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Source: Mammal Study, 45(4) : 1-6

Published By: Mammal Society of Japan

URL: <https://doi.org/10.3106/ms2019-0081>

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Infant pelage color change and infant handling in captive black-and-white colobus

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Abstract. Colobine monkeys generally spend less time each day engaged in social interactions than other primates. However, a notable feature of their social interaction involves females exchanging infants (i.e., infant handling). Here, we report on the handling of an infant in relation to pelage color change in a group of black-and-white colobus (*Colobus guereza*) housed in the Japan Monkey Centre. We found large variation in the speed of infant pelage color change among body parts (range 100–216 days) and documented that infant handling by non-mothers was related to the infant pelage color and/or moving ability (infant independence). Non-mothers, especially females, were clearly attracted to the newborn infant and often handled the infant in a few weeks of its birth, but handling decreased with infant age and corresponded both with the loss of the natal coat color and the infant acquiring effective locomotory independence. We document interesting patterns, but the conclusions we can draw are limited and future research should consider separating effects of infant pelage color and infant locomotory independence and evaluate the effect of infant body mass.

Key words: allo-mothering, colobine, guereza, natal attraction.

Infant care by individuals other than their genetic parents is widely reported in social mammals including primates (Hrdy 1976; Riedman 1982). Colobine monkeys include at least 78 species grouped into ten genera and are found in Asia and Africa. These animals have a diversity of social organizations (Oates and Davies 1994; Mittermeier et al. 2013), but in general they spend less time in social interactions than other primates (Grueter et al. 2013). However, a notable feature of their social interaction involves non-mothers handling infants (McKenna 1979; Newton and Dunbar 1994; Kirkpatrick and Grueter 2010; Matsuda et al. 2012), though this behavior is uncommon in cercopithecines (Kohda 1985). Maestripieri (1994) presented the comprehensive review of infant handling and outlined 15 hypotheses of its adaptive significance; however, a clear understanding remains elusive as dif-

ferent contexts and species are associated with different functions. As a result, detailed descriptive studies are useful to provide data for comparative meta-analysis to evaluate these hypotheses.

The conspicuous infant pelage coloration of colobines is unique among primates (note that many cercopithecines have contrasting neonatal coloration). Infant coloration takes on a variety of forms; for example in black-and-white colobus (*Colobus guereza*) infants have white hair with pink skin, which gradually darkens to black-and-white adult coloration (Oates 1977; Onderdonk 2000), while *Trachypithecus* spp. infants (silvered langur: *T. cristatus*, François' langur: *T. francoisi*, and Cat Ba langur: *T. poliocephalus*) have orange hair with pale skin, in marked contrast to the grey, black and/or white adult coloration (Bernstein 1968; Henderschott et al. 2019),

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Fig. 1. Images and scores of the blackness of each body part (i.e., arm, face, belly, back, and tail), using a scale from 0 to 3: 0, < 1/3 full blackness color; 1, 1/3 < 2/3 full blackness color; 2, almost full blackness color but blackness is slightly lighter; 3, full blackness.

and proboscis monkey (*Nasalis larvatus*) infants have black hair with bluish facial skin which differs from the coloration of adults (Bennett and Sebastian 1988; Sha et al. 2011). It is frequently suggested that the conspicuous infant pelage promotes infant handling by non-mothers (Emerson 1973; Oates 1977; Bădescu et al. 2015), though little is known how such behavior changes as infant pelage color changes.

Colobus guereza is widely distributed in the central and eastern parts of tropical Africa and is one of the most studied colobines. Infant handling by non-mothers in *C. guereza* has previously been described (Wooldridge 1971; Emerson 1973; Horwich and Manski 1975; Dunbar and Dunbar 1976; Oates 1977; Kohda 1985), although detailed analysis focusing on the infant handling in relation to infant pelage color change has received little attention. Therefore, here, we report on how infant handling behavior of *C. guereza* housed in the Japan Monkey Centre changes in relation to their pelage color.

Materials and methods

We studied a group of *C. guereza* consisting of three adult males (15, 9, and 8 years old) and two adult females (9 years old each), in the Japan Monkey Centre from July 2015 to May 2016 on 94 days for 51 hours (range per day, 13 to 100 min). Focal animal observation of an infant was started shortly after its birth on 12 July. We recorded the duration of infant handling by adults, including the mother and non-mothers, and when the infant was away from the adults. To evaluate the development of infant's pelage color, we collected images and scored the blackness of each body part, (i.e., arm, face, belly, back, and tail) using a scale from 0 to 3 (0, < 1/3 full blackness

color; 1, 1/3 < 2/3 full blackness color; 2, almost full blackness color but blackness is slightly lighter; 3, full blackness) (Fig. 1). Only one author (TO) conducted the image evaluation to eliminate inter-individual bias for subjective image assessment. We interpolated daily pelage color changes using a spline smoothing. We also interpolated the relationships between infant pelage color change (the overall mean: see Fig. 2) and the time spent with adults/away from adults, using a spline smoothing. All analyses were performed in the R statistical computing environment (R Core Team 2019).

Results

On average it took 150.0 days (standard deviation: 60.7 days) from birth for the different body parts to reach adult pelage coloration; however, there was great variation among body parts (arm: 100 days, face: 111 days, belly: 105 days, back: 216 days and tail: 216 days; Fig. 2). The time non-mother females spent handling the infant decreased as the infant pelage color changed to the mature pattern. The steepest decline in this handling occurred early in the infant's development (i.e., between 0 and 1 pelage color scores; Fig. 3a). The infant increased the time spent engaged in activities away from others as the pelage color developed (Fig. 3b). In contrast, the time spent being handled by its mother was almost constant throughout the study, though the infant pelage color changed (Fig. 3c). The infant was handled by only one of the three adult males and only twice (< 1% of the time) when all pelage color scores were those of a young infant, i.e., score: < 1.

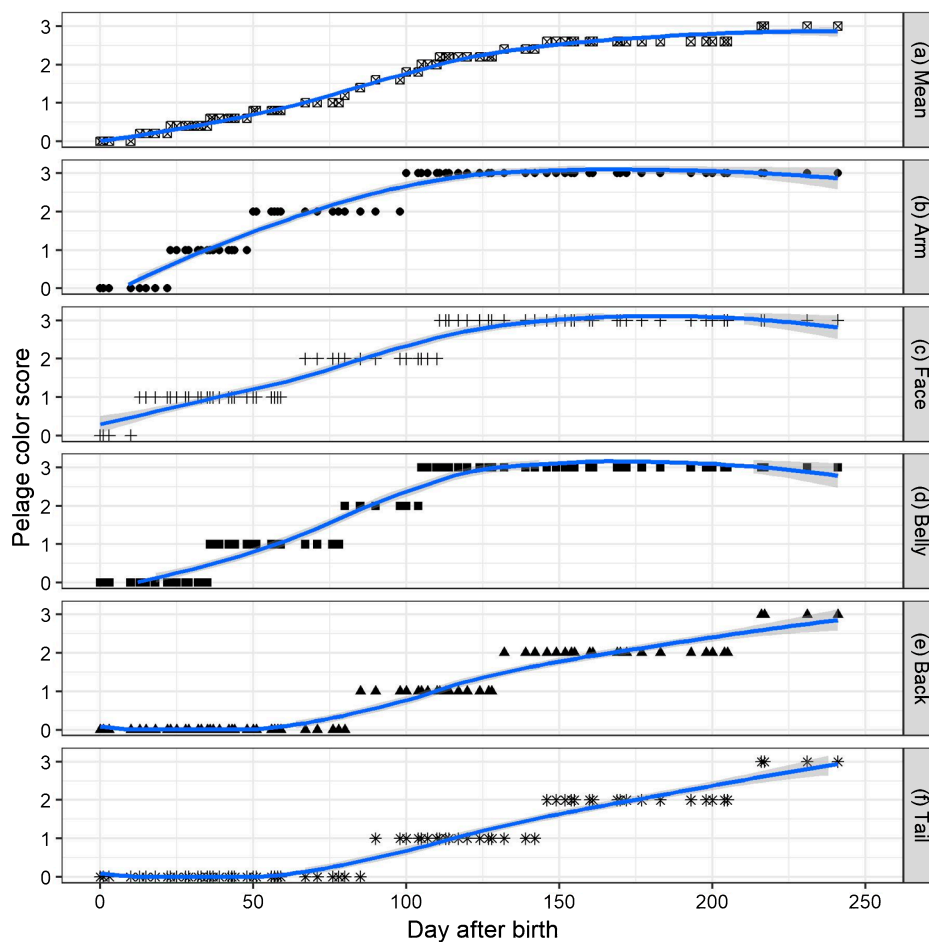


Fig. 2. Development of infant *Colobus guereza* pelage color in each body part and the overall mean. We interpolated daily pelage color changes using a spline smoothing. Shaded areas indicate 95% confidence intervals.

Discussion

We documented large temporal variation (100–216 days) among body parts in the rate with which the infant pelage lost its neonate color and took on an adult coloration, but the average time to reach adult coloration was 150 days. In contrast, previous studies of various species of black-and-white colobus have described that it takes approximately 100 days for infants to develop adult coloration (Horwich and Manski 1975; Oates 1977; Bădescu et al. 2016; Dunham and Opere 2016). Differing environmental conditions (captive/free-ranging, nutritional status, etc.) may have created this inconsistency, though factors, such as predation risk and feeding competition, should not have significant effects on natal coat durations in free-ranging *C. vellerosus* (Bădescu et al. 2016). The reason that our estimate of 150 days is longer than the 100 days previously found maybe because we used image evaluation that allows very detailed evalua-

tion of color (i.e., image magnification of specific body parts), while the other studies used direct observation. However, we only evaluated one infant, thus until infant pelage color change can be evaluated on more infants, our results must be considered preliminary.

Our study suggested that pelage color has an important effect on whether the infant is handled by non-mothers. The fact that the more visible body parts, the back and tail, change to adult coloration slower than other less visible parts, the belly, suggests that it is advantageous for the infants to maintain the neonate coloration as long as possible, and then make a rapid transition to the adult coloration. This occurs despite a possible elevated risk of infanticide associated with the neonate coloration (Onderdonk 2000; Bădescu et al. 2016), suggesting that the benefit of infant handling to the infant and mother is substantial.

Males did not handle the infant much at all, which was consistent with that of other studies of colobines

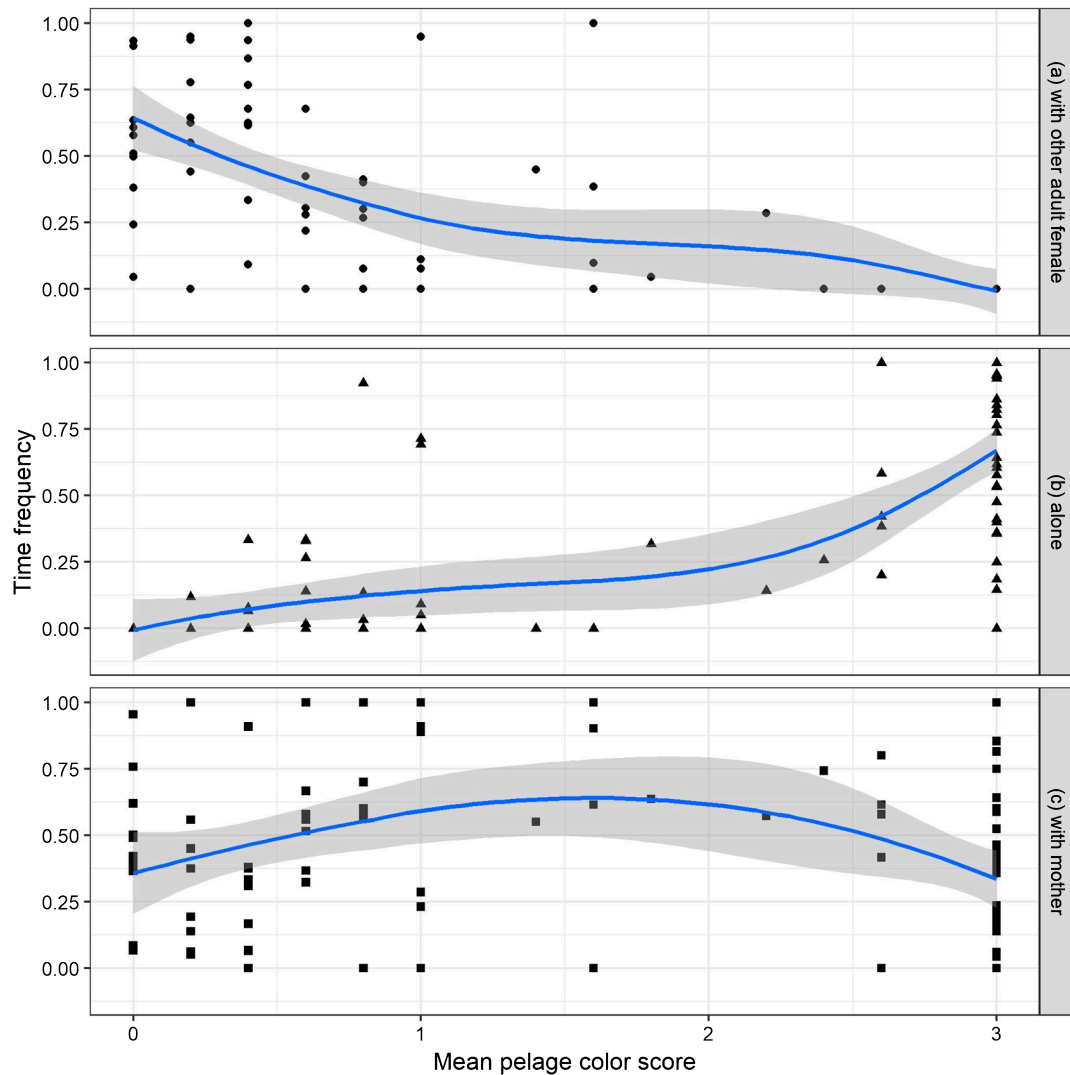


Fig. 3. Relationships between mean infant pelage color score and frequency that the time spent with females (a: non-mother female; c: mother) or for being away from adults, i.e., staying alone (b: alone). We interpolated the relationships between infant pelage color change (the overall mean: see Fig. 2) and the time spent with adults/away from adults, using a spline smoothing. Shaded areas indicate 95% confidence intervals.

(Brent et al. 2008), though some studies describe that males positively interact with infants (Wooldridge 1971). This pattern is also consistent with the fact that affiliative behaviors, like grooming, are primarily done by females, while males are generally peripheral to social interaction across colobines (Matsuda et al. 2012). Thus, not only grooming, but also infant handling in colobines, may facilitate female–female associations (Matsuda et al. 2012, 2015; Zhang et al. 2012).

As previously reported in *Colobus* spp. (Emerson 1973; Oates 1977; Bădescu et al. 2015), the infant handling by non-mothers was related to the infant pelage color and/or level of independence from the mother. In this study, a non-mother female (or nulliparous female)

seemed to be attracted by the new born infant with white pelage color and often handled the infant in the first few weeks after birth, but this gradually decreased as the infant got older, their natal coats disappeared, and the infant gained locomotory independence. Echoing observation of infant-handling behaviors in this study, Henderschott et al. (2019) suggested that in other colobine species (*T. francoisi* and *T. poliocephalus*), the coat signals dependence and promotes allocare of infants as they found an association between increased infant independence and decreased infant-handling behaviors that were progressively developing adult coat coloration. The current information is, nonetheless unfortunately, too limited to differentiate the independent effects of infant

pelage color and infant locomotory independence on female-handling behavior. Research that focuses on both of these factors across a number of colobine species, and considers body mass, are needed to clarify their evolutionary significance.

In general, our study supports the hypothesis that inexperienced females benefit by handling infants and learning maternal skills that they will need for their own infant (Lancaster 1971). In contrast to the well-skilled infant handling behaviors by the multiparous mother, the infant handling skill by the nulliparous female appeared to improve over time. In the beginning, the nulliparous female awkwardly carried the infant, nearly dropping it on several occasions. This nulliparous female successfully nurtured her own infant when she gave birth in March, 2016.

The time spent handling the infant by the mother was unexpectedly stable throughout the study. This supports the hypothesis that infant handling by non-mothers allows mothers to engage in beneficial activities, such as feeding (Hrdy 1976) and the conspicuous pelage color of infants functions to promote non-mother infant handling.

We suggest that in the future quantifying the relative costs/benefits of the interaction among the mother, the infant, and the third party under a variety of ecological settings, e.g., high and low food availability, risk of infanticide (see Bădescu et al. 2016), will be key to understanding the function and evolution of infant handling across the order Primates. Colobines offer a useful taxonomic group to make such a quantification of infant-handling behaviors as those behaviors are commonly observed both in captive and wild populations (Maestripieri 1994) and they can be found in a variety of settings that vary in ecological and demographic conditions (Chapman et al. 2017).

Acknowledgments: We thank the Japan Monkey Centre, in particular, T. Matsuzawa, G. Idani, S. Sakaguchi, M. Uchikoshi and K. Watanuki, for facilitating the project and sharing their knowledge of the monkeys. Finally, we are grateful to two anonymous reviewers for their fruitful comments. This study was partially funded by the Chubu University Grant (to IM) and the Leading Graduate Program of Primatology and Wildlife Science (PWS) of Kyoto University. This study was conducted in compliance with guidelines for care and use of nonhuman primates by the Japan Monkey Centre.

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Received 4 December 2019. Accepted 15 May 2020.

Editor was Yamato Tsuji.