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The adoption process of a hand-reared chimpanzee infant

A behavioural study of a captive group

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Abstract

Adoption and alloparental care are found in a wide range of animals, including numerous anthropoid species. Considering the high cost of caring for an infant other than your own, the adaptive significance is poorly understood. Here, I describe a study of the introduction and subsequent adoption of a one-year old hand-reared female chimpanzee (*Pan troglodytes*) infant into a captive group of conspecifics at Furuvik Zoo, Gävle, Sweden. I also discuss possible adaptive explanations for this adoption occurrence. Behavioural data on the integration and adoption process was collected over nine consecutive weeks. Frequency and time dedicated to infant care exhibited by group members was examined, as well as the infant's secure base behaviour. An adult primiparous female chimpanzee adopted the infant and thus an attachment figure shift occurred from human to chimpanzee. However, the female initially showed very limited interest in the infant. It was, in fact, two other younger female group members who showed most interest and cared for the infant at first. The infant's secure base behaviour patterns (examined by proximity to attachment figure, bout frequency and duration) show that the infant got more secure as the integration progressed. This study shows that an individual who initially exhibits most care does not necessarily become the adopter in the end and that there is a behavioural flexibility in displaying maternal motivation in adult chimpanzee females. These findings contribute to a better understanding of introduction procedures and attachment in chimpanzees and can also give insights in foster mother – infant relationships.

Contents

Introduction

Permanent adoption and alloparenting care are found in a wide range of animals, including numerous anthropoid species (for reviews see Theirry & Anderson, 1986; Hrdy, 1976). Adoption and caregiving behaviour are known to be costly activities, both in terms of time investment and energy expenditure. Therefore, it could be argued that adoption presents an example of altruism and can thus be difficult to explain with classic evolutionary theory (Reidman, 1982). Consequently, questions about the adaptive significance and evolution of the phenomenon arise: why would an individual invest in an infant, other than their own, considering the substantial costs? What are the benefits?

For a behaviour to be adaptive and persist in a population, it has to provide benefits through direct or inclusive fitness, which outweigh the costs involved (Hamilton, 1964). The benefits of getting adopted seen through an orphan's perspective are pretty clear: food, protection, transportation etc. (Thierry & Anderson, 1986). The advantages seen from an adopter's perspective are, however, less obvious. The costs seem to be higher, especially those that affect reproduction. Many primate species that exhibit adoption typically have slow reproductive life traits, such as delayed reproductive and social maturity, single births, long interbirth intervals, high parental investment and prolonged infant dependency (Reidman, 1982; Kennedy, 2005). An adoption might therefore implicate a huge cost for the adopter and interfere with the adopter's reproductive effort and ultimately reduce its fitness.

Adoption and alloparental care have been studied for a long time (Reidman, 1982; Hrdy, 1976; Lancaster, 1971; Thierry & Anderson, 1986; Maestripieri, 1994.), yet the mechanisms involved and the function of these behaviour are poorly understood. Several hypotheses have been proposed to explain these types of behaviour, including kin-selection theory, which is based on that the adopter increases its inclusive fitness by caring for an infant other than its own, provided that the adopter is related to the infant in question (Theirry & Anderson, 1986). Yet other cases might reflect gaining of valuable maternal skills, the so called "learning to mother"-hypothesis (Lancaster, 1971; Hrdy, 1976). It has also been suggested that some adoptions might reflect a "reproductive error" from the foster mother's side, that the tendency to give care to neonates is a by-product of otherwise adaptive mechanisms. Naturally, there is no single evolutionary hypothesis that explains every case of adoption and adaptive explanations for adoption differ depending upon the caregiver (Gould, 2000).

An area of study closely related to adoption and allomothering is the processes affecting mother – infant attachment. In order for an adoption to occur, there has to be a change or shift of attachment from the primary caregiver, the mother, to another attachment figure (Dolhinow & DeMay, 1982). Bowlby (1969) developed a theory, called Attachment Theory, aimed at explaining attachment patterns between a human infant and its primary caregiver, particularly the mother. This gave rise to extensive research on the attributes, strengths, and other aspects of attachments among human (Ainsworth 1969; Ainsworth & Bell, 1970; Bowlby, 1969, 1973, 1980) and non-human primates (Harlow *et al*., 1965; Kaufman & Rosenblum, 1967; Suomi *et al*., 1973; Maestripieri, 2001b; Ferrari *et al*., 2009). Maternal deprivation, contact, mutual gaze, proximity and approaches are all measurements that have been examined to give a reflection of the characteristics of attachment and loss. Ainsworth, who extended the Attachment theory, worked particularly with early emotional attachment and with the so called "strange situation procedure", which examines patterns of attachment between a parent and a child (Ainsworth & Bell, 1970). Ainsworth coined the term "secure base" which describes an infant's characteristic behavioural pattern of exploration of its

surrounding environment by making short trips away from the mother, returning back and moving away again with the mother as a secure base (Ainsworth & Bell, 1970; Okamoto-Barth *et al*., 2007). This type of exploring behaviour is present when the infant is comfortable in a setting and is less likely to be there if the infant is sick, anxious, tired or insecure (Okamoto-Barth *et al.*, 2007).

There are many similarities in attachment patterns between humans and apes. Human infants, as well as ape infants, will show less attachment behaviour towards their mothers as they mature, since the number of situations that activate the attachment system decrease (Broberg *et al*., 2006). The circumstances which activate the attachment system in apes are basically the same as in humans, and include separation, hunger, pain and fear (Okamoto-Barth *et al*., 2007; Broberg *et al*., 2006). It has also been shown that human-reared chimpanzee infants use their primary caregiver as a secure base when exploring novel environments (Miller *et al*., 1986).

Here, I describe a study of the introduction of a one-year old hand-reared female chimpanzee (*Pan troglodytes*) infant into a captive group of chimpanzees at Furuvik Zoo, in Gävle, Sweden. The infant, a female named Selma, was born at Kolmården Zoo in June 2008. Her mother showed no caregiving behaviour and rejected her. The infant had to be removed from her natal group and reared by human caregivers until the infant was old enough to get integrated into the chimpanzee group at Furuvik Zoo. Behavioural data was collected on the integration and adoption process over nine consecutive weeks. Frequency and time dedication of infant care behaviour exhibited by group members was examined as well as the infant's secure base behaviour.

Objectives and hypotheses

The overarching aim of this paper is to present a unique case of introduction process of a chimpanzee infant into a new group. I present a behavioural study of this introduction with focus on caregiving behaviour exhibited by group members and infant secure base behaviour. In addition, I will discuss adaptive explanations for this particular case of adoption.

Since it was not clear from the beginning of the introduction which individual would become the adopter of the infant, the first objective was to examine this aspect. My hypothesis was that there would be a difference in care behaviors exhibited between the individuals in the group and that there would be one individual who would display the highest frequency of infant care and dedicate most time to this activity from the beginning. This individual, according to my prediction, was most likely to become the infant's primary caregiver. Continuous-time animal data on frequency and duration of caregiving behaviour were collected to examine this (Altman, 1974).

The second objective addressed the infant's outwardly signs of confidence and attachment with the primary caregiver. I examined this by looking at the infant's secure base behavior as it provides unambiguous data on the infant's state of security; exploring and playing behaviour are exhibited by an infant when it is comfortable in a setting, and absent otherwise. In turn, this data can give an indication on how well the introduction progress and enable one to see the infant's shift of secure base over the course of the integration period, from human caregiver to chimpanzee. My prediction was that in a successful integration the

infant would become more secure and it would explore its surroundings more frequently and for longer periods of time as well as increase the distance away from the attachment figure (in this case a human caregiver for the first half of the study period and an adult female chimpanzee for the second half).

This study extends our knowledge in both introduction procedures in chimpanzees as well as providing useful information and better understanding of foster mother – infant attachment in non-human primates (hereafter, primates). I will use adopter, foster mother and primary caregiver interchangeably.

Theoretical background

Adoption and alloparenting

Interactions with primate infants by group members can range from mere interest, to caregiving activities such as carrying or grooming, to long-term adoption involving suckling (Clarke & Glander, 1981). In a wide range of primate species all over the world adoptions and alloparenting have been reported and documented; in the wild as well as in captivity. It has been observed in species such as vervet monkeys (*Cercopithecus aethiops*) (Lancaster, 1971), baboons (*Papio ursinus,*) (Hamilton *et al*., 1982), macaques (*Macaca mulatta*) (Berman, 1982), howler monkeys (*Alouatta palliata*) (Clark & Glander, 1981), ring-tailed lemur (*Lemur catta*) (Gould, 2000) and chimpanzees (*Pan troglodytes*) (Goodall, 1986; Nishida, 1983).

Alloparenting is described as the phenomenon when an individual, other than the genetic parent, provides care for a conspecific young (Wilson, 1975). This may also include adoption, which according to Reidman (1982) is when an individual provides exclusive care for another's offspring. It could, however, be argued that this definition is overrestrictive since many cases of adoption in nonhuman primates involve several individuals (Thierry & Anderson, 1986). There are some common reproductive and social features that characterize species that exhibit adoption and alloparental behaviour, most of which are associated with K-selected species. These are, in accordance with Reidman (1982):

(1) production of a single offspring;
(2) prolonged or energetically intensive parental investment;
(3) limited lifetime reproductive output;
(4) small groups with tight kinship bonds;
(5) highly social or cooperative group structure; and
(6) young that are raised in high-density breeding colonies.

For chimpanzees, which this paper will focus on, all of the features correspond, except the last one.

To restrict and simplify the present discussion of adoption, a few preconditions are recognized, stated by Thierry & Anderson (1986). These are: a) adoption is unidirectional: the adopter gives care and the adoptee receives it. Therefore, attachments between same-aged orphans or between peer-reared infants, do not count as adoption. b) only immature individuals – specifically infants and juveniles – can be adopted. c) cross-species adoptions are excluded.

Adoption occurrences

Adoptions might arise in varying contexts. In the wild, spontaneous adoptions might occur if a genetic parent of a young dies, for example, due to predation, injury or disease (Thierry & Anderson, 1986). Temporary or "transient" adoptions might also occur, typically in situations when a mother of an infant is alive but sick, injured or removed from the group. However, temporary adoptions could also take place in kidnapping scenarios (Hrdy, 1976; Silk, 1980b). A kidnapping occurrence is usually transitory and the infant is typically returned or retrieved by the mother. If this is not the case, the infant often dies, usually through starvation (Quiatt, 1979). In rare situations, kidnapping leads to permanent adoption (Thierry & Anderson, 1986).

There are also manipulated adoptions where infants get introduced to new caregivers. These manipulated adoptions often take place in captive settings, like the present case. The orphaned infants might have been rejected by their mother from birth or their mother might have been unable to care for them due to circumstances mentioned earlier. The orphaned infants are typically hand-reared for a period of time before being introduced to conspecifics. Ideally, resocialization of infants with conspecifics should take place as soon as possible to promote species-typical behaviour and social learning (Porton & Niebruegge, 2006). Spontaneous mother – infant swapping is also a type of adoption that might occur, albeit rarely. It has been reported for example in a captive group of lowland gorillas (*Gorilla gorilla gorilla*) (Nakamichi *et al*., 2007).

Who adopts?

When adoption of an orphaned primate occurs, it is typically a relative of the infant who becomes the adopter. Sisters, aunts, or sometimes even grandmothers have been reported to adopt, both in captivity and in the wild (Quiatt, 1979; Nozaki, 2009; Wroblewski, 2008; Ing-Marie Persson, pers. comm.). For unweaned infants, mothers who already have a newborn and are lactating are most likely to adopt (Quiatt, 1979). In other cases the female adopters have recently lost their newborn (van Wulfften Palthe & van Hooff, 1975), or are in late stages of pregnancy. Nulliparous females i.e. females that have never borne offspring, present an example of individuals that are especially prone to allomother (Quiatt, 1979). They sometimes also adopt, given that individuals who already are secondary caregivers tend to become primary caregiver if something happens to the biological mother (Uehara & Nyundo, 1983). Older infants or juveniles, on the other hand, usually get adopted by individuals other than adult females. They are actually more likely to be adopted by juveniles or subadults, who often are known or assumed to be related to the adoptee (e.g., Berman, 1982; Goodall, 1986). There are also cases where adult males have been reported to adopt juveniles or older infants (Boesch *et al*., 2010). Although genetic relations usually are unsure, male adopters are sometimes assumed to be the adoptees' fathers (Theirry & Anderson, 1986).

Who gets adopted?

The mere presence of a solitary infant does not necessarily cause group members to exhibit caregiving behaviour towards it (Clarke & Glander, 1981). An adoptee's behaviour and initiative on getting adopted, by vocalizing and being persistent in contact seeking, is therefore an important contributing factor to a successful adoption (Dolhinow & DeMay, 1982). Thierry and his colleagues (1984) suggest that the protest and despair-reactions an infant displays after the loss of its mother can be an approach to solicit care and to invoke a response from other conspecifics. If an orphan does not try to seek substitute care from other

members, the infant may not get adopted (Clarke & Glander, 1981). Studies on howler monkeys (*Alouatta palliata*), show that a non-vocalizing infant has a low chance of getting rescued in threatening situations, (e.g. if it falls out of a tree, engages in too rough a play or gets left behind) if it does not solicit care (Clarke & Glander, 1981).

There are other examples where adoption of an orphan never takes place, despite efforts from the adopter. One explanation for such a scenario might be the adverse reactions an infant can experience due to the loss of its mother. Harlow's classic experiments in the 1960's on maternal deprivation in rhesus macaques (*Macaca mulatta*), had a big influence in the evolving science of attachment and loss, and gave insights in the importance of an attachment figure. Signs of depression due to maternal deprivation might entail; lack of playing, increasing self-directed activities, increased isolation and, related to this discussion; indifference to the adoptive mother (Dolhinow, 1980).

Caregiving behaviour

The care behaviour associated with adoption is similar to alloparental or allomothering care behaviour. They include nursing, carrying, grooming, cuddling, proximity during foraging or travel, protecting and nest-sharing, but not necessarily all of them (Thierry & Anderson, 1986). These activities contribute to and reflect the strong social tie between the adopter and the adoptee. However, these activities represent costs of some kind (Theirry & Anderson 1986). Lactating is, for example, very energetically costly (Kennedy, 2005). An unweaned infant is extremely vulnerable, and an orphaned infant with no alternative source of milk from a substitute caregiver, has a low chance of survival (Theirry & Anderson 1986). For orphaned, unweaned chimpanzees below the age of 4.5, this probability of mortality is high (Goodall, 1986).

Foster mother-infant relationship

Research in mother – infant attachment is extensive. A related subject matter is the relationship between a foster mother and an adoptee. It has, for example, been investigated whether there are any differences between how a biological mother treats her biological infant compared to a foster infant (Ellsworth & Andersen, 1997; Maestripieri *et al*., 2000; Fontenot *et al*., 2004). Ellsworth and Andersen's (1997) examined cases where rhesus macaque mothers both had a biological offspring and an adopted "twin". The results showed that the biological infants spent more time in maternal contact than their adopted "twin" siblings and that the latter spent less time in ventro-ventral position than the genetic offspring when having contact with the mother. The mothers also initiated contact more frequently with the biological infant. This correlation of giving more care to the biological offspring has also been reported in Japanese macaques (*Macaca fuscata*). A female who adopted a newborn two days after the birth of her own infant, gave more care to her own infant. For example, she retrieved her own offspring during aggression while the adoptee had to follow (Kurokawa, 1974 cited in Thierry & Anderson, 1986). However, when a foster infant is adopted without the presence of a biological "sibling", foster mother – infant relationship seem to substitute fully for that of mother – offspring (Berman, 1982; de Waal, 1982).

Study species

Reproduction

Chimpanzees are characterized, amongst other things, by their social complexity, tool use and multi-male multi-female societies with fission-fusion structures (Goodall, 1986). They also have a slow reproductive life history with delayed reproductive and social maturity, with females reaching sexual maturity between 9–13 years of age (Jones *et al*., 1996; Goodall, 1986). Females provide the bulk of the parental care and very strong social bonds are formed between females and their offspring. The offspring is highly dependent on the mother for approximately 5–6 years with a prolonged learning period, hence long interbirth intervals. Chimpanzees typically raise a single offspring, with a gestation period between 202–260 days (mean 230 days) and the offspring is weaned between the age of 30–54 months. This long period of dependency of the mother is the main reason why chimpanzees up to 4 years old are termed "infants" (Uehara & Nyundo, 1983). The age when female chimpanzees typically give birth for the first time differ largely. Wild female chimpanzees have been reported to give birth to their first infant between the ages of 11–23 years. However, well fed female chimpanzees in captivity usually have their first infant at 10.5–11.5 years of age. They also reach sexual maturity earlier than their wild conspecifics. Nishida *et al*., (2003) report that the lifetime reproductive output for wild chimpanzee females of the Mahale Mountains National Park, Tanzania was on average 3.9. Though males do not provide any direct parental care for young, they provide indirect care through protection for the young. It is not unusual either that males play with young members of the group and treat them gently, especially if they have a white tail tuft. This tail tuft signals their young age and it gradually disappears at approximately 4–5 years of age (Goodall, 1986).

Infant development

In chimpanzees, the offspring is carried ventrally by the mother for approximately 3–6 months, after which it gradually starts to ride on the mother's back more frequently. By the age of 1.5 years, the infant is independent enough to spend about 25 % of its awake time away from its mother, playing and exploring, but frequently returning to its mother for comfort. By the age of 3 the infant spends more time further away from its mother, but continues to sleep by her side during the nights and rides on her back when travelling longer distances (Broberg *et al*., 2006). It is not until 4–7 years of age that the juvenile becomes independent enough to travel, eat and sleep by itself. However, it continues to visit its mother regularly, even in adulthood and after the mother has had new offspring. Chimpanzee-, bonobo- and gorilla mothers are not reluctant to these visits, in contrast to many monkeys, like macaque- and baboon mothers (Broberg *et al*., 2006).

Offspring will develop socially as a member of its mother's lineage, which is also the case for adopted infants (Thierry & Anderson, 1986). It has been suggested that rank is not technically inherited from the mother to the offspring, but that a mother's behaviour and interactions with other group members affect the rank of the offspring. A high ranking mother is relaxed and confident, and is therefore likely to have offspring who behave in the same fashion. Subsequently, this correlation works the other way around too; offspring of nervous mothers may not do well in dominance competitions, and therefore typically get a lower rank (Goodall, 1986).

Hypotheses for adoption

Considering the cost and the big investment that caring for an infant entail, adoption or allomothering of an infant other that your own, seems illogical. What could an individual gain? Below, I take a closer look at hypotheses that have been proposed to explain these types of behaviour.

Kin selection

The kin selection hypothesis for adoption is based on the possibility that the foster mother increases her inclusive fitness by caring for an infant other than her own, provided that the she is related to the infant in question. This is in line with classic kin-selection theory (Hamilton, 1964). Usually, this correlation between adopter and adoptee is seen in chimpanzees (Goodall, 1986; Nishida, 1983; Wroblewski, 2008), where the foster mother typically is known or suspected members of the same matriline as the adoptee, often individuals with 50 or 25 % of their genes in common. However, this is not necessarily always the case. An experimental study of hanuman langurs (*Presbytis entellus*) by Dolhinow and DeMay (1982) showed that even though the adoptee was related to individuals in the group, unrelated individuals became adopters.

The fact that humans and chimpanzees are genetically very similar and share evolutionary history (humans and chimpanzees diverged from a common an ancestor approximately 5-7 million years ago), makes comparisons of similar behaviour intriguing and interesting. For example, Joan Silk (1980a; 1987) has examined the nature of adoption in humans. She studied the occurrence of adoption in 11 different cultures in Oceania, and examined relatedness of the foster parent and the adoptee. Her findings showed that most cases of adoptions were highly kin-based and that adoptees typically were related to the foster parents in varying degrees (Silk, 1980a). These results support the kin selection hypothesis, and cast doubt on the view that adoption is mainly cultural based. Nevertheless, Silk found that a minority of adopters in Oceania do adopt children they are not genetically related to. One possible explanation for this is that in some agricultural cultures, the benefits (i.e. contributing work force) can outweigh the costs. Silk's prediction for this was that small families should be more likely to adopt than large ones, a predication that was later proven (Silk, 1980a).

"**Learning to mother**"

An alternative hypothesis is the "Learning to mother"-hypothesis and it has received much support for explaining allomothering behaviour. It refers to the maternal skills the allomothers acquire that ultimately makes them more successful themselves when they sire their own offspring (Lancaster, 1971). Another support for the hypothesis is that it usually is nulliparous females who exhibit allomothering behaviour, since they are the ones who typically need the experience. Studies on vervet monkeys also show that offspring of females which had exhibited previous allomothering behaviour had a higher chance of survival (Fairbanks, 1990). Alloparental experience also facilitates the acceptance of an infant in an adoption occurrence, and it is not unusual that individuals who already are secondary caregivers adopt orphaned infants (Uehara & Nyundo, 1983).

Reciprocal altruism

Yet another potential adaptive explanation of adoption invokes reciprocal altruism (Thierry & Anderson, 1986; Trivers, 1971). This refers to the prospect that the adoptee might function as future social support and ally for the adopter, which could be beneficial in situations of conflict or competition. This represents a long-term reciprocal social bond, though another positive aspect of adoption might be immediate, such as warmth or as an "agonistic buffer" (see next section). Reciprocal altruism has been suggested to explain instances when orphaned infants get adopted by elder siblings (e.g. Goodall, 1986). Besides, the cost associated with a sibling adoption might not be that high given that the adopter usually is young and the adoption therefore does not interfere with its reproductive effort. Thierry and Anderson (1986) suggest that the psychological state of an older sibling that adopts might also be a factor contributing to the adoption, considering it has itself lost an important attachment figure and wants replacement.

Social benefits

Primates often live in very socially complex communities and it has been suggested that there may be numerous social advantages for both males and females that adopt (Hrdy, 1976; Riedman, 1982). For example, there is an increased opportunity of becoming a source of interest to others in the group by carrying an infant (Theirry & Anderson, 1986), as well as it can facilitate the integration into a new group. There are also examples of when individuals use infants as a method to reduce the amount of aggression received from other group members (Hrdy, 1976; Riedman, 1982). This phenomenon has been reported in for example male baboons (*Theropithecus gelada*) (Dunbar, 1984) and macaques (*Macaca thibetana*) (Ogawa, 1995) and it is called "agonistic buffering" or triadic interactions. It usually occurs when subordinate males feel threatened and pick up infants and thus become less vulnerable to attack from other males (Dunbar, 1984). Mothers or allomothering primates also get infant-related benefits, such as becoming less susceptible to aggression by other group members, getting enhanced social status, and/or getting extra protection from predators (Reidman, 1982). Hrdy (1976) noted, however, that these benefits are more exploited by males than females.

Another possible explanation for adult males to exhibit caregiving behaviour towards infants is that it may be a strategy related to affiliation with adult females which could potentially lead to enhanced mating opportunities and enhancement of rank (Gould, 2000; Reidman; 1982). In humans, it has also been proposed that adoption can be a form of charitable behaviour that raises the social reputation of adopters (Alcock, 2005).

Reproductive error

Finally, there is the possibility that adoption is non-adaptive; that the costs may outweigh the gains. To rear an infant or juvenile despite the high costs, with the possibility of reducing your own fitness, might present a consequence of motivational systems that cause a general desire and a tendency to give care to neonates (Quiatt, 1979). This means that adoption might present behaviour patterns that are a by-product of otherwise adaptive proximate mechanisms (Theirry & Anderson, 1986; Quiatt, 1979; Alcock, 2005). Natural selection has not eliminated this kind of behaviour since it is *usually* adaptive given that adoption is typically kin-directed. Hence selection has favoured individuals who have an attraction to young infants, an important behavioural mechanism increasing inclusive fitness (Theirry & Anderson, 1986). This behaviour of employing generally adaptive parental behaviour in an unusual, non-adaptive fashion is called reproductive error.

It is usually females that are near parturition or that have recently lost their own infant that exhibit these patterns. Theirry & Anderson (1986) suggest that these females are both psychologically as well as physiologically prepared to care for an infant and thus more likely to adopt an infant than other individuals. Maestripieri (1999; 2001a) suggests that the enhanced maternal motivation after during the early postpartum weeks the may depend on the hormonal changes that are associated with late pregnancy, parturition, and lactation, which make sure that mothers take care of their biological offspring. This period is called maternal sensitive period. van Wulfften Palthe & van Hooff (1975) describe a case of adoption of an unrelated infant in captive chimpanzees in which the chimpanzee mother, who had lost her offspring almost immediately after birth, adopted and nursed without problems a five-week-old hand-reared infant. Other examples of this kind of maladaptive application of the parental drive are seen in kidnappings scenarios of unweaned primate infants and some cross-species adoptions. There are, however, examples of when female primates have been able to heighten their maternal motivation and adopt an infant even after the sensitive period (Nakamichi *et al*., 2007). In one unusual adoption case, described by de Waal (1982), a nonlactating chimpanzee female adopted an orphaned infant and learned how to bottle feed it. Initial training was used, though she added her own patterns as the time went on.

Materials and Methods

Study animals and study site

Background

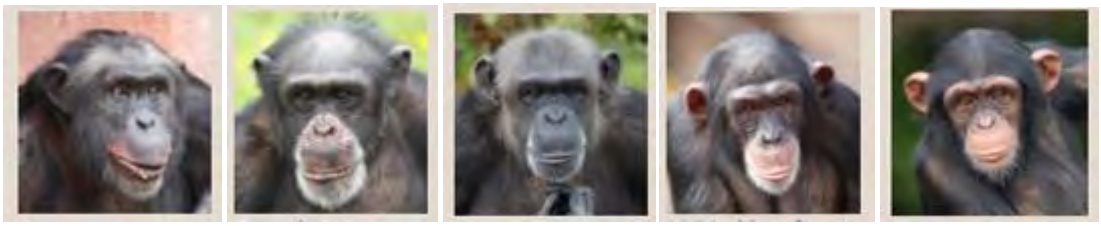
The infant, named Selma, was born at Kolmården Zoo, Sweden, in June 2008. Her mother did not show any signs of caregiving behaviour, apart from occasional carrying of the newborn. For long periods of time she neglected the infant and even loaned her to young males (Ing-Marie Persson, pers comm.). After three days, zoo personnel could finally get Selma out with the help from Selma's grandmother who handed her over. Selma was by then in a very bad condition, with low body temperature and exhausted after being without nourishment and care for several days. Human caregivers had to take over. Ideally, a chimpanzee female who just lost her own infant and was still lactating, would adopt Selma. This was, unfortunately, not possible in this case. Instead, Ing-Marie Persson (IP), head of the primate department at Furuvik Zoo, outside Gävle in Sweden, became Selma's primary caregiver within two weeks from the rejection. In addition, there were several secondary caregivers who stepped in when necessary. Since an almost identical introduction of another infant was carried out successfully approximately four years earlier at Furuvik Zoo, IP was the right person for this job. In addition, IP's relationship to the chimpanzee group at Furuvik Zoo is unique. Even with an adult male in the group, she is able to go into the group and interact with them. This is usually impossible and very dangerous since adult males are typically aggressive and unpredictable. In this case, however, it is possible since IP spent a lot of time with Santino, the male, during his time in quarantine when he first came to the zoo. This ability facilitates introductions of new group members, given that a gradual familiarization from everybody's part is possible. Selma was between 16–18 months of age when the study was conducted. As mentioned earlier, chimpanzee infants are not yet weaned by this age and no female in the present group was lactating. This concern was resolved by bottle feeding several times a day through the enclosure mesh once the new member was fully integrated into the group.

The group

The chimpanzee group (Tab 1. & Fig. 1) consisted of one dominant adult male; (age during study period in brackets): Santino (31), two adult females; Linda (25) and Penny (28), one sub-adult female named Maria Magdalena, but called Magda (9) and one female juvenile; Manda (5). The group members were unrelated to each other and it was a non-reproducing group. The two adult females, Penny and Linda were both primiparous i.e. they have borne one offspring each. Their offspring unfortunately did not survive their first year. Linda was wild-caught and came to Sweden at the age of two. Manda, the group's juvenile, was born at Kolmården Zoo and was the other infant that got introduced into the group in 2005, whereby Linda took on the role as her foster mother. Manda has the same father as Selma.

Table 1. Members of the chimpanzee group

Study animals	**Santino**	**Penny**	**Linda**	**M. Magdalena**	**Manda**
Born	20/4-1978	11/12-1980	Oct-1984	21/9-2000	7/9-2004
Status	Adult male	Adult female	Adult female	Adolescent female	Female juvenile
Dominance rank	Upper	Middle	Middle	Low	Not applicable
No. of prior offspring	0	1	1	0	0
Reared	Hand-reared	Mother-reared	Hand-reared	Mother-reared	Hand-reared



Santino Penny Linda M. Magdalena Manda

Fig. 1.The chimpanzee group in which Selma was introduced at Furuvik Zoo, Gävle, Sweden. Photos: Furuvik Zoo

Facility design

The chimpanzee indoor facility consisted of several enclosures of different sizes interconnected to each other, with possibility of division between them (Fig. 2). This to allow mixed-age and mixed-sex social groups, with room for sub-grouping, isolation and cooperation among members (Coe *et al*., 2001 cited by Patterson, 2003). The building was also connected to two separate outdoor islands. However, since the introduction study took place in the winter, the outdoor area was not used. During the first 4 weeks of the study, an integration enclosure was used, in which the infant and a human caregiver were located (Fig. 2). The room was approximately 3 x 3 m and connected to the other enclosures that the chimpanzee group were in by a little entry through which only Selma could fit (Fig. 2).

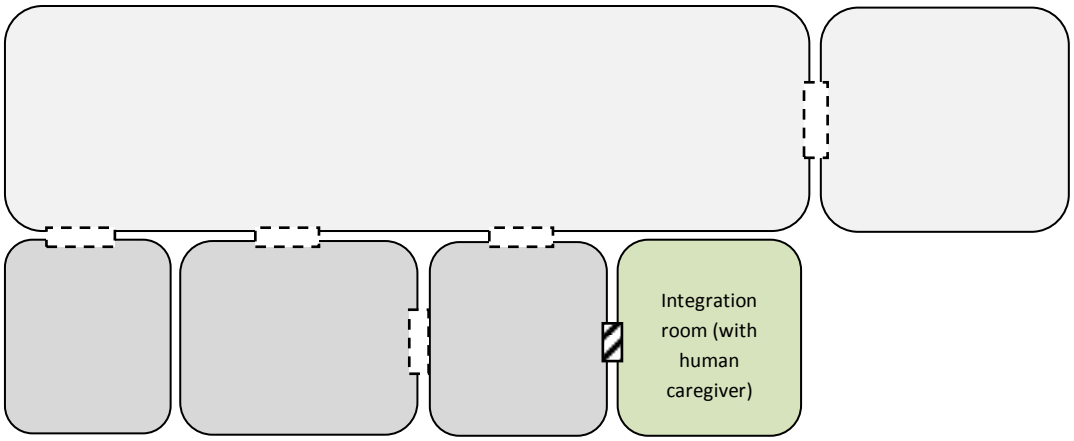


Fig. 2. Generalized scheme of the indoor facility. The dashed lines illustrate closable doors and the diagonal black lines illustrate an open shutter door which only the infant could fit through.

Data collection

Continuous-time animal data (Altman, 1974) were collected three times per week, four hours per day (two consecutive hours before noon, two hours in the afternoon), by myself, using a handheld computer for collecting the data. A total of 108 h of data were collected and analyzed. The study was carried out during Oct–Dec 2009, over a period of nine weeks; four weeks with gradual introduction, (where the infant and a human caregiver were located in the integration enclosure) (Fig. 2), and five weeks where the infant was fully integrated into the new group and had no access to a human caregiver. The observations did not interrupt the daily routines which were carried out as usual and the chimpanzees had to, at least once a day, change enclosures to enable facility maintenance and cleaning. The study was conducted at Lund University Primate Research Station Furuvik and was approved by Uppsala djurförsöksetiska nämnd (Dnr. C199/9, "Observationer av vardagligt och spontant beteende hos schimpans, orangutang och gibbon").

Caregiving behaviour

Frequency and duration of all caregiving behaviour exhibited by the group members were recorded four hours per day. The caregiving behaviour I chose to record consisted of dorsal and ventral carrying, grooming the infant, resting and sitting in contact with the infant, hugging/holding and protecting. No suckling or attempt of suckling was recorded, thus excluded as caregiving behaviour here. Data on social play was also collected. Playing was, however, counted as interest behaviour in contrast to caregiving behaviour (see the separate figures in the result section). Play entailed both rough and gentle activities such as; tickling, holding, wrestling, chasing, play biting, pushing, and swinging the infant. Ad libitum notes were taken as well as contextual data, e.g. visitors, predominant group activity, members present, conflicts and disturbances etc.

The duration of all caregiving behaviour exhibited by the group members was analyzed by adding the time an individual showed caregiving behaviour towards Selma over a three observational days. This sum was then divided by the total time a specific group member's potential interaction time with Selma. Sometimes one or several individuals were separated from the others for a few hours or a day. In addition, the observation time was not always exactly 240 minutes the first four weeks. By using % time as a measure, this difference in interaction time with Selma was accounted for. The data for interest behaviour was analyzed in the same way.

Secure-base behaviour

To examine the infant's secure- base behaviour I measured 1) the number of bouts she made during an observation session, 2) the duration (min) of a bout, 3) the maximum distance (m) from her secure base. I divided the distances into three categories, where 1 = 1–5 m, 2 = 6–10 m, and 3 = 11–15 m represented the distance away from the caregiver. Since the integration enclosure was connected to the others by a little entry through which only Selma could fit, the visits to the other group members were on her terms (whether or not to go in, when and for how long). The criteria for a secure base bout (SBB) with a human caregiver were that the infant had to: a) fully leave the integration enclosure to start a bout (standing in the doorway did not count) b) fully return into the integration enclosure again to terminate a bout.

Checking and waiting outside the entry by the group members occurred frequently during the gradual integration period and data on this behaviour were collected and was included as interest behaviour. This behaviour entailed bending down their head into the entry and look into the integration enclosure where the infant and her human caregiver were (Fig. 3). Sometimes group members also called and/or reached in and made inviting gestures for the infant to come out.

Fig. 3. A group member, Manda, waiting outside the integration enclosure. Photo: Maria Thunström

The five following weeks, in which the infant was integrated into the group with no access to a human caregiver, the infant's secure base behaviour with her new chimpanzee caregiver was examined to see any pattern changes. The criteria for a secure base bout with the

chimpanzee caregiver were: a) letting go of the individual, no contact b) maintaining a distance of more than 1 meter, not sitting or resting a meter away.

Initiation and inhibition

Data on whom or what initiated and inhibited a SBB was also collected, but only the first four weeks of the introduction, when the integration enclosure was used. This was because the different initiation and inhibition factors were too difficult and unclear to distinguish once Selma was fully introduced into the group. For an individual to initiate a SBB, she or he had to influence Selma to come out of the integration enclosure. This entailed waiting outside Selma's entry, and sometimes using gestures and emitting calls (Fig. 3). Selma herself could also initiate a bout. For a bout being induced by Selma, no one had to be outside the enclosure or do anything to influence her to go out. Moreover, for an individual to inhibit a SBB, she or he had to make Selma retreat to her human caregiver in the integration enclosure. There were numerous factors contributing as to why a SBB was terminated: 1) a fast approach or movement by group member, 2) too rough play, 3) loud distress calls, aggression calls, pant hoots etc. emitted by the chimpanzees, and 4) conflicts between group members. There were also other factors that were not group related, but human related, such as conversations, a visit of a caregiver, movements by Selma's caregiver which could be interpreted as if she was leaving.

Results

Descriptive results: Observational data on caregiver shift

The infant's contact with human caregivers was terminated by week 5. From this time point on it was intended that Selma permanently would stay with the chimpanzee group. At this breaking point Selma exhibited acute separation distress. She emitted high distress calls and ran frequently in and out of the integration enclosure, which was still open but with no caregiver present. The other group members seemed confused and stayed in the background and occasionally approached Selma. Linda, on the other hand, periodically followed Selma around and initiated contact, by opening her arms or reaching after her. Selma sporadically sought refuge in Linda, and clung to her back or belly, but it was not until after 45–60 min of exhibiting distress behaviour that Selma clung to Linda almost permanently, though still emitting distress calls. Selma exhibited anxious behaviour for approximately two weeks after the caregiver change, especially when a former human caregiver was sighted or heard. It took approximately four weeks for the infant to display all the normal behaviors that reflect a secure emotional state, such as social- and solitary playing, exploring, eating and be relaxed enough to get groomed by the other group members. By week 8, Selma did not cling to Linda much nor did she emit distress calls, even when a previous human caregiver was present. The most frequent caregiving behaviour exhibited by Linda was dorsal carrying. However, as the introduction progressed, activities such as grooming and playing increased.

Percentage of time and frequency of caregiving behaviour

As noted, a sudden and clear shift of primary caregiver occurred in week 5 when Selma's contact with humans was terminated. As from that point, Linda exhibited more caregiving behaviour towards Selma than any of the other group members (Fig. 4; 5 & 6). The frequency of care-giving behaviour was highly unequal among the five group members (χ^2 = 951.9, P < 0.001) (Fig. 6). Percentage time dedicated to infant care behaviour was also very clear; in week 6, Linda dedicated 75.7 % (~9 hr) of the observation time (12 hr per week) carrying or being in contact with Selma when the same percentage for other group members was close to 0 % (Fig. 4). However, during the initial four weeks with gradual introduction, Linda's participation and interest in Selma was very limited, with an average of 1.1 % time dedicated to infant care. Manda and Magda, on the other hand, exhibited the most caregiving behaviour during the same time period, with an average of 12.6 % and 22.4 % time for respective individual (Fig. 4), which thereafter rapidly declined when Linda "took over". When interest behaviour, such as playing with Selma was accounted for, all the group members had a higher percental value of time dedicated to Selma (Fig. 5). Two weeks into Selma's full integration Santino exhibited aggressive behaviour towards Linda and Selma and was as a result separated from them during week 7, 8 and 9, thus his data is missing at these time points (Fig. 4 & 5).

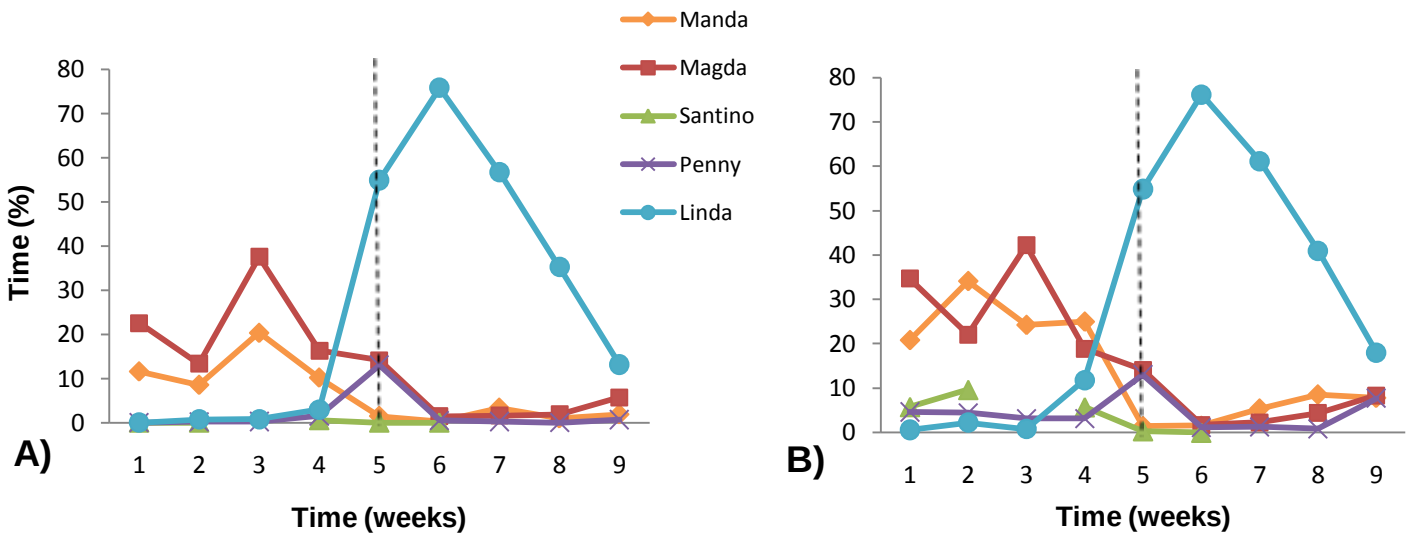


Fig. 4. A) Percentage time a specific group member exhibited caregiving behaviour (grooming, carrying, contact, hugging/holding and protecting) towards Selma over nine consecutive weeks. B) Diagram B combines caregiving behaviour with interest behaviour (such as playing). The dotted line illustrates the point at which Selma's contact with human caregivers was terminated.

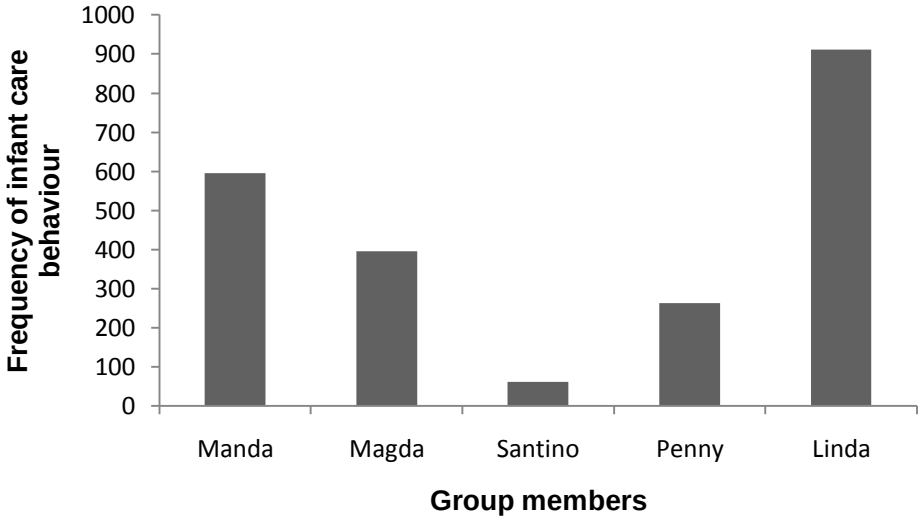


Fig. 6. The frequency of caregiving behaviour exhibited by group members over the nine week study period ($\chi^2 = 951.9$, $P < 0.001$).

Secure base patterns

Duration

The percentage of time that Selma was not in Linda's immediate proximity increased progressively with every week after the caregiver shift (Fig. 7). The last week of the study Selma spent 9 h of the observation time (11 h for that week) interacting with the other group members or exploring the surroundings herself (Fig. 7). The weekly average duration of a SBB also increased over the last five weeks (Fig. 8).

Distance from attachment figure

The number of SBB's with a maximum distance of 11-15 meters from Selma's caregiver increased over the study period ($k = 3{,}55$, $R^2 = 0{,}48$) (Fig. 9). Correspondingly, the number of SBB's with a shorter distance (1-5 meters away from the caregiver) decreased (Fig. 9).

Number of secure base bouts

The number of SBB's was constantly increasing in the beginning of the introduction (except in week 4) and peaked in week 7, with 251 SBB's over a 4-hour period. Then the number steadily decreased over the last two weeks (Fig. 10).

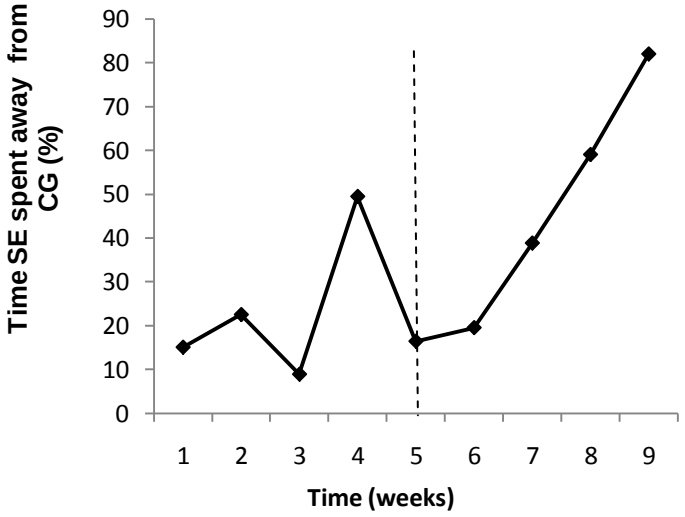


Fig. 7. Percentage time Selma (SE) spent away from her caregiver (CG). The first 4 weeks, the secure base was a human caregiver, the following 5 weeks the secure base was her chimpanzee caregiver Linda.

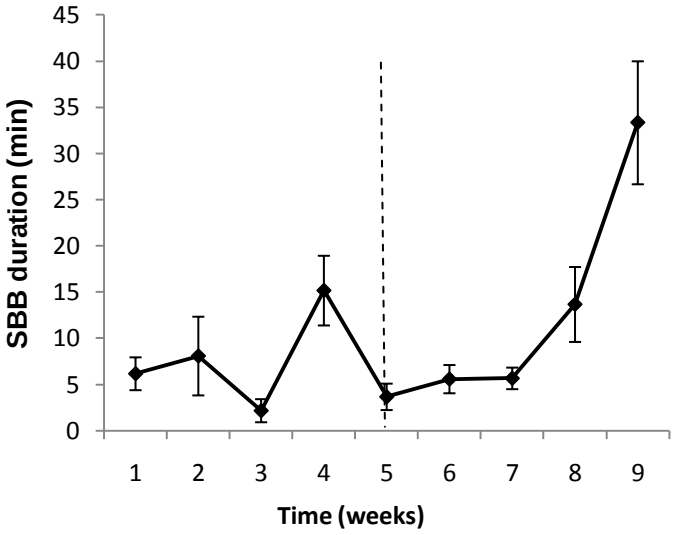


Fig. 8. Weekly average of the longest SBB duration during an observational session (n = 6 per week). Error bars depict standard error of the mean. The dotted line illustrates when the Selmas contact with human carcaregivers ended.

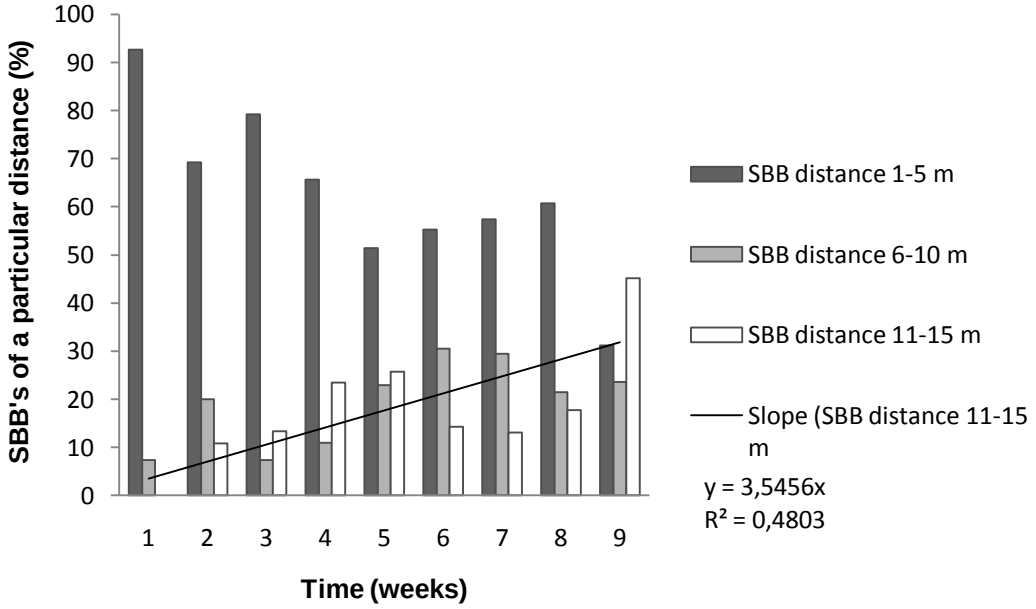


Fig. 9. The difference in secure base bout distance over the study period. The figure shows the percentage of secure base bouts with a particular distance.

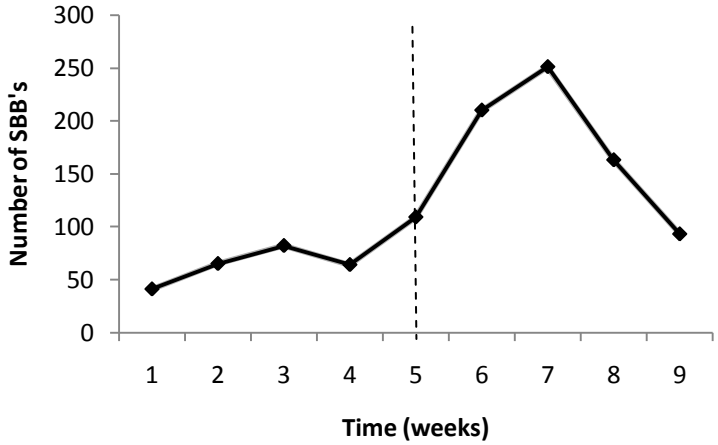


Fig. 10. Sum of SBB's per week. The dotted line illustrates when Selmas contact with human carcaregivers ended.

Initiation and inhibition of secure base bouts

Data on initiation and inhibition of secure base bouts was collected during the four first weeks when the integration enclosure was used. Magda and Manda were the only group members engaging in an initiating behavior, except in week 4 when Linda initiated 1 out of 64 SBB's (Fig. 11). Magda initiated most of the bouts with an average of 26.5 % of the total (compared to Manda's 15.3 %), if you exclude that Selma herself initiated many trips. Magda initiated half of the SBB's the first week (20 out of 41 SBB's) (Fig. 11). Inhibition of secure base behavior was, on the other hand, exhibited by all of the group members. Penny inhibited most SBB's (average of 15.4 %) (Fig. 12), though most of the SBB's were inhibited of other factors such as human induced or it was unknown.

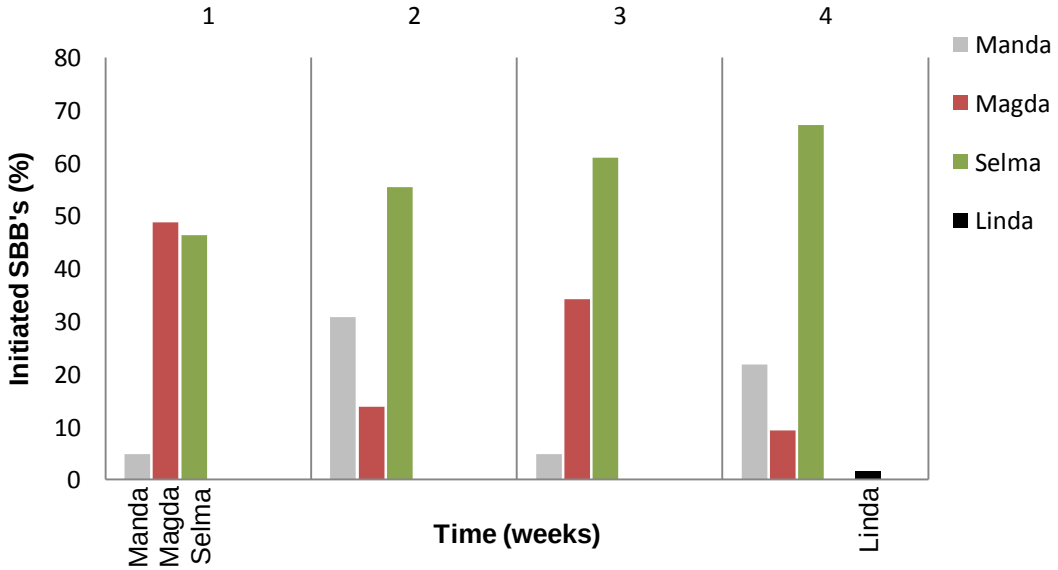


Fig. 11. The percentage of secure base bouts that were initiated by a specific group member. Penny and Santino did not engage in this behaviour.

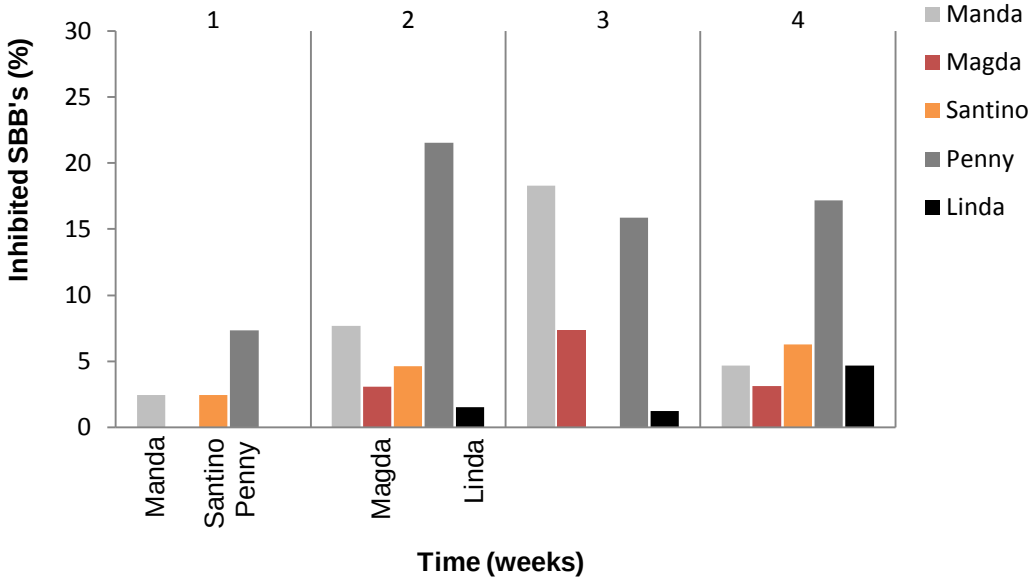


Fig. 12. The percentage of secure base bouts that were inhibited by a specific group member.

Discussion

Adoption process

Since Linda had previous experience of foster parenting, and the task was thus familiar to her, the fact that she adopted Selma was unsurprising. Previous studies have shown that alloparental experience facilitates the acceptance of an infant (Cleveland & Snowdon, 1984; Holman & Goy, 1980). However, the adoption was unusual in that it was not until week 5 and Selma was permanently in the group, with no access to her human caregiver that Linda "stepped in" and took on the role as primary caregiver. From basically not having exhibited any caregiving behaviour at all during the first four weeks of gradual integration of Selma, Linda now cared for Selma exclusively. The percentage of time she exhibited caregiving behaviour gradually decreased from week 7. This was, however, due to Selma's increasing confidence (see secure base results e.g. Fig. 10), rather than lack of care from Linda's side.

Bashaw and her colleagues (2009) report a similar case of two hand-reared chimpanzee infants that were introduced into a new group of conspecifics at a zoo. They concluded that though "each infant formed a relationship with a specific female that involved nest-sharing, carrying, retrieval, and intervening to reduce risk to the infant; these relationships could be classified as allomothering because they involved maternal behavior but occupied significantly less of the infants' time than a maternal relationship". Considering the rapid decrease in time Selma spent in proximity to Linda, the present case might too be classified

as allomothering. However, since allomothering assumes that a biological mother is present, I would argue that this case qualifies as an adoption.

My prediction on who would become Selma's new primary caregiver was based on the hypothesis that there would be one individual who would display the highest frequency of infant care and dedicate most time to infant care from the beginning. If you look at to the initial integration period, in which Magda and Manda showed the most caregiving and interest behaviour, this prediction was wrong and the hypothesis must be rejected, since none of them ended up becoming her foster mother (Fig. 4). There are a few possible reasons as to why Linda might have shown limited interest and care behaviour in the beginning of the introduction. One possible reason could be that Manda, Linda's previous adoptee, was not fully independent of her and could have influenced her initial behaviour. Chimpanzees are, as mentioned, dependent on their mothers for up to six years (Goodall, 1986), and Manda was five years of age during the study. Another possible explanation could be that Linda did not feel comfortable with the setting and the other caregivers in the integration enclosure. Linda is somewhat reserved and selective in the humans she interacts with (Ing-Marie Persson, pers comm.).

Individual variation

It is obvious that there is considerable individual variation in the potential to adopt. The personality and motivational state of an adopter are two important factors influencing adoption outcomes and there is no doubt that certain individuals appear more susceptible than others (Thierry & Anderson, 1986; Gould, 2000). The difference between Linda and Penny is a good example of this. Although both Linda and Penny are almost the same age and the same reproductive status and rank they behaved very differently in relation to the newcomer. Though Linda showed limited care behaviour towards Selma initially, she exhibited the most maternal behaviour. She used typical gestures and vocalizations. She also played calmly in bouts and made nests out of hay in which she lay down on her back and put Selma on her feet and ventrum. She also calmly deterred other group members. Penny on the other hand, was not so motherly. Even though she showed interest in Selma, she was often rough in her manner and scared her away repeatedly (Fig. 12). Even when Penny had her own baby she could leave it for hours (Ing-Marie Persson, pers comm.).

The infant's role in the process

Selma was persistent in her behaviour and pushed, followed, initiated contact, maintained proximity and clung to Linda in a very determined fashion. She also emitted distress calls when she felt insecure. Selma was also the one initiating most of the SBB's (Fig. 11). These observations support earlier findings that the infant itself has an important role in an adoption process, and that its behaviour affects the outcome and the maintenance of it (Dolhinow & DeMay, 1982; Clarke & Glander, 1981). Moreover, Dolhinow and DeMay (1982) suggests that it is possible that a foster mother allows contact and being clung on because it is less work than to expend the energy necessary to discourage a highly motivated and persistent infant. Based on my observations, this may very well have been the case in the present study.

In the same way as the adopter's motivational state and personality are key factors in an adoption outcome, I would argue that this is also true for the adoptee. In comparison to the previous introduction and subsequent adoption of Manda, one can notice considerable individual variation in the potential to accept new situations. Manda got adjusted to the

group faster and easier, and she did not show the same distress as Selma did in the beginning (Ing-Marie Persson, pers. comm.). Manda was reared by her biological mother until she was 4 months old and in that respect she might have become more secure and grounded than Selma. Seven months of mother-rearing is suggested to be enough to produce wildtype behavior in chimpanzees (Bashaw *et al*., 2009; Menzel *et al*., 1963). In addition, the group composition was also different when Manda got introduced.

Sudden caregiver shift

Linda stepped in and took on the role as the primary caregiver of Selma when the latter showed clear signs of acute distress and had no longer access to a human caregiver. This was illustrated by Linda's rapid increase in percentage of time dedicated to infant care in week 5 (Fig 4. & 5). This apparent change in behaviour could be argued to be signs of empathy and altruism. de Waal (2008) states that "empathy is an ideal candidate mechanism to underlie so-called directed altruism, i.e., altruism in response to another's pain, need, or distress." He also distinguishes between three different levels of empathy: *emotional contagion* as the lowest level, *sympathetic concern* as the middle level, and *empathic perspective-taking* as the highest level. Emotional contagion is when one party is affected by another's emotional or arousal state, causing a matching emotional state in the observer. Sympathetic concern, the second level of empathy, is represented by consolation behaviour. In chimpanzees, this often occurs when an uninvolved bystander comforts the loser of a fight. This type of behaviour is only found in Hominoidea (i.e. humans and apes), and has not been found in monkeys (de Waal, 2008). Targeted helping is according to de Waal an expression of the third level of empathy; empathic perspective-taking. This is when an individual provides fine-tuned help in response to another's specific situation and goals. Hirata (2009) argues that this is exhibited when, for example, a chimpanzee mother understands the situation her infant is in and attempts to meet its needs without emotional cues from the infant.

Regarding this specific case, I would argue that Linda's response probably involved both emotional contagion and sympathetic concern. Linda too became anxious and distressed when Selma displayed anxious behaviour and Linda, an uninvolved bystander, showed consolation behaviour when Selma was left alone without possible contact with a human caregiver.

Possible adaptive explanations for the adoption

In order to put forward possible adaptive explanations associated with this adoption occurrence, there are numerous of factors to take into consideration. Social- and kin relationships, age, sex, costs and reproductive status of the adopter are all factors that affect the outcome of an adoption (Theirry & Anderson, 1986).

Since Selma came from outside the group, it is likely to presume that Linda did not consider her as kin. Thus, this case does not support *kin selection* as an adaptive explanation. Yet another explanation unlikely to explain this case is *reciprocal altruism*, since it primarily accounts for male adopters, and adopters and adoptees closer in age to each other. The idea behind the hypothesis is the prospect that the adoptee might function as future social support and ally for the adopter. In my view, the *"Learning-to-mother"-hypothesis* cannot satisfyingly explain this case either. The oppositions for this alternative are that it primarily

explains allomothering behaviour and that it usually is nulliparous females who exhibit this behaviour, since they are the ones who typically need the experience. Linda was primiparous and already had extensive experience in infant care.

The *social benefit-hypothesis* is based on the potential social advantages an adopter can gain by caring for an infant, such as enhancement of the adopter's social status and/or increase the opportunity for the adopter of becoming a source of interest to others in the group (Theirry & Anderson, 1986). Considering that Linda is relatively low-ranked, this hypothesis could be possible, though this alternative is mainly considered in temporary adoptions and kidnapping scenarios. Another social benefit can be reduced aggression from other group members. This, however, turned out to be the opposite in this case. Yet, one has to remember that this did not take place in the wild where females are usually less sociable with males when they have a young offspring (Goodall, 1986), and therefore, in this case, the conditions were different.

The non-adaptive alternative *reproductive error* does not fit this present case of adoption either, since Linda does not fit into the typical characteristics that females who exhibit these patterns usually show. She did not care and suckle an infant of her own, nor was she near parturition or had recently lost her own infant. Thus I have the reason to suggest that an already heightened maternal motivation was not the reason why she accepted the new infant despite the high cost. However, this means that Linda could raise her maternal motivation and adopt an infant even after the maternal sensitive period and even though she was not lactating and was still caring for a juvenile offspring Manda, something that is also described in gorilla females by Nakamichi *et al*., (2007).

As noticed, none of the adaptive explanations fit really well to this present adoption occurence. However, one has to keep in mind that this was a manipulated adoption and not natural. The adaptive explanations are better suited to explain adoptions in the wild.

Secure base behaviour

In order for this adoption to occur, there had to be a shift or realignment of attachment for the infant, from one attachment figure, a human caregiver, to Linda, a chimpanzee. It was visible that it was psychologically stressful for Selma to quickly transfer attachment figure to Linda when the former attachment figure was sighted or heard, which is similar with the case study of gorilla infants by Nakamichi *et al*. (2007). The caregivers involved in the introduction of Selma tried not to be sighted by her so the new attachment period with Linda would not be interrupted. However, when a familiar human caregiver was present, Selma would (at least week 5, 6 and 7) run to the caregiver, emit distress calls and then use that person as a secure base through the enclosure bars. However, all data recorded of Selma's secure base behaviour indicates that she got more secure as the integration progressed, as predicted. She explored the surroundings more frequently (Fig. 10) and for longer periods of time before returning to the attachment figure (Fig. 7 & 8), as well as making trips further away from the secure base (Fig. 9). There is also a clear correlation between a decrease in the frequency of SBB's, an increase of SBB's with greater distance from Linda and longer SBB-durations the two last weeks. The observed secure base behaviour patterns exhibited by Selma also show that the behavioural patterns were similar, independent of the species of the caregiver acting as a secure base; chimpanzee as human. Selma used the different

attachment figures similarly, by making short trips away from the secure base to explore and returning for consolation and comfort.

Conclusion

Rejection of neonates by chimpanzee mothers does occur from time to time, and the majority take place in captivity by first-time mothers who often have no prior experience of infant care (Bloomsmith *et al*., 2003). Manipulated adoptions of orphans and introductions of older chimpanzees into new groups are therefore seen fairy frequently in zoos and sanctuaries. Thus, future empirical research on introduction procedures and on acceptance of infants by adoptive mothers is of importance. This case represents an example of a successful integration and adoption. A gradual familiarization period such as the one presented here is, in my opinion, one important factor in easing the transition for an infant, although future studies are needed in this field to further point out factors that contribute to a successful result in an adoption process.

Further research should also include long-tem systematic behavioural research on adult social behaviour and reproduction in hand-reared vs. mother-reared chimpanzees. The effect of loss is also, in my opinion, an important but difficult area to examine. Although an infant's outwardly observable behaviour indicates that the major impact of the loss of the attachment figure has diminished or ended, the long-term psychological effects and impact of the circumstance are still poorly understood.

This study gives an example of a sudden caregiver shift in chimpanzees and shows that an individual who initially exhibits most care does not necessarily become the adopter in the end. These findings reflect a behavioural flexibility in displaying maternal motivation in adult chimpanzee females as Linda could activate maternal behaviour without being in a maternal sensitive period. My observations also support that the personality and motivational state of both the adoptee and the adopter play an important role in adoptions, as pointed out in the discussion about the differences in personality of the two adult females Penny and Linda, as well as in Selma's determined requests for care from Linda and the fact that Selma initiated the majority of the SBB's.

Although this study is based on a single case of introduction and adoption, it extends our knowledge in introduction procedures of non-human primate infants by providing useful information about the method used (with the integration enclosure and gradual familiarization). It also set the stage for further investigations on foster mother-infant attachment by providing secure base behavioural data on an adoptee infant, which can be compared to other similar cases.

Acknowledgements

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