Primates (2016) 57:187–194
DOI 10.1007/s10329-016-0515-5

ORIGINAL ARTICLE

A unique case of extra-group infant adoption in free-ranging Angola black and white colobus monkeys (*Colobus angolensis palliatus*)

Noah Thomas Dunham[1] · **Paul Otieno Opere**[2]

Received: 31 August 2015 / Accepted: 20 January 2016 / Published online: 12 February 2016

Abstract Infant adoption has been reported in a variety of primate taxa both in captive and natural settings. Adoption by females may be adaptive by increasing inclusive fitness via shared genes between adoptive mother and adoptee or by providing valuable maternal practice which, in turn, may increase the female's future reproductive success. Others have argued that adoption may be non-adaptive and the result of a general attraction toward infants. Our study examines a unique case of adoption by an adult female Angola black and white colobus monkey (*Colobus angolensis palliatus*) who adopted an extra-group infant alongside her own biological infant. We compare infant behaviors and mother-infant interactions between biological infant and adoptee and then compare both biological infant and adoptee behavioral profiles to those of infants under normal circumstances. Data were collected from July 2014 to June 2015 on three habituated groups in the Diani Forest of Kenya. Scan sampling and pooled data were used to create daily and monthly behavioral profiles for the biological infant and adoptee, as well as a mean monthly profile of four infants under normal circumstances. Data include time spent (1) clinging to mother/adoptive mother, (2) clinging to another individual, (3) behaving independently, and (4) behaving in close proximity to mother/adoptive mother. Initially, the adoptee struggled to achieve behavioral profiles consistent with those of the biological infant and normal colobus infants of the same age as he spent significantly more time moving independently and significantly less time clinging to the adoptive mother. After the mysterious death of the biological infant in mid-January 2015, the adoptee assumed a behavioral profile similar to that of infants under normal conditions. This case does not support adaptive hypotheses for adoption (i.e., inclusive fitness or learning to mother). Instead, because the biological infant died, possibly due to the presence of the adoptee, we argue that this case of infant adoption was non-adaptive. Ultimately, this adoption appears to have been an outcome of the adoptee's persistent desire to be cared for and the female's strong propensity to engage in allomaternal behavior.

Keywords Maternal behavior · Orphan · Inclusive fitness · Allomothering · Colobine monkey

Introduction

While adoption is an uncommon behavior among nonhuman primates, instances have been documented both in the Old World and New World, as well as in captive settings (Hamilton et al. 1982; Thierry and Anderson 1986; Waters and Thomas 1996; Ellsworth and Andersen 1997; Ogawa 1998; Gould 2000; Izar et al. 2006; Pelé and Petit 2015). Biological mothers may forfeit primary care of an infant as a result of death (e.g., predation or disease) or general neglect. In either case, adoption occurs when the primary care of a dependent offspring transfers from the biological mother to another individual or individuals (Thierry and Anderson 1986). Although there are instances of adult males, subadults, and juveniles adopting weaned infants and young juveniles (Hrdy 1976; Gould 2000; Boesch et al. 2010), adult females often assume the role of adoptive

✉ Noah Thomas Dunham
dunham.102@osu.edu

[1] Department of Anthropology, The Ohio State University, Columbus, OH, USA

[2] Department of Conservation Biology, University of Eastern Africa, Baraton, Kenya

mother, carrying, grooming, and nursing younger, more dependent infants (Thierry and Anderson 1986).

Adaptive explanations for females adopting infants generally encompass (1) the direct benefit of increasing inclusive fitness via shared genes between adoptive mother and adoptee or (2) the indirect or selfish benefit of practicing mothering behavior which, in turn, may increase the female's future reproductive success. The direct inclusive fitness benefit of adoption is particularly evident among taxa characterized by female philopatry such as free-ranging macaques (*Macaca* spp.) (Taylor et al. 1978; Hasegawa and Hiraiwa 1980), but has also been observed in non-female philopatric howler monkeys (*Alouatta* spp.) (Izawa 1989; Agoramoorthy and Rudran 1992). The indirect or selfish benefit to adoption typically applies to cases of juveniles and nulliparous females gaining valuable mothering experience before giving birth to their own offspring (Lancaster 1971). While there is no conclusive evidence supporting this hypothesis in direct relation to adoption, Fairbanks (1990) found that female vervet monkeys (*Cercopithecus aethiops*) who had more experience caretaking and carrying infants as juveniles ultimately had better survival rates for their first born offspring.

It is important to stress that adoption can also be viewed as non-adaptive and a behavior so rare that it has not been selected against (Thierry and Anderson 1986). Under this view, adoption is merely the manifestation of a keen interest in infants associated with normal maternal and allomothering behaviors (Quiatt 1979). In fact, Hrdy (1976: 128) emphasized that the "foundations for adoption have been laid before the actual transfer became necessary, through aunting behavior" (i.e., allomothering). This behavioral system is a hallmark of many Asian and African colobine monkeys and is believed to be greatly facilitated by reduced intragroup feeding competition, more relaxed social hierarchies, and dispersal patterns characterized by male and female emigration in many of these taxa (McKenna 1979; Maestripieri 1994; Matsuda et al. 2012; Wikberg et al. 2012). Allomothering enables other adult females and juveniles to hold, carry, protect, and in some cases, nurse infants that are not their own (Poirier 1968; McKenna 1979; Bădescu et al. 2015). These interactions also help to solidify bonds between infants and other group members which are believed to ease the transition of primary infant care from biological mother to another female in circumstances where adoption is necessary (Lancaster 1971; Kriege and Lucas 1974; Hrdy 1976; Quiatt 1979; Riedman 1982). Despite the high frequency of allomothering in colobines and Hrdy's (1976) claim that allomothering can serve as a precursor to adoption, there are virtually no published accounts of long-term infant adoption in wild colobine monkeys (Boggess cited in Hrdy 1980) and only a handful of examples from experimental and captive settings (Dolhinow, 1980; Waters and Thomas 1996).

We add to this literature by examining a free-ranging female Angola black and white colobus monkey (*Colobus angolensis palliatus*) who spontaneously adopted an infant alongside her own infant. Our study is unique in that (1) it is the first published account, to our knowledge, of infant adoption in a free-ranging African colobine monkey, (2) the infant originated from another group, and (3) the adoption did not occur just after the birth or death of the biological infant, as is typically described in the literature, but when the biological infant was 3.5 months old and the adoptee was estimated to be 4–5 months old. Here, we compare behaviors between the biological infant and adoptee to determine if the female cared differently for the two infants. We also compare the behavioral profiles of the biological infant and adoptee with those of four *C. a. palliatus* infants under "normal" circumstances. Finally, we discuss this case within the context of adaptive explanations for adoption and the role of allomothering behavior in colobine monkeys.

Methods

Study site and study species

The Diani Forest is located in the Kwale District of south coastal Kenya and is one of the few remaining patches of biodiversity-rich coral rag forests in East Africa (Metcalfe et al. 2009). The forest measures approximately 4.6 km^2 and is characterized by patches of intact forest interspersed with degraded areas (Anderson et al. 2007; Dunham and McGraw 2014). The Diani Forest is home to a variety of primate taxa including Peters' Angola black and white colobus monkey (*Colobus angolensis palliatus*).

Throughout their ranges in eastern and Central Africa, *Colobus angolensis* generally live in groups of 2–20 members; however, *Colobus angolensis ruwenzorii* from Nyungwe, Rwanda, sometimes form groups of greater than 300 members (Fimbel et al. 2001; Fashing et al. 2007). Group size at Diani averages six individuals with groups typically consisting of one or two adult males, multiple adult females, and their offspring (Moreno-Black and Maples 1977; Dunham pers. observation). Like most *Colobus angolensis* subspecies and other *Colobus* spp., *Colobus angolensis palliatus* are highly arboreal, spend much of their time feeding and resting in the main canopy, and are renowned for their spectacular leaping ability (Dunham and McGraw 2014; Dunham 2015). Research has shown that *Colobus angolensis* are largely folivorous throughout their ranges but may also rely heavily on seeds and/or lichens (Bocian 1997; Maisels et al. 1994; Lowe and

Sturrock 1998; Fimbel et al. 2001). In Diani, *Colobus angolensis palliatus* primarily feed on young and mature leaves while consuming unripe fruits, seeds, and flowers to lesser degrees (Moreno-Black and Maples 1977; Dunham unpublished data).

Case history

Beginning in July 2014 our Ufalme study group contained five individuals: one adult male, three adult females, and one juvenile female. Over a 2.5-week period from late August to early September, one female disappeared while another female, Malkia, gave birth to an infant male named Kaskazi. These changes to the group composition were first documented on September 10, 2014. Similarly, our third female gave birth to a female infant sometime during the first week of December and was first documented on December 10, 2014.

Also, on December 10th at 6:40AM an extra-group male infant, Okoa, was first observed crying and struggling to follow the study group. Okoa continued to cry and remain in close proximity to Malkia and Kaskazi throughout the day. Based on his slightly larger body size relative to the 3.5 month old Kaskazi, we estimated Okoa to be approximately 4–5 months old at this initial observation. Okoa's larger body size and longer tail with a more prominent white tip made him easily distinguishable from Kaskazi (Fig. 1). At 4:15PM on December 10th Malkia was first observed simultaneously nursing Kaskazi and Okoa (Fig. 2). This pattern continued for the remainder of our December observation days (December 11th–12th and 15th–18th) and into January 2015 (January 11th–13th) with Malkia continuing to care for Kaskazi and Okoa. On January 15th, Kaskazi was mysteriously found dead with no apparent external injuries. Malkia continued to care for the adoptee Okoa through January 2015 and throughout the remainder of the study, ending in June 2015. The identity of Okoa's biological mother remains unknown as no extra-group females have been observed trying to reconnect with the infant. It is likely she inhabits one of the neighboring colobus groups or has died.

Observational methods

Data for this paper were collected as part of an ongoing study examining the behavioral ecology and food selection of three groups of *C. a. palliatus* in the Diani Forest. Each group was followed for 5–7 days per month before rotating to another group. Data presented here includes 183 full-day follows spanning from July 2014–June 2015. Scan samples were collected at 15-min intervals in which the activity and nearest neighbor of each individual was recorded. Only

Fig. 1 Malkia holding Kaskazi (*center*) while Okoa (*right*) remains in close proximity. Note the slightly larger body size and longer, bushier white portion of the tail that clearly differentiates Okoa from Kaskazi

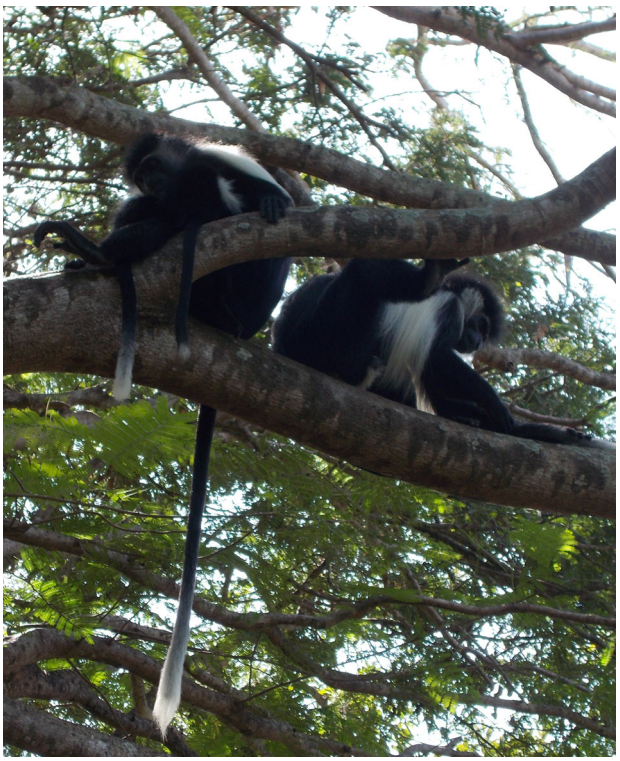

Fig. 2 Malkia simultaneously nursing Okoa (*left*) and Kaskazi (*right*) with the resident male resting nearby

Table 1 Summary of *Colobus angolensis palliatus* infant data

Infant name	Group name	Infant age range (in months) During observations	Months infant observed	Number of days infant observed	Notes
Kaskazi	Ufalme	1–5	Sep 2014–Jan 2015	31	Born Sep 2014, died Jan 2015
Okoa	Ufalme	4–10[a]	Dec 2014–Jun 2015	40	Joined Ufalme group on Dec 10, 2014
Ufa1	Ufalme	1–7	Dec 2014–Jun 2015	40	–
Uja1	Ujamaa	1–10	Aug 2014–Jun 2015	89	–
Nyu1	Nyumbani	5–10	Jan 2015–Jun 2015	32	–
Nyu2	Nyumbani	1–6	Jan 2015–Jun 2015	32	–

[a] Age estimated based on body size and pelage color

infant data are included in the analyses of this study. Infant activities include rest, feed/forage, socialize, move, and cling. Clinging includes grasping onto a stationary or moving individual and also cuddling. Because it was often impossible to determine if an infant was suckling or just clinging (particularly when located in the upper canopy), clinging is used as a proxy for suckling. We report data on four normal colobus infants in addition to Kaskazi and Okoa (Table 1). For each infant, data are presented as frequencies of time spent clinging to mother (i.e., adoptive mother for the case of Okoa), clinging to non-mother, and independent (i.e., not clinging to another individual). Proximity data include frequencies in which the nearest neighbor is the mother/adopted mother vs. another individual.

Statistics

Non-parametric Mann–Whitney *U* tests were used to compare daily frequencies of the aforementioned behaviors between the biological infant and adoptee during the period in which both infants were alive and present in the study group. In order to determine if behavioral profiles of Kaskazi and Okoa differed significantly from those of infants under normal circumstances, linear regressions relating month of age to the mean behavioral frequencies of four normal colobus infants were compared to those of Kaskazi and Okoa using non-parametric rank analysis of covariance (Quade 1967). Data on the four normal infants were pooled because there were no significant differences in their monthly behavioral profiles.

Results

Biological infant vs. adoptee

There were a total of 10 observation days in which both Kaskazi (biological infant) and Okoa (adopted infant) were alive and present in the study group. During this time Kaskazi spent significantly more time clinging to Malkia [$\text{median}_{\text{Kaskazi}} = 54.2\ \%$ (IQR = 30.5–77.9), $\text{median}_{\text{Okoa}} = 25.0\ \%$ (IQR = 12.2–37.8), $P < 0.01$] while Okoa spent significantly more time independent of all group members [$\text{median}_{\text{Kaskazi}} = 44.4\ \%$ (IQR = 20.7–68.1), $\text{median}_{\text{Okoa}} = 73.2\ \%$ (IQR = 60.4–86.0), $P < 0.01$]. Time spent clinging to individuals other than Malkia did not differ significantly between biological infant and adoptee [$\text{median}_{\text{Kaskazi}} = 0.0\ \%$ (IQR = 0.0), $\text{median}_{\text{Okoa}} = 0\ \%$, (IQR = 0.0), $P = 0.47$]. Likewise, the frequency in which Malkia was the nearest neighbor did not differ significantly between infants [$\text{median}_{\text{Kaskazi}} = 83.4\ \%$ (IQR = 51.5–100.0); $\text{median}_{\text{Okoa}} = 69.5\ \%$ (IQR = 46.5–92.5), $P = 0.29$].

Biological infant and adoptee vs. normal infants

Monthly behavioral frequencies for Kaskazi, Okoa, and the mean values of four normal infants are show in Fig. 3, 4, 5, 6. Under normal conditions, time spent clinging to mother generally decreased with each month of age (Fig. 3). A similar trend was evident for time spent clinging to non-mother (Fig. 4). Infants generally became more independent with age (Fig. 5) and spent less time in close proximity to their mother (Fig. 6).

Behavioral frequencies during Kaskazi's lifetime (i.e., months 1–5) are compared to the mean frequencies of four normal infant cases during their respective months 1–5. In all cases behavioral profiles for Kaskazi did not differ significantly from the mean normal infant profiles: cling to mother ($F = 0.13$; $P = 0.73$), cling to non-mother ($F = 0.77$; $P = 0.41$), independence from other individuals ($F = 0.13$; $P = 0.73$), and mother as nearest neighbor ($F = 0.33$; $P = 0.86$).

Behavioral frequencies during Okoa's tenure in the study group (i.e., months 4–10) are compared to the mean frequencies of four normal infant cases during months 4–10 of their respective lifetimes. Unlike Kaskazi, Okoa's behavioral profiles do not mirror those of the normal infants as significant differences were found with respect to cling to adoptive mother ($F = 6.01$, $P = 0.03$), cling to

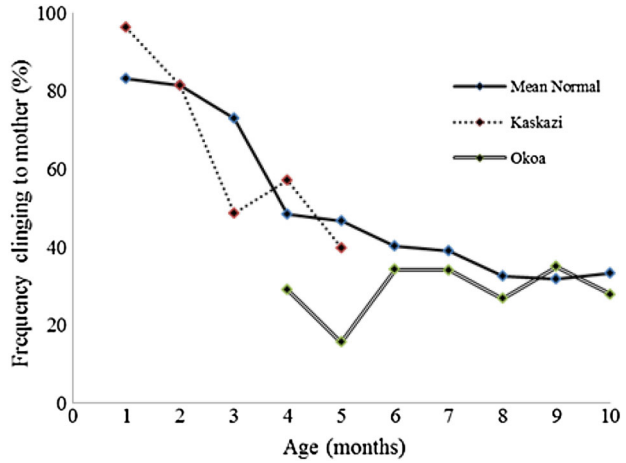

Fig. 3 Monthly frequency of cling to mother/ adoptive mother

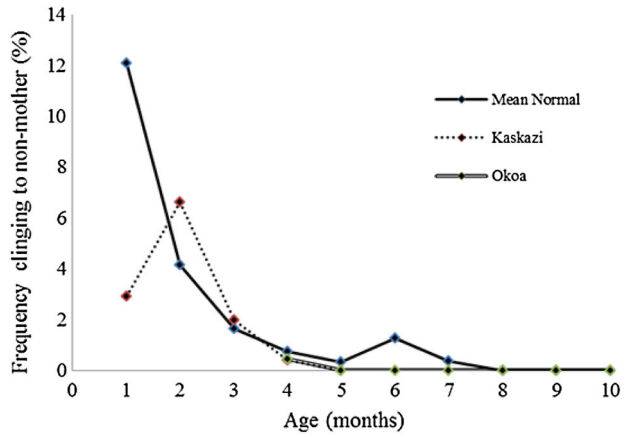

Fig. 4 Monthly frequency of cling to non-mother

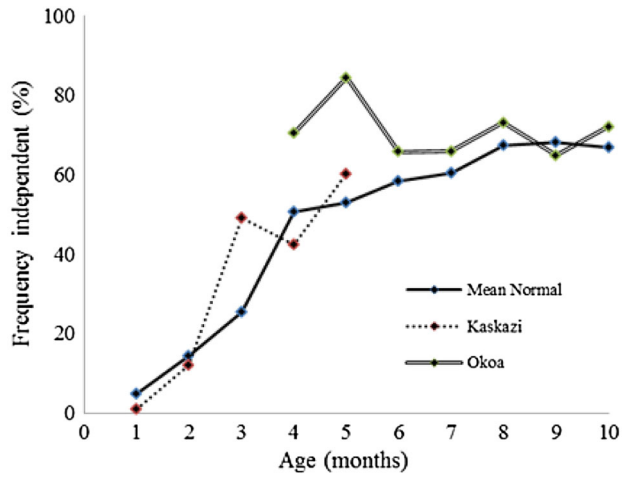

Fig. 5 Monthly frequency of time spent independent

non-adoptive mother ($F = 6.01$, $P = 0.03$), independence from other individuals ($F = 6.01$, $P = 0.03$), and adoptive mother as nearest neighbor ($F = 5.21$, $P = 0.04$). Okoa spent significantly more time independent and significantly less time in close proximity and clinging to his adoptive mother and other individuals.

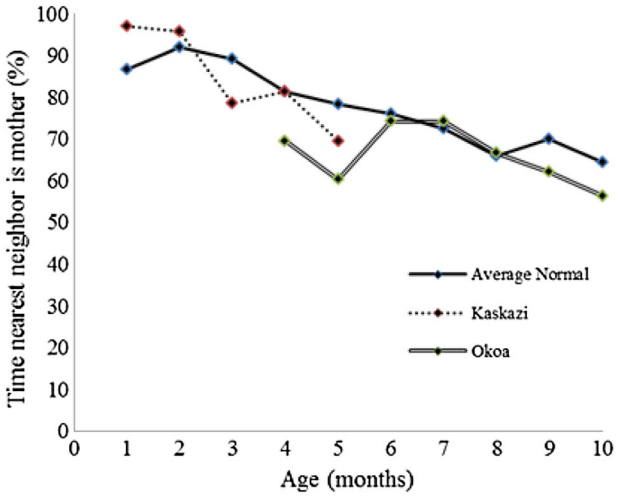

Fig. 6 Monthly frequency in which mother/ adoptive mother is nearest neighbor

Discussion

This study examines a unique case of infant adoption in free-ranging *C. angolensis* in which an adult female adopted an extra-group infant alongside her own biological infant. During the time the infants lived contemporaneously, the biological infant, Kaskazi, spent significantly more time clinging to his mother, Malkia, than did the adoptee, Okoa. While caring for two infants simultaneously engenders greater energetic costs for the mother (Agoramoorthy and Rudran 1992; Ellsworth and Andersen 1997; Link et al. 2006), there is no obvious indication in our data that Malkia's added investment in Okoa occurred at the expense of Kaskazi. This notion is supported by the fact that monthly behavioral profiles for Kaskazi–including the period of overlap with Okoa—were statistically indistinguishable from those of infants under normal conditions at the same age.

However, because we were not able to quantify suckling frequencies and durations, it is possible that milk intake differed significantly between Kaskazi and Okoa. By sharing a mother, it is also likely that both infants suffered from reduced milk intake relative to infants nursed singularly. For example, in common marmosets (*Callithrix jacchus*) where twinning is common, smaller bodied adult females raising twins had lower fat content, lower gross energy in their milk, and lower nursing bout frequencies (Tardif et al. 2001). In other words, "small mothers were investing less in twin litters both through less energy placed in a given volume of milk and by producing less milk overall" compared to their counterparts raising

singletons (Tardif et al. 2001: 23). Twinning is exceptionally rare among medium to large bodied anthropoids; therefore, comparable lactational data are not available for colobus monkeys (Chapman et al. 1990). If there was indeed a deficiency in the quantity and/or quality of Malkia's milk during the time she was nursing the two infants, it is possible that the larger bodied Okoa was able to persist longer than Kaskazi.

Regardless of Kaskazi's cause of death, his absence created an opportunity for Okoa. In the months after Kaskazi's death, the time in which Okoa spent moving independently sharply declined and his time spent in the proximity of and clinging to Malkia sharply increased to values resembling those of infants under normal conditions at the given ages. That is, after the death of Kaskazi an outside observer would simply assume that Okoa was the biological infant of Malkia.

Adoption is clearly adaptive from an infant's perspective. If its biological mother is incapable or unwilling to provide care, an infant should actively seek another individual to provide nourishment and safety as receiving this care greatly enhances its chance of survival (Dolhinow and DeMay 1982; Agoramoorthy and Rudran 1992). Okoa clearly typifies this point: After whining and relentlessly following the group for several hours, Malkia eventually allowed him to cling and suckle in the evening of that initial day. This trend continued for the next month, however, Okoa remained more peripheral as Kaskazi maintained closer proximity and more frequent interactions with Malkia. In the days after Kaskazi's death, Malkia occasionally forcefully resisted Okoa's attempts to nurse. Only after several attempts did she succumb and allow him to suckle. His persistence surely played a major role in the adoption ultimately being successful and long-lasting (Dolhinow and DeMay 1982).

While adoptions can also be adaptive for the adoptive mother in some instances, neither the direct inclusive fitness nor indirect learning to mother hypothesis is supported by Malkia's adoption of Okoa. Inclusive fitness can be directly enhanced by adopting an infant with whom the mother shares genes. Because Okoa was born into another group and the identity of his biological mother remains unknown, hypothesizing that the adoption provides a direct inclusive fitness benefit for Malkia is untenable. Furthermore, the absence of genetic data prevents us from analyzing the relatedness of Malkia and Okoa. Adoption may also provide an indirect inclusive fitness benefit by allowing a female the opportunity to practice infant care on the adoptee without major consequences if the infant dies (Hrdy 1976). This hypothesis is better suited for juvenile and subadult females and does not apply well to Malkia as an adult female already caring for her own biological infant.

Given that neither adaptive hypothesis is supported, and that Kaskazi died possibly as a consequence of Okoa's adoption, we argue that this specific adoption event is non-adaptive. Malkia continued to care for Okoa after Kaskazi's death and in doing so experienced high energetic costs of lactation and maternal care, delaying her sexual receptivity, her ability to conceive, and thus the capacity to propagate her genes (Altmann et al. 1978; Winkler et al. 1984; Agoramoorthy and Rudran 1992). In a similar study, Agoramoorthy and Rudran (1992) found that a howler monkey female who cared for an unweaned adoptee alongside her own biological infant had a subsequent interbirth interval of 21.7 months compared to the 16.6 months average associated with infants raised singularly. Ellsworth and Andersen (1997) found a similar trend in rhesus macaques that raised adoptees alongside their biological infants. The struggle to balance adoptee care with conceiving her own offspring was apparent in the months immediately after Kaskazi's death as Malkia attempted to nurse Okoa while actively presenting to and mating with the group's resident male—occasionally at the same time (Fig. 7).

Others have argued that adoption is not necessarily adaptive, but that it is the consequence of a more general attraction toward infants, and that adoption occurs so rarely that it has not been strongly selected against (Quiatt 1979; Thierry and Anderson 1986). Perhaps more than any other primates, colobine monkeys are particularly infatuated with young infants and have a strong tendency toward alloparenting (McKenna 1979; Maestripieri 1994). Alloparenting is particularly geared toward young infants as the stark color contrast associated with newborns (i.e., during the first 2–3 months of life) of many colobine species, relative to their adult counterparts, is believed to convey vulnerability (Horwich and Manski 1975; Hrdy 1976; Alley 1980; Brent et al. 2007). In this study, the white coloration of *C.*

Fig. 7 Malkia simultaneously nursing Okoa and mating with the resident male

a. palliatus infants corresponds to the higher frequencies of clinging to non-mother behavior observed during the first three months of life (Fig. 4). Still, Malkia adopted Okoa around 4–5 months of age and after his white pelage had completely shifted from the newborn white coloration to the black and white coloration characteristic of adults. This suggests that some individuals retain their affinity for infants and a predisposition to care for them even after pelage color change.

In another species of black and white colobus monkey (*Colobus vellerosus*), Bădescu et al. (2015) found that alloparenting behavior (i.e., natal attraction and infant handling) was more common among maternal kin and nulliparous females, regardless of rank. Thus, they argue alloparenting in colobines is particularly ubiquitous because it can provide potential inclusive fitness benefits to alloparents and valuable mothering experience for nulliparous females, without substantial costs to the biological mother or individuals engaging in alloparenting (Bădescu et al. 2015). We argue that Malkia's adoption of Okoa was the result of a natural and potentially adaptive tendency toward alloparenting; however, this behavior was exacerbated to the extent that it became non-adaptive due to the death of her biological infant, the high costs accompanying primary care of a presumably unrelated adoptee, and the likely associated delay to conceiving future offspring.

Acknowledgments This material is based upon work supported by the National Science Foundation Graduate Research Fellowship under Grant No. 2012136655, Columbus Zoo and Aquarium, Nacey Maggioncalda Foundation, National Geographic Society, and Pittsburgh Zoo & PPG Aquarium. We recognize the Kenya Wildlife Society for permission to conduct this research. Thanks to Pam Cunneyworth and Andrea Donaldson of Colobus Conservation for providing logistical support for this study. We thank Dr. Ikki Matsuda and one anonymous reviewer for their comments on earlier versions of this manuscript.

References

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

Alley TR (1980) Infantile colouration as an elicitor of caretaking behaviour in Old World primates. Primates 21:416–426

Altmann J, Altmann SA, Hausfater G (1978) Primate infant's effects on mother's future reproduction. Science 201:1028–1030

Anderson J, Rowcliffe JM, Cowlishaw G (2007) The Angola black-and-white colobus (*Colobus angolensis palliatus*) in Kenya: historical range contraction and current conservation status. Am J Primatol 69:664–680

Bădescu I, Sicotte P, Ting N, Wikberg EC (2015) Female parity, maternal kinship, infant age and sex influence natal attraction and infant handling in a wild colobine (*Colobus vellerosus*). Am J Primatol 77:376–387

Bocian CM (1997) Niche separation of black-and-white colobus (*Colobus angolensis* and *C. guereza*) in the Ituri forest. Ph.D.thesis, City University of New York

Boesch C, Bole C, Eckhardt N, Boesch H (2010) Altruism in forest chimpanzees: the case of adoption. PLoS One 5(1):e8901. doi:10.1371/journal.pone.0008901

Brent LJN, Teichroeb JA, Sicotte P (2007) Preliminary assessment of natal attraction and infant handling in wild *Colobus vellerosus*. Amer J Primatol 69:1–7

Chapman CA, Walker S, Lefebvre L (1990) Reproductive strategies of primates: the influence of body size and diet on litter size. Primates 31:1–13

Dolhinow P (1980) An experimental study of mother loss in the Indian langur monkey (*Presbytis entellus*). Folia Primatol 33:77–128

Dolhinow P, DeMay MG (1982) Adoption: the importance of infant choice. J Hum Evol 11:391–420

Dunham NT (2015) Ontogeny of positional behavior and support use in *Colobus angolensis palliatus* of the Diani Forest, Kenya. Primates 56:183–192

Dunham NT, McGraw WS (2014) Positional behavior and habitat use of Peters' Angola black and white colobus monkey (*Colobus angolensis palliatus*) in structurally distinct areas of the Diani Forest, Kenya. Afr Primates 9:1–14

Ellsworth JA, Andersen C (1997) Adoption by captive parturient rhesus macaques: biological vs. adopted infants and the cost of being a "twin" and rearing "twins". Am J Primatol 43:259–264

Fairbanks LA (1990) Reciprocal benefits of allomothering for female vervet monkeys. Anim Behav 40:553–562

Fashing PJ, Mulindahabi F, Gakima J, Masozera M, Mununura I, Plumptre AJ, Nguyen N (2007) Activity and ranging patterns of *Colobus angolensis ruwenzorii* in Nyungwe Forest, Rwanda: possible costs of large group size. Int J Primatol 28:529–550

Fimbel C, Vedder A, Dierenfeld E, Mulindahabi F (2001) An ecological basis for large group size in *Colobus angolensis* in the Nyungwe Forest, Rwanda. Afr J Ecol 39:83–92

Gould L (2000) Short communication: adoption of a wild orphaned ringtailed lemur infant by natal group members: adaptive explanations. Primates 41:413–419

Hamilton WJ III, Busse C, Smith KS (1982) Adoption of infant orphan chacma baboons. Anim Behav 30:29–34

Hasegawa T, Hiraiwa M (1980) Social interactions of orphans observed in a free-ranging troop of Japanese macaques. Folia Primatol 33:129–158

Horwich RH, Manski D (1975) Maternal care and infant transfer in two species of *Colobus* monkeys. Primates 16:49–73

Hrdy SB (1976) Care and exploitation of nonhuman primate infants by conspecifics other than the mother. In: Rosenblatt JS, Hinde RA, Shaw E, Beer C (eds) Advances in the study of behavior, vol 6. Academic Press, New York, pp 101–158

Hrdy SB (1980) The langurs of Abu. Harvard University Press, Cambridge

Izar P, Verderane MP, Vilsaberghi E, Ottoni EB, de Oliveira MG, Shirley J, Fragaszy D (2006) Cross-genus adoption of a marmoset (*Callithrix jacchus*) by wild capuchin monkeys (*Cebus libidinosus*): case report. Am J Primatol 68:692–700

Izawa K (1989) The adoption of an infant observed in a wild group of red howler monkeys (*Alouatta seniculus*). Field Stud New World Monkeys La Macarena Columbia 2:33–36

Kriege PD, Lucas JW (1974) Aunting behavior in an urban troop of *Cercopithecus aethiops*. J Behav Sci 2:55–61

Lancaster JB (1971) Play-mothering: the relations between juvenile females and young infants among free ranging vervet monkeys (*Cercopithecus aethiops*). Folia Primatol 15:161–182

Link A, Palma AC, Velez A, de Luna AG (2006) Costs of twins in free-ranging white-bellied spider monkeys (*Ateles belzebuth belzebuth*) at Tinigua National Park, Colombia. Primates 47:131–139

Lowe AJ, Sturrock GA (1998) Behaviour and diet of *Colobus angolensis palliatus* Peters 1868, in relation to seasonality in a Tanzanian dry coastal forest. Folia Primatol 69:121–128

Maestripieri D (1994) Social structure, infant handling and mothering styles in group living Old World monkeys. Int J Primatol 15:531–553

Maisels F, Gautier-Hion A, Gautier JP (1994) Diets of two sympatric colobines in Zaire: more evidence on seed-eating in forests on poor soils. Int J Primatol 15:681–701

Matsuda I, Zhang P, Swedell L, Mori U, Tuuga A, Bernard H, Sueur C (2012) Comparisons of intraunit relationships in nonhuman primates living in multilevel social systems. Int J Primatol 33:1038–1053

McKenna JJ (1979) The evolution of allomothering behavior among colobine monkeys: function and opportunism in evolution. Am Anthropol 81:818–840

Metcalfe K, French-Constant R, Gordon I (2009) Sacred sites as hotspots for biodiversity: the three sisters cave complex in coastal Kenya. Oryx 44:118–123

Moreno-Black GS, Maples WR (1977) Differential habitat utilization of four cercopithecidae in a Kenyan Forest. Folia Primatol 27:85–107

Ogawa H (1998) Brief report: Adoption and social interactions between mother and "twin" offspring in *Macaca fuscata*. Folia Primatol 69:100–105

Pelé M, Petit O (2015) Equal care for own versus adopted infant in tufted capuchins (*Sapajus* spp.). Primates 56:201–206

Poirier FE (1968) The Nilgiri langur (*Presbytis johnii*) mother-infant dyad. Primates 9:45–68

Quade D (1967) Rank analysis of covariance. J Am Stat Assoc 62:1187–1200

Quiatt D (1979) Aunts and mothers: adaptive implications of allomaternal behavior of nonhuman primates. Am Anthropol 81:310–319

Riedman ML (1982) The evolution of alloparental care and adoption in mammals and birds. Q Rev Biol 57:405–435

Tardif SD, Power M, Oftedal T, Power RA, Layne DG (2001) Lactation, maternal behavior and infant growth in common marmoset monkeys (*Callithrix jacchus*): effects of maternal size and litter size. Behav Ecol Sociobiol 51:17–25

Taylor H, Teas J, Richie T, Southwick C, Shrestha R (1978) Social interactions between adult male and infant rhesus monkeys in Nepal. Primates 19:343–351

Thierry B, Anderson J (1986) Adoption in anthropoid primates. Int J Primatol 7:191–215

Waters SS, Thomas D (1996) An observation of adoption in colobus monkeys (*Colobus guereza kikuyuensis*). ABWAK 23:59

Wikberg EC, Sicotte P, Campos FA, Ting N (2012) Between-group variation in female dispersal, kin composition of groups, and proximity pattern in a black and white colobus monkey (*Colobus vellerosus*). PLoS One 7:e48740

Winkler P, Loch H, Vogel C (1984) Life history of Hanuman langurs (*Presbytis entellus*): reproductive parameters, infant mortality, and troop development. Folia Primatol 43:1–2