarm call most frequent without visual stimulus followed by Fiona, Kiki and Tammy and Chica having the same number of change of behaviour (Table 8.3). With visual stimulus Chica had the highest number of change of behaviour followed by Cheyenne, Tammy, Fiona and Kiki had the lowest. Kiki was the only orphan that was with other troop members without visual stimulus. With visual stimulus Cheyenne and Fiona was with other individuals in the troop followed by Chica. Tammy and Kiki was not with other troop members.

Table 8.3. Percentage of occurrence individual vervet monkeys changed their behaviour and was with the foster mother or another individual before, during and after the snake call playback alone and with a visual stimulus.

		Change behaviours from before to during to after		Spent with a foster mother before, during and after		Spent with another monkey before, during and after	
Troop	Individual	Call alone	With visual stimulus	Call alone	With visual stimulus	Call alone	With visual stimulus
Goliath	Zoro	67	100	0	0	0	0
	Dana	67	83	0	0	0	8
	Maggie	0	83	0	0	0	0
D and D	Tammy	42	83	0	0	0	0
	Chica	42	90	0	0	0	10
	Cheyenne	67	87	0	0	0	20
	Kiki	44	67	0	0	33	0
	Fiona	50	80	0	0	0	20

Chi-square analyses for snake alarm call on the behaviour of infants is shown in Table 8.4. None of the Goliath troop orphans significantly changed their behaviour from before to during to when a call alone was played (Table 8.4). However, all three showed significant changes in behaviour when a visual stimulus accompanied the call. No infant showed significant changes in behaviour during the time they spent with the foster mother or another monkey (Table 8.4).

In the D and D troop, there was no significance for change in behaviours for all infants when a call only was presented (Table 8.4). Chica, Cheyenne, and Fiona showed significant changes in behaviours when a stimulus was presented. No infant showed significant changes in behaviour during the time with foster mother with or without the visual stimulus. In addition, no infant showed significant changes in behaviour during the time spent with other troop members when calls only were played. When a visual stimulus was presented, With the visual stimulus, Chica, Cheyenne, and Fiona showed significant changes in behaviour during their time with other troop members (Table 8.4).

Table 8.4. Chi-squared test for snake alarm call without and with visual stimulus, for Goliath and D and D troop. Changes in behaviours, time spent with foster mother, and time spent with another individual before, during and after the alarm call playback. Significant values are shown in bold. NA = no statistics possible.

		Changed behaviours from before to during to after				Time spent with a foster mother before, during and after				Time spent with another monkey before, during and after			
		Call alone		With visual stimulus		Call alone		With visual stimulus		Call alone		With visual stimulus	
		x^2	p	x^2	p	x^2	p	x^2	p	x^2	p	x^2	p
Goliath	Zoro	0.33	0.566	**9.00**	**0.003**	0	NA	0	NA	0	NA	0	NA
	Dana	0.67	0.413	**5.33**	**0.021**	0	NA	0	NA	0	NA	**8.33**	**0.004**
	Maggie	0	NA	**5.33**	**0.021**	0	NA	0	NA	0	NA	0	NA
D and D	Tammy	0.33	0.566	2.67	0.102	0	NA	0	NA	0	NA	0	NA
	Chica	0.33	0.566	**13.76**	**0.000**	0	NA	0	NA	0	NA	13.76	<0.001
	Cheyenne	0.67	0.613	**8.07**	**0.005**	0	NA	0	NA	0	NA	**5.4**	**0.020**
	Kiki	0.11	0.413	1.00	0.317	0	NA	0	NA	3.00	0.083	0	NA
	Fiona	0	NA	**5.40**	**0.020**	0	NA	0	NA	0	NA	**5.4**	**0.020**

I next focused on the responses of orphans during the time when alarm calls (with and without visual stimuli) were played. For the leopard predator, in the Goliath troop, responses to the alarm call alone was recorded on 14 occasions without visual aid. Individuals were startled but continued their previous activity on 20% of the 14 occasions, ran to cover in the trees at 53% of the 14 occasions or displayed no reaction 27% of the 14 occasions. With the visual stimulus, reactions were recorded on four occasions in all individuals. On all four occasions, infants ran for in the trees.

During the leopard alarm call playback in the Goliath troop, Maggie had the highest proportion of startled and orientation response when calls alone were played, followed by Zoro and Dana (Table 8.5). With accompanying the visual stimulus, none of the orphans showed startled and orientated towards the stimulus responses. Dana did not react to the alarm call alone compare to the other two orphans. Including the visual stimulus, none of the orphans showed a no response (i.e. all responded). When calls alone were played, Zoro and Maggie responded by running to the cover of the trees, and with the inclusion of a visual stimulus, Zoro, Dana and Maggie responded by running to the trees for cover. None of the orphans was in an observational stance with or without the visual stimulus (Table 8.5).

In the D and D troop, responses to the leopard predator alarm call alone was recorded on seven occasions. Individuals were startled but continued their previous activity on 29% of the seven occasions or displayed no reaction to the alarm call on 71% of the seven occasions reaction. With the visual stimulus, reactions were recorded on 24 occasions, with orientation toward source was occurring on 13% of 24 occasions, individuals ran for cover in the trees on 83% of 24 occasions, or displayed no reaction to the alarm 4% of 24 occasions (Table 8.5). For the D and D troop, no orphans was observed startled and orientated toward the source of the calls alone (Table 8.5). Chica, Cheyenne and Kiki were startled and orientated toward the source of the call accompanied by the visual stimulus. Tammy, Kiki and Fiona did not respond to the alarm call without visual the stimulus. With the visual stimulus, Tammy had a low percentage(20%) of not responding to the alarm call. Without the visual stimulus, no orphans ran to the cover of the trees. With the visual stimulus, however, all orphans ran to the cover of the trees. None of the orphans were in an observational stance with or without the visual stimulus (Table 8.5).

Table 8.5. Responses to alarm call during leopard alarm call for Goliath and D and D troop.

		Startled and orientated (combined)		No response		Ran to tree cover		Observational stance	
Troop	Individual	Call alone	With visual stimulus	Call alone	With visual stimulus	Call alone	With visual stimulus	Call alone	With visual stimulus
Goliath	Zoro	13	0	0	0	83	100	0	0
	Dana	0	0	100	0	0	100	0	0
	Maggie	40	0	0	0	60	100	0	0
D and D	Tammy	0	0	100	20	0	80	0	0
	Chica	0	14	0	0	0	86	0	0
	Cheyenne	0	33	0	0	0	67	0	0
	Kiki	0	20	100	0	0	80	0	0
	Fiona	0	0	100	0	0	100	0	0

Chi-squared analyses for the leopard alarm call responses showed that, in the Goliath troop, no orphan showed a significant startle response and orientated towards the call with and without the visual stimulus (Table 8.6). In addition, there was no significant occurrence of no response, running for cover adopting an observational stance. Similar, non-significant occurrences for all variables occurred in the D and D troop (Table 8.6).

Table 8.6. Chi-squared test done for responses to leopard alarm call with and without visual stimulus for Goliath and D and D troop. Significant values are shown in bold. NA = no statistics possible.

		Individual was startled and orientated (combined)				No response				Individual in tree cover				Observational stance			
		Call alone		With visual stimulus		Call alone		With visual stimulus		Call alone		With visual stimulus		Call alone		With visual stimulus	
Troop	Individual	x^2	p	x^2	p	x^2	p	x^2	p	x^2	p	x^2	p	x^2	p	x^2	p
Goliath	Zoro	2.67	0.102	0	NA	0	NA	0	NA	0.09	0.764	1.00	0.317	0	NA	0	NA
	Dana	0	NA	0	NA	3.00	0.083	0	NA	0	NA	1.00	0.317	0	NA	0	NA
	Maggie	1.29	0.257	0	NA	0	NA	0	NA	0.20	0.655	0	0	0	NA	0	NA
D and D	Tammy	0	NA	0	NA	2.00	0.157	1.80	0.180	0	NA	1.80	0.180	0	NA	0	NA
	Chica	1.00	0.317	3.57	0.059	0	NA	0	NA	0	NA	3.57	0.059	0	NA	0	NA
	Cheyenne	1.00	0.317	0.33	0.564	0	NA	0	NA	0	NA	0.33	0.566	0	NA	0	NA
	Kiki	0	NA	1.80	0.180	2.00	0.157	0	NA	0	NA	1.80	0.180	0	NA	0	NA
	Fiona	0	NA	0	NA	1.00	0.317	0	NA	0	NA	4.00	0.046	0	NA	0	NA

For all the snake predator alarm calls alone, in the Goliath troop, responses were recorded on three occasions. Individuals were startled but continued their previous activity on one of the three occasions, orientated toward the source one of the three occasions, and did not respond on one of the three occasions. With the visual stimulus, reactions were recorded on 11 occasions. Of these, individuals orientated towards the stimulus source on 18% of 11 occasions, ran to covers in the trees on 55% of 11 occasions, observational stance was recorded on 18% of 11 occasions, and no response to the alarm call was recorded on 9% of 11 occasions.

In the Goliath troop, Zoro and Dana responded with startled and orientating towards the alarm call alone (Table 8.7). With the visual stimulus, Dana and Maggie showed a startled response and orientated towards the call. Dana did not respond to the alarm call alone. With the visual stimulus, Maggie did not respond while the alarm call played. For calls alone, no orphan responded to the alarm call by running to the cover in the trees, and with the visual stimulus, Zoro, Dana and Maggie responded by running to the trees for cover. None of the orphans adopted an observational stance when calls only were played. With the visual stimulus, only Dana responded by adopting an observational stance (Table 8.7).

In the D and D troop, responses were recorded on 19 occasions to the call alone. Individuals were startled on 21% of 19 occasions, orientated toward the source on 11% of 19 occasions, ran for cover in the trees on 5% of 19 occasions, adopted an observational stance on 5% of 19 occasions, and displayed no reaction to the alarm call was on 58% of 19 occasions. With the visual stimulus, reactions were recorded on 22 occasions. Individuals were recorded startled on 23% of 22 occasions, orientated toward the source on 27% of 22 occasions, orientated toward the source on 27% of 22 occasions, ran to the cover of the trees on 23% of 22 occasions, adopted an observational stance on 23% of 22 occasions, or showed no reactions on 4% of the 22 occasions.

For the D and D troop, Chica, Cheyenne, Kiki and Fiona were startled and orientated toward the alarm call source played alone (Table 8.7). Kiki and Fiona were startled and orientated toward the source of the call and the visual stimulus. Tammy, Chica, Kiki, and Fiona did not respond to the alarm call alone. With the visual stimulus, only Kiki did not of not respond to the alarm call. During calls alone, Fiona was the only infant that ran to the cover of the trees, and when there was the visual stimulus, Chica, Cheyenne and Fiona ran to the cover of the trees. Fiona was the only infant to adopt an observational stance to the alarm calls alone. Chica, Kiki and Fiona were adopted an observational stance to calls and the visual stimulus (Table 8.7).

Table 8.7. Responses to alarm call during snake alarm call for Goliath and D and D troop.

		Startled and orientated (combined)		No response		Ran to tree cover		Observational stance	
Troop	Individual	Call alone	With visual stimulus	Call alone	With visual stimulus	Call alone	With visual stimulus	Call alone	With visual stimulus
Goliath	Zoro	100	0	0	0	0	100	0	0
	Dana	50	25	50	0	0	25	0	50
	Maggie	0	25	0	25	0	50	0	0
D and D	Tammy	0	0	100	0	0	0	0	0
	Chica	50	0	50	0	0	14	0	29
	Cheyenne	100	0	0	0	0	60	0	0
	Kiki	33	33	67	33	0	0	0	33
	Fiona	17	40	50	0	17	20	17	40

Chi-squared analyses for the snake alarm call responses showed that that no orphan in the Goliath and D and D troops showed a significant behavioural responses to the alarm call alone or accompanied by the visual stimulus (Table 8.8). Tammy (D and D troop) was the only orphan who showed a significant response by not reacting to the call alone (Table 8.8).

Table 8.8. Chi-squared test done for responses to snake alarm call with and without visual stimulus for Goliath and D and D troop. Significant values are shown in bold. NA = no statistics possible.

		Individual was startled and orientated (combined)				No response				Individual in tree cover				Observational stance			
		Call alone		With visual stimulus		Call alone		With visual stimulus		Call alone		With visual stimulus		Call alone		With visual stimulus	
Troop	Individual	x^2	p	x^2	p	x^2	p	x^2	p	x^2	p	x^2	p	x^2	p	x^2	p
Goliath	Zoro	0	NA	0	NA	0	NA	0	NA	0	NA	3	0.083	0	NA	0	NA
	Dana	0.33	0.566	1	0.317	0	NA	0	NA	0	NA	1	0.317	0	NA	0	NA
	Maggie	0	NA	1	0.317	0	NA	1.00	0.317	0	NA	0	NA	0	NA	0	NA
D and D	Tammy	0	NA	2	0.157	**4**	**0.046**	0	NA	0	NA	1.8	0.180	0	NA	0	NA
	Chica	0	NA	0.14	0.706	0	NA	0	NA	0	NA	3.57	0.059	0	NA	1.29	0.256
	Cheyenne	2	0.157	0	NA	0	NA	0	NA	0	NA	0.2	0.655	0	NA	0	NA
	Kiki	0.33	0.566	0.33	0.566	0.33	0.566	0.33	0.566	0	NA	0	NA	0	NA	0.33	0.566
	Fiona	2.67	0.103	0.2	0.655	0	NA	0	NA	2.67	0.102	1.8	0.180	2.67	0.102	0.2	0.655

Discussion

The aim of my study was to assess the success of the fostering protocol implemented by the Vervet Monkey Foundation to foster orphaned vervet monkey offspring to conspecific females in established troops. The Foundation adopted a step-wise process of integration, comprising of a quarantine phase to a Disneyland phase to develop independent bottle feeding, an integration phase to assist in the adoption of a foster vervet monkey female, and finally release into the troop of the foster mother. I observed and recorded the behaviours of eight orphans from their integration to release into one of two troops: the Goliath and the D and D troops.

The Goliath troop was presented with four orphans in the integration cage during my study. Three orphans, Dana, Maggie and Neville, shared one foster mother in the integration cage and Zoro was adopted by another foster mother. Only three orphans were released into the Goliath troop: Zoro, Dana, and Maggie. In D and D troop, five orphans were presented to females in the study. Tammy and Chica shared a foster mother, Fiona was adopted by a single foster mother, Kiki and Cheyenne shared a foster mother in the integration cage, but when Cheyenne was released into the troop, she was fostered by another female. The success of the fostering protocol was 89%, with Neville not being released into Goliath troop but being adopted into another troop within the Foundation.

The orphans in the Goliath troop had similar duration of inactive behaviour for their three weeks in the integration cage, and the duration of inactivity of all orphans decreased over the three weeks in the integration cage. Once released into the troop, Dana and Maggie had a similar duration of inactive behaviour to each other, and Zoro had the lowest duration in the first week of release. During the second week, all three had a similar duration of inactive behaviour. The duration of inactivity decreased from the first to second week of observations. The D and D troop orphans varied in their inactive behaviour duration in the integration cage in each week of observation. The duration of inactive behaviour decreased over the three weeks. Once released into the troop, the orphans varied in their inactivity. The duration of inactive behaviour decreased over time in all orphans except for Fiona whose duration increased from the first week to the second week.

The duration of active behaviour in the integration cage increased from week one to week two and decreased in week three for Goliath troop orphans. Once released into the troop, two of the three orphans released, Zoro and Maggie, had higher duration of active behaviour than that of the other orphan, Dana. Over time, active behaviour decreased for all orphans. In the D and D troop, the duration of active behaviour varied between individuals, with activity generally decreasing over time. Once released into the troop, individuals again varied in the activity patterns, and activity decreased from the first week to the second week of observation. The study period was during summer with temperatures that ranged from 26ºC to 35ºC during the day time. Menbere and Balakrishnan (2016) investigated how different habitat types influenced vervet monkey activity and inactivity and found that vervet monkeys were more active in the morning and late afternoon when the temperatures were lower. I conducted my research during the warmer periods of the day between 8am and 4pm, which could explain the low activity behaviours of the vervet monkeys in my study.

The association with the foster mother behaviour in Goliath troop varied between the individuals while in the integration cage, and the duration of this behaviour decreased for each individual. Once released into the Goliath troop, one individual, Maggie, had low duration of association with foster mother. Over time, the duration of the association with foster mother decreased. In D and D troop, the association with foster mother also varied between individuals, and there was a decrease in the association with the foster mother for all individuals, except for Chica who had an increase in her association with the foster mother. Once released into the troop, the association with the foster mother again varied between individuals in the first week of release and decreased to no association with foster mother a week later, except for Kiki whose association with the foster mother increased.

All foster mothers were adults that had previous fostering experience (as per information from The Vervet Monkey Foundation), so the decrease in association was not due to the lack of experience of foster mothers. The reduction in association did not influence the successful adoption of orphans, supporting the findings of a study on captive vervet monkeys by Hauser and Fairbanks (1988). Instead, the reduced association resembles the situation of free-living vervet monkeys (Struhsaker 1971). My findings thus suggest that offspring reduced their association with the foster mother because of their growing independence (Stovall–McClough and Dozier 2004), and a reduction in their initiation of contact with the mother, as demonstrated in chimpanzees (Yamamoto *et al.* 2009) and vervet monkeys (i.e. reduced grooming as infant becomes older Struhsaker 1971).The orphans were up to five months old at the end of the study which matches the growth phase and emerging independence of young vervet monkeys (Struhsaker 1971). Another important consideration is that the foster mother was not lactating and young fed on provisioned food, which would have reduced their contact between offspring and the foster mother (Rosenblum and Andrews 1994). Another consideration is that primate mothers modify their contact with their offspring as offspring age, such as when infants seek comfort and sucking (in free-roaming infants) (Barrett *et al.* 1995).

All Goliath troop individuals showed similar feeding and drinking behaviour in the three observation weeks. In week two, the duration of feeding and drinking behaviour increased and then decreased in week three. Once released into the troop, individuals varied in their feeding and drinking behaviour in each week of observations, which also decreased over time. In the D and D troop, the duration of feeding and drinking behaviour varied between individuals in each week of observation, and also showed a decrease over time. Over time, feeding and drinking behaviour decreased. The changes in feeding could be related to a stress response (i.e. often reducing feeding bouts; Connan and Treasure 1998). However, the changes in levels of feeding were variable by week and were not associated with any observable stress. The reasons for the changed in feeding and drinking were not apparent.

Allo-grooming behaviour in the Goliath troop differed among the individuals, and decreased over time. Once released into the troop, only Dana did not engage in allo-grooming behaviour, while a decrease in this behaviour occurred over time. In the D and D troop, individuals also differed in their allo-grooming behaviour and a decrease in this behaviour was seen in the second week, with Tammy engaged in allo-grooming. Once released into the D and D troop, individuals varied in their duration of allo-grooming behaviour, which decreased in the second week. A decrease in allo-grooming has been found to accompany the aging of the offspring. In a study on lesser bush babies *Galago senegalensis moholi*, Doyle *et al.* (1969) found that allo-grooming decreased as offspring became older, which was linked to their growing independence.

Socio-positive behaviour in the Goliath troop orphans also varied between individuals in the integration cage for all three weeks of observations. The duration of socio-positive increased in week two compared to week one and then decreased in week three. Once released into the enclosure, the duration of socio-positive behaviour varied between individuals in the first week of release. Over time, there was a decrease in socio-positive behaviour for Zoro and Maggie but an increase for Dana. In the D and D troop, individuals varied in their socio-positive behaviour, which also decreased from week one to week two. Once released into the troop, a similar pattern of individual variation and decrease over time was observed. Struhsaker (1971) also observed a decrease in socio-positive behaviour as individuals aged in free-roaming vervet monkey offspring. The decrease could be linked to the fact that the first week of introduction or release into the troop could have been highly stressful for the offspring. Thus, the level of socio-positive behaviour could be a coping mechanism as suggested by Cheney and Seyfarth (2009).

For the Goliath troop, socio-negative behaviour varied for all individuals in the integration cage. Socio-negative behaviour was not observed when orphans were released into the troop. In the D and D troop, Tammy, Chica and Cheyenne displayed socio-negative behaviour in the first week but not the second week. Once released into the troop, Cheyenne was the only individual that displayed socio-negative behaviour but showed no socio-negative behaviour in the last week of observation. The display of socio-negative behaviour, such as biting other individuals, fighting and displaying teeth in a "grin", from the different individuals in the integration cages could be a possible result of stress of the new environment (Ellis *et al.* 2011). Isbell (1991) maintained that female primates have increased socio-negative behaviour while they become accustomed to increasing group size (i.e. new members coming into the group).

In Goliath troop, orphans varied in the duration of self-grooming over the observation weeks. When orphans were released into the enclosure, Dana was the only individual to display self-grooming behaviour during the last week of observation. Chica and Cheyenne of the D and D troop were the only orphans observed self-grooming. In the second week, no self-grooming was observed. Isbell and Young (1993) observed increased self-grooming in larger groups of free-roaming vervet monkeys, possibly due to greater parasitic load. Higham *et al.* (2009) suggest that there is a possible stress link to self-grooming, as seen in olive baboons *Papio hamadryas anubis.* Whether one or both of these factors (parasite load or stress) are potential causes of self-grooming requires further investigation.

In the integration cage for the Goliath troop, Zoro displayed abnormal behaviour (i.e. sucking of digits) in the first week and showed none in the last week of observations; other individuals showed no abnormal behaviours. No abnormal behaviour was observed once orphans were released into the troop. In the D and D troop, only Chica and Kiki displayed abnormal behaviour (i.e. sucking of digits) which decreased over time. Once released into the enclosure, Kiki was the only individual displaying abnormal behaviour (i.e. sucking of digits) but no abnormal behaviour was observed in the last week of observation. Hosey (2005) suggested that abnormal behaviour was related to stressors of unfamiliar housing environments. This might also explain the findings here but the general low incidence of abnormal behaviour indicates the orphans were not prone to developing abnormal behaviour during my sampling period.

Overall, there appeared to be a general decrease in all behaviours in the sampling period. This could be a consequence of the high ambient temperatures reducing general activity. In addition, the decrease could indicate developing social stability in the groups following introduction of the orphans (Olsson and Westlund 2007). Often when there is an increase in stress or social instability, there will be a decrease in social behaviour but an increase in socio-negative or abnormal behaviour (DeVries *et al.* 2003) and vice versa (Panksepp *et al.* 1980). The low duration of socio-negative, possibly self-grooming and abnormal behaviour also suggest a low stress environment, suggesting a positive outcome of the fostering protocol used and that group stability was not negatively affected (Dazey *et al.* 1977).

I compared the fostering protocol of the Foundation to that of published studies. I found seven studies for comparison. Generally, the outcomes of my study compared favourably with the other studies in terms of the success of fostering. I report the success (if known) and outcomes of these studies below. However, it must be noted that the differences in the studies could be because of species differences as well as unreported protocols as well as environmental and social influences on the fostering processes.

The only vervet monkey study available for comparison mentioned successful fostering but no success level was reported (Anon, 2018). The starting ages of the orphaned offspring ranged from three weeks to eight weeks in my study, which were not reported in the other vervet study. At the Foundation, the intention was to minimise human intervention, whereby human-caregivers cared for orphans and trained them to drink formulated milk in baby bottles in feeding cages (Disneyland) mainly, whereas the other study focused on human-minding offspring, where humans cared for and reared orphans and also surrogate reared offspring where female vervet monkeys were given orphans as soon they arrived at the centre (Anon 2018). If the success rate of that study was as high as assumed by the author/s, it suggests that the protocol of rearing (greater or lesser human contact; different times of presentation to foster females) is not important for successful adoption of vervet monkeys.

In a study of yellow baboons *Papio cynocephalus*, the success was not reported numerically but was based on the behaviours observed (Coelho *et al.* 1984). Baboon young were peer raised with other baboon young of the same age. The success of the study reported that behaviours seemed age-appropriate for baboons but there was a lack of strong bonds in early development in social groups (Coelho *et al.* 1984). As the success was based on behaviours observed (interpreted as normal for baboons) and no human contact occurred (compared to the three month human rearing in my own study), it suggests that peer-rearing young is a possible avenue of rearing offspring but the outcome of this rearing will need to be studied in vervet monkeys.

In African green monkeys *Chlorocebus sabaeus*, offspring that were rejected by mother were given to a foster mother (Fontenot *et al.* 2004). The success rate of that study was 75%. There was no human interaction. The starting age ranged from one to five days old in the study (age of orphans in my study ranged from three weeks old to eight weeks old). Since the success rate of the study was lower than that of my study, the differences could be differences in protocol or even starting age of young at fostering.

In a study of gorillas *Gorilla gorilla*, the success level of adoption was 100% (Abello and Colell 2009), higher than the 86% in my study. Human-minding was a year and higher than my study's three month human-minding. The starting age of the gorillas ranged from three to eight months old. The introduction protocol to females was similar to my study. Since the success levels of that study was higher than that of my study, the greater level of human care does not seem to affect adoption at least in gorillas.

In a study on chimpanzees *Pan troglodytes,* the success was not reported numerically but reported as a success of the behaviours observed in different rearing protocols (Ijzerndoorn *et al.* 2008). Human interaction was one year long, higher in comparison to the three months of my study. The starting age ranged from new born to 12 weeks old; not overtly different to my study. The study reported that offspring given more care from human-caregivers showed fewer abnormal behaviours in later stages of development, suggesting that a longer period of human-rearing could result in more well adapted offspring if no conspecifics foster females were available for adoption

I found two different studies on Rhesus macaques *Macaca mulatta* for comparison. In both studies, the success level was not reported numerically but behaviours outcomes were reported. The first study used a similar level of human interaction as in my study (about three months) (Champoux *et al.* 1991). Offspring were all new born and younger than those in my study (ranging from three weeks to eight weeks). The focus of integration was on peer-raising and low human care and no adult conspecific female care). The young developed undesired abnormal behaviour (Champoux *et al.* 1991). The other Rhesus macaques study also reported on behavioural outcomes (Rommeck *et al.* 2009). Human contact was for a shorter period of one month but human-rearing was limited to changing diapers and feeding orphans. For this study, offspring were new born. The integration was peer-reared with offspring of the same age group. Orphans again developed abnormal behaviours, suggesting that peer-rearing is not successful.

The predator alarm call response study was used as another measure of success for the fostering of orphaned young at the Vervet Monkey Foundation. I predicted that newly fostered offspring would seek the protection of the foster mother or another troop member when the predator alarm call was played back to the troops. Briefly, offspring did not seek protection of adults when the predator alarm calls were played back with or without visual stimuli. However, they did change their behaviour before, to during, to after the alarm calls to a leopard and snake was played.

I generated three hypotheses to explain the lack of association with their foster mother in alarm call experiments. 1) The age of the offspring suggest that they were independent and not reliant on their foster mother. Lowland gorilla *Gorilla gorilla gorilla* offspring decreased contact with the mother (even during threats) as they became older (Hoff *et al.* 1981). In my study, there was already a decrease in association with the foster mother when offspring where released into the troop enclosure, which might explain why offspring did not seek them out during alarm call playback experiments. 2) There could perhaps been no bond/trust between the adopted offspring and the foster mother. This assumption is difficult to assess, though, since it is not always easy to identify measures of trust in primates (Maestripieri 2001). 3) There is a possibility offspring perceived the predator alarm calls as novelty and not as a threat. Magrath *et al.* (2008) found that fairy-wrens *Malurus cyaneus* responded to the novelty of honeyeater *Phylidonyris novaehollandiae* alarm calls which were not perceived as a response to potential threat. It is also possible that offspring could not associate the alarm calls produced by vervet monkeys not from their own troop as a response to a threat, as suggested by Oda and Masataka (1996) in ringtailed lemur *Lemur catta*. In addition, the response to alarm calls could be learned over time if perceived as novelty. Fischer *et al.* (2000) found that infant baboons *Papio cynocephalus ursinus* take time to learn predator alarm calls.. Fischer *et al.* (2000) found that infant baboons *Papio cynocephalus ursinus* take time to learn predator alarm calls.

For the leopard alarm call with and without the visual stimulus, orphans of both the Goliath and the D and D troop showed both observational (i.e. startled and orientated toward the source of the alarm call, and observational stance) and predator avoidance responses (i.e. ran to cover of the trees) to the alarm calls. For alarm calls alone, orphans made observational responses or no response to the alarm call on its own. With the visual stimulus, for both Goliath and D and D troop orphans showed observational and predator avoidance responses and no response to the alarm call. For the snake alarm call with and without a visual stimulus, both the Goliath and D and D troop orphans showed observational and predator avoidance response as well as no response to the alarm call. For calls alone, observational responses observational and predator avoidance responses were observed. Seyfarth *et al.* (1980a) observed free-roaming vervet monkeys to show mainly observational responses to snake alarm call and a rarely running to the cover of the trees. In my study, I observed orphans in an observational stance more commonly when visual stimulus was absent and with visual stimulus offspring ran to the tree cover more often.

In both troops, it appeared that responses to predator alarm calls were more frequent or heightened when calls were accompanied by a visual stimulus. This does not necessarily imply that the inanimate visual stimulus was threatening but rather that both acoustic and visual stimuli illicit behavioural responses to alarm calls (Verhall and Luksch 2016). In contrast, Seyfarth *et al.* (1980a) and Seyfarth and Cheney (1990) observed that free-roaming vervet monkeys ran to the cover of the trees when a vervet alarm call for a leopard predator was played-back without visual stimuli.

The general lack of responses in some orphans (during leopard and snake alarm call without visual stimulus) could be because they did not associate the alarm call with a threat but as a novelty as suggested above. Moreover, young might rely on cues from older individuals to respond to particular cues. For example, Seyfarth and

Cheney (1986) showed that vervet monkey offspring responded to alarm calls by first observing adults' reactions, which could explain the no responses observed to both alarm calls in my study. The behaviour of adults was not documented in any detail in my study, so I cannot comment on whether offspring cued onto the behaviour of adults.

Conclusion

The fostering protocol at The Vervet Monkey Foundation was considered successful from the high success of adoptions. I recorded the behaviours of fostered offspring alone and with the foster female as finer scale markers of adoption success. Behaviours of the orphans that indicate success of the fostering protocol were a reduction in socio-negative behaviour and a virtual absence of abnormal behaviour. In addition, orphans showed active behaviour, association with the foster mother, feeding and drinking, and socio-positive behaviour. The responses to the alarm call were age appropriate even though newly fostered orphans did not seek out the foster mothers while the alarm call played.

Fostering is not a common occurrence in primates since it is considered costly to the individual (Stanford 1992), and is perhaps non-adaptive (Roulin 2002). One could consider hormonal priming (e.g. through oxytocin and vasopressin) as modulators of adoption (Pedersen and Prange 1979). However, since none of the females were bred by the Foundation and none had their offspring at the time of adoption, hormonal priming is an unlikely explanation. Another interesting consideration is the oestrous cycle of the female vervet monkeys, since the females become socially motivated, associated with an increase in oestradiol (Rapkin *et al.* 1995). Interestingly, an increase in oestradiol has been linked to females being more accepting of offspring in macaques *Macaca fuscata* (Bardi *et al.* 2001). By rotating individual female vervet monkeys into and out of the integration cage by Foundation staff might have serendipitously paired an orphan with a willing female at an appropriate hormonal state for accepting an orphan. However, little to no research on hormonal influences on adoption in vervet monkeys is known. All female foster mothers had previous experience with fostering which possibly might have also contributed to females being motivated to foster orphans.

Overall, orphans appeared to integrate well into the two troops, and I cannot tell 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 adoption. In comparing my study with other studies, I found that the duration off human-care was less important when fostering orphans to adult females but the protocol used (human, peer, older conspecifics) was important in the development for appropriate behaviours. An important caveat to the my assumptions is that studies of fostering and rehabilitation of primates do not report success levels, making it challenging to compare and evaluate success rates. In addition, consequent behavioural development of fostered young are not often reported. Nonetheless, the high success rate in my study provides a useful benchmark for future comparative studies. Moreover, the protocol reported here has conservation salience for primates generally and vervet monkeys particularly.

I suggest that future studies should consider alternative protocols (human-minders, conspecific foster mothers) conducted in the same rehabilitation centres to assess their efficacy on a particular target species (i.e. to assess if some protocols are better than others). The fostering protocol used by the Foundation should also be repeated at different vervet monkey rehabilitation centres to assess whether the protocol adopted is widely applicable. For the alarm call playback experiments, there is a need for better recording equipment and visual stimuli and collection of alarm calls from the troops into which orphans are released.

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