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## Natal-to-juvenile pelage change in free-living François' (*Trachypithecus francoisi*) and Cat Ba langurs (*T. poliocephalus*)

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**Key words:** limestone langurs, pelage, natal coat, Cat Ba langur, François' langur

### Summary

This article discusses the timing, patterning, and implications of natal pelage loss for two species of limestone-dwelling Asian colobines – François' (*Trachypithecus francoisi*) and Cat Ba (*Trachypithecus poliocephalus*) langurs. It considers why some primate species, such as those in the *Trachypithecus* genus, are born with a flamboyant, orange natal coat and what purpose it may serve in promoting allocare and reducing the threat of infanticide. With 11-12 months of observation of each species, this study assesses the pattern of natal coat loss for three François' langur infants living in Mayanghe Nature Reserve (China) and three Cat Ba langur infants living on Cat Ba Island (Vietnam). There was conflicting evidence for our first hypothesis, as the pattern of natal coat loss is similar in both species, although the timing is sped up in François' langur infants. Using previous data on these species, and confirming our second hypothesis, there does appear to be an association between increased independence and decreased group member interest in infants that were progressively developing an adult coat colouration, suggesting that the coat does signal dependence and promote allocare. Finally, in analysing the pattern of where the natal coat is lost first, observations suggests that both species of langurs may be using a paternity cloaking approach to avoiding infanticide. Ultimately, it is unclear if François' and Cat Ba langurs are experiencing different degrees of infanticidal threat given the contradictory evidence, nor is it known how or if their divergent patterns of development are related to habitat quality.

## Sự thay đổi màu lông từ lúc sinh ra đến tuổi bán trưởng thành ngoài tự nhiên của loài Voọc đen má trắng (*Trachypithecus francoisi*) và voọc Cát Bà (*T. poliocephalus*)

### Tóm tắt

Bài báo này thảo luận về thời gian, mô hình, và ý nghĩa của việc thay đổi màu lông khi mới sinh của 2 loài Voọc thuộc nhóm Asian colobines gồm Voọc đen má trắng và Voọc cát bà. Giả thuyết là các con non mới sinh của các loài linh trưởng thuộc nhóm *Trachypithecus* có bộ lông với màu vàng cam sặc sỡ có mục đích tăng cường sự quan tâm chăm sóc từ các cá thể khác trong đàn và giảm thiểu nguy cơ bị giết chết. Qua 11-12 tháng thu dữ liệu với 3 con nhỡ của loài Voọc đen má trắng François' ở khu bảo tồn thiên nhiên Mayanghe (Trung Quốc) và 3 con nhỡ của loài Voọc cát bà ở Vườn quốc gia Cát bà (Việt Nam), nghiên cứu này kiểm nghiệm quá trình mất màu lông tự nhiên của cả 2 loài Voọc này. Có bằng chứng mâu thuẫn cho giả thuyết thứ nhất được ghi nhận ở cả 2 loài này về quá trình thay đổi bộ lông, mặc dù thời gian thay đổi màu lông ở loài Voọc François' nhanh hơn.

Cùng với các dữ liệu đã ghi nhận trước đây và xác nhận trên giả thuyết thứ hai cho thấy có mối liên hệ giữa sự tự lập tăng lên và sự quan tâm của các thành viên trong đàn giảm xuống với con non có bộ lông đang dần biến đổi sang bộ lông của con trưởng thành, điều này gợi ý bộ lông là dấu hiệu của sự tự lập và thúc đẩy sự quan tâm.

Cuối cùng, kết quả phân tích dữ liệu cũng chỉ ra rằng con non của cả 2 loài đều có phương thức

giấu mối quan hệ cha con để tránh việc bị giết trong tiến trình thay đổi màu sắc bộ lông.

Sau cùng, không rõ liệu 2 loài Voọc này trải qua các mức độ đe dọa bị giết khác nhau với các bằng chứng mẫu thuẫn, cũng không rõ các quá trình phát triển khác nhau có liên quan đến chất lượng môi trường sống hay không.

## Introduction

Some primates are born with coats that differ from adult coat colouration and patterns (Ross & Regan 2000). Of these, a particular group is born with coats that are flamboyant and stand in sharp contrast to the adults of those species. Asian langurs fall within this category, with bright orange natal coats that conspicuously stand out against the grey, black and/or white adult colouration (Blaffer Hrdy 1976; Oates & Davies 1994; Groves 2001; Nadler et al. 2003).

The eventual loss of the natal coat can be used to age individuals (Treves 1997) as infants tend to show increased independence by spending less time proximate to (Horwich 1974; Stanford 1991) and nursing from (Treves 1997) their mother at approximately the same time that the natal coat changes. It is also around this stage that nonmaternal group members lose interest in handling infants (Jay 1963).

The timing of the loss of natal coat colouration may be affected by available resources, habitat quality, and social pressures. For example, it is proposed that Pharye's leaf monkeys (*Trachypithecus phayrei*) in larger groups experience an increase in scramble competition, resulting in a delay of the acquisition of adult coats by infants (Borries et al. 2008). This is presumably due to mothers being nutritionally deprived, thus limiting the nutrients they can pass on to their developing young. This effect of food-limitation is supported by the fact that places (e.g. captivity) or periods (e.g. provisioning) with reliable availability of higher-quality resources increases maturation and reproductive rates for primates (Altmann et al. 1981; Sugiyama & Ohsawa 1982; Newton 1987; Altmann et al. 1993; Mori et al. 1997; Altmann & Alberts 2005).

Additionally, the speed at which natal coats are lost may be related to infanticidal pressures. Ursine colobus (*Colobus vellerosus*) infants that live under high threat of infanticide (specifically, male infants and infants living in multimale groups) develop adult colouration faster than those that do not face as high of infanticidal pressures, possibly because of increased maternal investment (Bădescu et al. 2016). This hastened transition away from natal coats may reduce infanticide risk despite the fact that the infants are still nursing (Bădescu et al. 2016). In other words, the loss of the natal coat is acting as a visual code for 'independent' to infanticidal males, even though the infants are behaviourally dependent on their mothers.

There is debate as to the advantages and disadvantages to a contrasting natal coat, with several hypotheses focusing on infanticide-avoidance benefits. This is because while dependent and unweaned infants that have a conspicuous natal coat may be more obvious to potentially infanticidal males, they are also highly attractive to group members; thus the high coat contrast may be indicative that the group will unite in protection of the infant against infanticidal males. This hypothesis has been termed the infant defense hypothesis (Treves 1997). This idea has been somewhat supported in Asian langurs as the orange natal coat seems to have care-eliciting effects on group members, which may reflect a psychological and evolutionary tactic to induce caretaking and to create a safe social environment for young at their most vulnerable and dependent stage, by increasing group member interest and tolerance and decreasing aggression; although natal coats certainly are not necessary for such purposes (Alley 1980). There is a pattern for species with high rates of allocare (caretaking by nonmaternal group members) to have more adult-to-infant colour contrast especially in areas that are highly-visible on clinging infants (Blaffer Hrdy 1976; Ross & Regan 2000). This suggests that areas such as the crown, legs, and back will be the last to change colouration, since these are the body parts that are most obvious to potential caretakers (Treves 1997). However, research suggests that these areas are often the first to change, as seen in a number of primates, such as Guatemalan black howler monkeys (*Alouatta pigra*), agile mangabeys (*Cercocebus agilis*), king colobus (*Colobus polykomos*), stump-tailed macaques (*Macaca arctoides*), hamadryas baboons (*Papio hamadryas*), and Hanuman langurs (*Semnopithecus entellus*) (Treves 1997).

Alternatively, the paternity cloaking hypothesis states that a natal coat may mask paternal phenotypic indicators, thus protecting infants from males that may recognise the infant as not being his own (Treves 1997). For example, when a female mantled howler monkey (*Alouatta palliata*) was born with white patches on her feet, similar to the male that took over the group and that the mother had previously consorted with – and dissimilar to the previous resident male or her mother – she was spared from infanticide, unlike some of her infant group mates (Clarke 1983). Only areas that a male is able to see on his own body are relevant to this hypothesis; thus, this hypothesis excludes backs, heads, and faces, as males cannot gauge how similar an infant is to these areas of his body (Treves 1997); instead this hypothesis predicts that ventrums, limbs, and tails will be the last features to change, so as to confuse paternity for potentially-infanticidal males.

Limestone langurs are Asian colobines that live on limestone karst in China, Vietnam, and Laos (Groves 2007; IUCN 2015). The species-group can be divided into a northern clade with François' (*Trachypithecus francoisi*), Cat Ba (*T. poliocephalus*), and white-headed (*T. leucocephalus*) langurs – and a southern clade with Delacour's (*T. delacouri*), Lao (*T. laotum*), Hatinh (*T. hatinhensis*), and Indochinese black (*T. ebonus*) langurs (Roos 2003; Roos et al. 2007), divided by the Red River (Groves 2007). Limestone langurs, as with several other primates with unimale-multifemale social structures (Struhsaker & Leland 1987), experience infanticide (Li & Rogers 2004; Zhao et al. 2011; Yao et al. 2012), and nonmother-group mates show an interest in allocare that declines with infant age (Hu 2007; Yao et al. 2012; Jin et al. 2015). Thus, both infanticide (which, as a reproductive strategy, is focused on unweaned individuals: Blaffer Hrdy 1979; Struhsaker & Leland 1987) and allocare are associated with neonates. For example, one-to-eight month-old white-headed langur infants disappeared after takeovers of unimale-multifemale groups by a strange male – i.e. those who were not old enough to be weaned and were still dependent on their mothers – which accounted for 42.9% of all white-headed langur infant mortality during this study period (Zhao et al. 2008; 2011). White-headed langur infants under one month spend 20-30% of daytime observations being handled by someone other than their mothers, but there is little handling for those over two months of age (Jin et al. 2015).

This study aims to document the progression of natal-to-adult coat colouration for François' and Cat Ba langurs in order to compare and contrast closely-related species to one another and to other Asian colobines living in different habitats, and to draw connections between natal coats, independence and allocare interest. We hypothesise (Hypothesis 1) that the two species will follow a similar timing and patterning of natal coat loss. We further hypothesise (Hypothesis 2) that the timing of the loss of the natal coats will be related to measures of independence and allocare interest (e.g. time spent in proximity), which will be analysed based on data from other sources. Our data can also be used to assess whether the pattern of natal coat loss is related to allocare interest (Alley 1980) or paternity cloaking (Treves 1997) on behalf of infanticide avoidance (Hypothesis 3); if the former, we would expect the dorsum, head, and legs to retain the natal coat the longest, and if the latter we would expect the ventrum, limbs, and tail to take the longest to shift to adult colouration. The methods used are an easy, noninvasive way of assessing development (Treves 1997), which is important for age-estimates by survey team members, researchers, and conservation groups as it will allow for more accurate censusing.

## Methods

### Study Species

This study looks closely at François' and Cat Ba langurs, who diverged 0.50-0.25 million years ago due to geographic barriers (Liu et al. 2013). François' langurs are 'Endangered' (Bleisch et al. 2008a), and live in southern China; Cat Ba langurs are 'Critically Endangered' (Bleisch et al. 2008b) and are endemic to Cat Ba Island (northeastern Vietnam). Both species live on limestone karst hills that are threatened with degradation and fragmentation, ultimately resulting in a loss of habitats; hunting is another cause for drastic population declines (Nadler et al. 2003; Hu et al. 2004; Stenke & Chu Xuan Canh 2004).

Author GH has documented two takeover events in François' langurs; one failed but another was successful and led to a group split. However, only one infant in seven years of study was

presumed to have died from an invading male (Hu 2007), suggesting that takeover may be a rare occurrence. There are two observations of infanticide and takeover among Cat Ba langurs from 1998-1999 (Nadler pers. comm.), in addition to a more recent (2018) observation of an adult male injuring an infant (Rawson pers. comm.). It is likely that with more hours of observation, reported infanticides would increase.

Both François' and Cat Ba langurs show the typical pattern of neonate attraction. Group members, including juvenile females, show great interest in being able to touch, groom, suckle, or hold François' langur infants, although mothers do not allow anyone else to handle their infants until they are over two weeks of age (Hu 2007). Although Cat Ba langur individuals were not individually recognisable, it is clear that nonmothers are interested in handling young group members because of the amount of infant transfers that have been observed, which are focused on newborns (68% of transfers) and infants (32% of transfers) but never occur in young juveniles or juveniles (Hendershott unpubl. data).

Both of the closely-related François' and Cat Ba langur adults have dark brown/black pelage, a crest on their head, white 'moustaches' that go ear-to-ear, and a black 'cape' of hairs (Nadler & Ha Thang Long 2000; Nadler et al. 2003; Groves 2007) (Fig. 1). While François' langurs are entirely black except for the moustache (Fig. 1b), Cat Ba langur shoulders, head, and crest are orange/golden and they have a V-shaped saddle band of grey hairs across their lower back, stretching from thigh to thigh (Groves 2007) (Fig. 1a). Both species exhibit flamboyant orange natal coats at birth (Groves 2001), and the only areas that are sexual dichromatic are pale pubic patches on the inner thighs (Brandon-Jones 1995; Nadler et al. 2003).



**Fig.1.** Adult Cat Ba (a) and François' (b) langurs with young attached.

### Behavioural Observations

François' langurs were studied by one of the authors (GH) in Mayanghe Nature Reserve (northeastern Guizhou, China) from January 2005 to January 2006, while Cat Ba langurs were studied by another author (RH) on Cat Ba Island (northeastern Vietnam) from February 2014 to January 2015. The François' langurs were observed on foot, with or without binoculars depending on distance between researcher and langurs, while the Cat Ba langurs were observed from a boat 50-300 metres away with binoculars. Boats are often used in the study of limestone langurs living nearby water (Schneider et al. 2010; Workman 2010; Agmen 2014; Phan Duy Thuc et al. 2014), as traversing the karst is dangerous and time consuming. At both field sites data collection began around sunrise and concluded at sunset.

Age-related changes to coat colouration and body size were noted ad libitum and documented with photographs; they are mentioned descriptively. Descriptions are roughly divided into the first (days 0-30), second (days 31-60), third (days 61-90), and fourth (days 90-120) months, followed by months 5-8 (days 121-240), 9-11 (days 241-330), and 12-36 (over 330 days). Note that when mentioning 'the second month' or 'months 5-8', this refers to changes that occur *during* those months (i.e. the 'second month' includes 'after the first month' and 'before the third month').

Among both species, the same individuals were observed over time to assess stages in natal

coat loss, and all immature individual coat colourations were documented. This includes the six infants born during the study (three François' and three Cat Ba langurs) as well as a Cat Ba langur female born January or February 2014 and three juvenile François' langurs and five juvenile Cat Ba langurs. During the study periods, there were three infants born (one in January and two in February 2005) to the François' langur group under study (LYY-G1; total 9-12 individuals), and three infants born (one in August 2014, one in October/November 2014, and one in December 2014/January 2015) to one of the Cat Ba langur groups under study (Group A; total 10-13 individuals). The date of birth is assumed to be between the last sighting of the group without a newborn and the first sighting with a newborn; this ranges from 1 to 13 days for individuals born during the study.

### A note on authorship

GH was collaborating with CG on a manuscript on pelage shifts, and had given him all of his photographs and some notes, at the time he died. When RH approached CG about a manuscript on pelage shifts, he provided useful feedback and recommended the data be combined with that of GH and passed on those photographs and notes. While working on this manuscript, CG died. Thus, RH and AB are left with data obtained by GH, shared with CG, and then passed on to them. Both RH and AB are extremely grateful for the hard work that both GH and CG put into this topic, and want to make it clear that the data have been given to them third-hand. Despite this, however, it seems a waste to not publish the results of GH and CG's hard work in combination with their own, as it is so similar. The holders of the estates of CG and GH have approved this manuscript and their co-authorship. All photographs were taken by the authors in the course of their fieldwork unless otherwise noted.

### Results

When first born, both langur species are completely bright orange with pink-grey face, ears, and hands, a small bald spot on the forehead (with no crest) and pinkish ischial callosities (Fig. 2a,b). While François' langur newborns have black hairs scattered along the tail, newborn Cat Ba langur tails are completely orange. By one month of age Cat Ba langurs have a slightly faded orange coat, especially on the head, where dark-tipped hairs – the beginnings of a crest – start to develop. Over the first month (days 0-30), the face and digits of both species of langur infants begin to darken (Fig. 2c,d), and the lower three-quarters of the François' langur tail shifts to black (Fig. 2d). In both species, the animals are extremely skinny, without the characteristic distended gut of a leaf-eating primate.





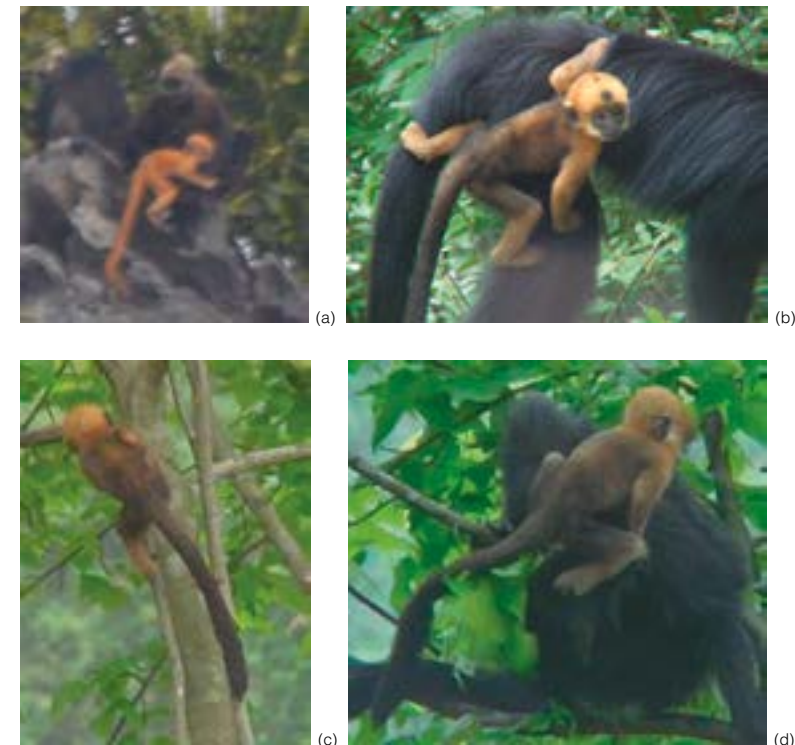
**Fig.2.** A newborn Cat Ba langur 3-6 days after birth (a), a 15-18 day-old (photo by Kayla Hartwell) (b) and 24-35 day-old (c) Cat Ba langur infant. A 13-15 day-old François' langur (d). Note the pink exposed skin and bright orange coat at birth; the skin darkens in two-week-old François' langurs, while Cat Ba langurs retain more of the natal coat throughout the first month.

In the second month (days 31-60), the face, ears, hands, and feet darken in both species (Fig. 3). Among Cat Ba langurs, the crest continues to darken, and although the orange natal coat is dulled (especially on the limbs), black hairs are not yet visible (Fig. 3a). Among François' langurs, black hairs appear on the torso, arms, and upper legs, and the beginnings of a yellowish-white moustache spread from both ears towards the mouth, and black hairs begin to form above the forehead (Fig. 3b).



**Fig.3.** Infant Cat Ba langur at 41-44 days of age (a). A 60-day-old François' langur (b). Note darkened skin in both species.

In the third month of life (days 61-90), both langur species' face, ears, hands, and feet have become a dark grey, which is still lighter than adult colouration (Fig. 4). Cat Ba langurs continue to become a duller orange colour, with dark hairs beginning to show (Fig. 4a). They have a small black spot above the base of the tail, and the tail is darker on the underneath side than the top. François' langurs develop a fully-darkened and pointed crest, their moustache lightens from yellow to white, and their fur continues to darken, including on the lower legs (Fig. 4b,c,d). In both species, ischial callosities start to become more white than pink.



**Fig.4.** A 57-68 day old Cat Ba langur (a). A 68 (b), 72 (c), and 88 (d) day-old François' langur infant. Note the drastic differences in pelage between the two species at this stage.

Drastic pelage changes occur for both species in the fourth month of life (days 91-120). Among Cat Ba langurs, all exposed skin is now dark (Fig. 5a,b), the beginnings of a white moustache appear, and the limbs are lighter-coloured than the torso. An undercoat of dark grey/black stretches across the lower back (making the coat a lighter shade of orange), as does the beginnings of the greyish saddle (Fig. 5a,b). The basal third of the tail is dark with black hairs, although the remaining tail is still mostly orange (Fig. 5a,b). Among François' langurs, the pelage has become almost entirely black in a short period (from days 125-130), with only some yellow fur retained on the head and shoulders (Fig. 5c,d). Both the moustache and crest become more adult-like (although the moustache is wider than those of older individuals), and it is at this stage that sex can be determined in François' langurs.





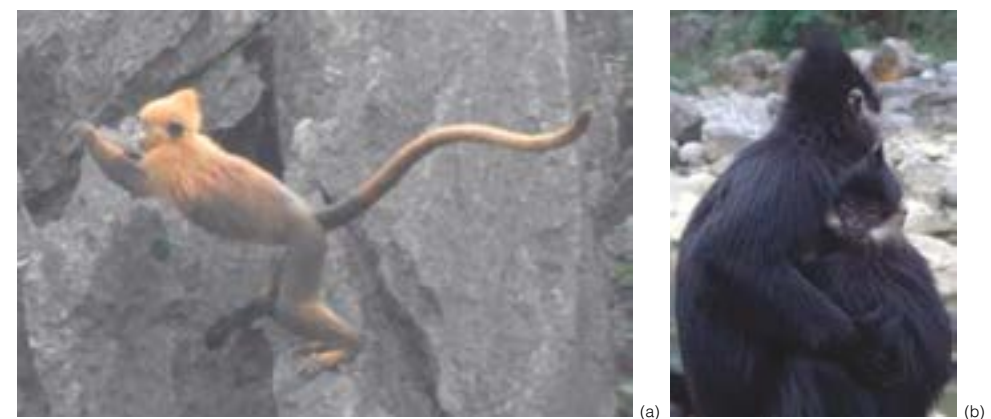
**Fig.5.** Young Cat Ba langur 99-102 (a) and 119-122 (b) days since birth. Infant François' langurs at 97 (c) and 115 (d) days old. Note the drastic difference between the dark coat of François' langurs and the slowly-transitioning coat of the Cat Ba langur.

From months five to eight (days 121-240), both langurs develop adult-coloured black skin. Among Cat Ba langurs, the back has shifted from an orange coat with a dark undercoat to being a dark coat with a slight orange tinge (Fig. 6a,b); there is a small orange spot between the shoulder blades. The neck and shoulders are still pale orange, as are the limbs (upper legs and lower arms are darker than lower legs and upper arms) and lower tail (by the end of this period only the lower third of the tail is orange, and the underside remains darker than the top). The blanched thigh patches of females and the saddle become more visible (Fig. 6a). It is at this stage that Cat Ba langurs gain the larger abdomen characteristic of leaf-eaters. François' langurs continue to have pelage darkening (albeit yellow hair is still visible on the head and crest), a whitening of the moustache, and a more pointed crest (Fig. 6c,d).



**Fig.6.** Young Cat Ba langur 168-199 (a) and 180-211 (b) days since birth. François' langurs at 130 (c) and 146 (d) days old.

From months nine to 11 (days 240-330), Cat Ba langurs' lower back is black while the upper back is grey; most of the limbs are dark with the exception of small orange patches on the tops of wrists and feet (Fig. 7a). Although a dark patch of hairs become visible on the tip, there are still some light patches in the lower third of the tail (Fig. 7a). François' langurs develop a jet-black coat, and the last of the yellow hairs on the head are lost (Fig. 7b). Their moustache is predominantly white, yet remains wider than those of older individuals (Fig. 7b).



**Fig.7.** A Cat Ba langur at 264-295 days of age (a). A François' langur at 320 days of age (b). Note that both species have gained the large abdomen, although they differ markedly in the retention of the natal coat.

Animals one to three years old (over 330 days old) are juveniles (based on their foraging and locomotor independence) in both langur species. Among Cat Ba langurs, colouration is also similar to adults and subadults, except that the orange colours on their head and neck are brighter and their torso, limbs, and skin are a duller black (more of a faded orange-brown, especially on the front of the torso and the lower legs, with small spots of pale yellow e.g. between the shoulder blades and on the tops of the wrists and feet) (Fig. 8a). A dark-tipped crest and light-grey saddle are easily visible, the tail retains some pale orange colouration, and the underside is still darker than the top. A fully distended stomach is visible in juveniles (Fig. 8a). Among François' langurs, the moustache narrows and becomes whiter during this stage; colouration is similar to adults (Fig. 8b).



**Fig.8.** Cat Ba juveniles over one year old (birthdate unknown) (a). François' langur at 13-14 months of age (b). Note the lighter pelage colouration of Cat Ba langurs in contrast to François' langurs.

## Discussion

This study is one of the first to assess natal pelage shifts in two [Critically] Endangered species, for which little is known on this topic (although the pelage development of Delacour's and Hatinh langur have been described by Nadler 1997). These shifts in pelage can be a useful way of aging individuals, as well as providing evidence for various theories related to dependence, allocare and interest by group members, as well as infanticidal pressures and resource availability.

## Hypothesis 1

### Similar Timing and Patterns for François' and Cat Ba Langurs

In regards to our first hypothesis: there are parallels and divergences in the timing and patterning of natal coats loss between François' and Cat Ba langurs, although generally the gradual shift from natal-to-juvenile pelage changes are similar to those noted for other Asian colobines (Horwich 1974; Blaffer Hrdy 1977), including another species of limestone langur – the Delacour's langur; although the latter was a study in captivity (Nadler 1997; Agmen 2014). Both study species are born bright orange with pink-white skin on the face, hands, and feet; by four months they have lost the majority of their natal coat; and by one year of age they are mostly adult-coloured with species-typical coats; including moustaches for both species, a grey saddle and a yellow head/neck for Cat Ba langurs and a black head/neck for François' langurs.

Cat Ba and François langurs differed in several aspects of developmental timing. François' langurs are born with black hairs on their tail, while Cat Ba langurs have a completely orange tail. In the first month, three-quarters of François' langur tails are black (Fig. 9b), whereas the tail does not start to darken for Cat Ba langurs until the third month, and faded orange colouration remains on the tail into the juvenile stage (12+ months) (Fig. 9a). Reports of Cat Ba langurs in captivity indicate that one year old juveniles have orange-brown on just over half of their tails, and the tail does not really begin to darken until six months of age (Nadler & Ha Thang Long 2000). In contrast, a captive Delacour langur infant of two weeks of age had a predominantly black tail (Nadler 1997; Agmen 2014).



**Fig.9.** A Cat Ba langur infant (left, 99-102 days old) and juvenile (right, 264-295 days old) (a). A François' langur newborn, less than 20 days old (b). Note the very different patterns of tail colouration.

François' langurs have the beginnings of a moustache by the second month, and a crest begins to develop in the third month; both are relatively adult-like by the end of the fourth month (the moustache continues to whiten and narrow, and the crest becomes more pointed, until François' langurs are juveniles). Conversely, Cat Ba langur moustaches start to become visible in the fourth month. Their crest is visible within the first month and starts to darken in the second month; it is more adult-like by the tenth month. The captive Delacour langur also had the beginnings of a crest at a month of age (Nadler 1997; Agmen 2014).

While François' langurs have black hairs appearing on their torso, arms, and upper legs by the end of the second month, this does not occur for Cat Ba langurs until the third month. François' langurs have an almost entirely jet-black pelage by the fourth month, while Cat Ba langurs still have a dull black coat with species-typical orange on the head and neck at 12+ months of age. Among captive Cat Ba langurs, the back does not darken until around six months of age, and two year olds have still not acquired a full adult colouration as their head and shoulders are more golden than those of adults (Nadler & Ha Thang Long 2000). In a captive male Delacour langur, the coat became dark orange in the second month, and by three months the chest started to darken while the dorsal side of the back and limbs were black; at five months he was 75% black, with patches of orange on the head, shoulders, and groin (Nadler 1997; Agmen 2014). Thus, François' and Delacour langurs develop dark colouration faster than Cat Ba langurs on their tails, torsos, and limbs. François' langurs also have moustaches that appear two months earlier than Cat Ba langurs. The Cat Ba and Delacour langurs, however, have earlier crest development. It is possible that the earlier loss of François' and Delacour langur natal coats is due to the fact that adult coats are darker black than the 'dark chocolate-brown' coats of Cat Ba langurs (who may retain yellow-brown hairs on the feet into adulthood: Groves 2007) (Nadler & Ha Thang Long 2000), thus making them easier to observe from a distance as they sharply contrast with orange natal coats and white moustaches. This does not, however, account for the drastic differences in tail colouration between these species, nor the fact that Cat Ba langurs in captivity (i.e. those that can be observed at a closer range) have similar development to those observed living in the wild, but not other captive Delacour langurs kept at the same facility (Endangered Primate Rescue Center - EPRC) in Vietnam.

## Hypothesis 2

### Independence and allocare interest

Across other primate species, this shift in natal-to-adult pelage is accompanied by an increase in independence (Jay 1963; Blaffer Hrdy 1976; Stanford 1991; Treves 1997), which is the same pattern we report here based on comparing our results with other data on measures of independence. For example, at the time when the skin darkens and dark hairs starts to show up on one-to-two month old François' langurs, the infants start to explore, rest, and play within a short distance of their mother or handler (Hu 2007). By the time drastic colouration shifts are happening in the fourth month, 42% of

infant locomotion is independent, and 50% of foods are solid (Hu 2007). By the time François' langurs are predominantly adult coloured, 90% of their food is solid (with weaning being complete around 12-14 months) and 98% of their locomotion is independent (Hu 2007). Among Cat Ba langurs, the 3-16 week old infants included in this study spent 26% of their time alone (i.e. not within arm's reach of another langur), 19% of their time on another langur, and are starting to locomote and forage on their own (Hendershott 2017). At about four months of age, around the time when the coat darkens significantly, Cat Ba langurs spend twice as much time alone as 3-16 week old individuals (50%) and only 1% of their time on another langur; their locomotion, foraging, and play rates also increase significantly compared to the previous age period (Hendershott 2017). A similar trend is seen in captive Delacour langurs. During their second and third months of life a drastic colour change is seen, which is also the same time that Delacour's langurs start foraging on their own more often and clinging to adults less often – their locomotion is frequently independent by one month of age (Agmen 2014).

This reported increase in independence associated with pelage changes is also related to a reduction in interest by group mates, at least in Cat Ba langurs. Among Cat Ba langurs, the average number of group members that are in proximity to young langurs (a proxy measure for interest) is inversely proportional to the infants' age category (Hendershott 2017), and newborns with full natal coats (0-3 week olds) receive twice as many transfer attempts as infants that have started to lose their natal coat (3-16 week olds) (Hendershott unpubl. data), despite the shorter time period of 'newborn'. Similarly, a captive Delacour's langur infant was handled by nonmaternal group mates most often during his second month of life (29% of the time), decreasing to 24% in the third month, which coincides with the darkening coat (Agmen 2014). This supports both our second hypothesis (pelage is related to dependence and allocate interest) and the infant defence hypothesis for Cat Ba langurs, in that group members are attracted to individuals with a natal coat, and their attraction, proximity, and caretaking may help in preventing the infant being killed by a strange male during their most vulnerable period (Alley 1980).

### Hypothesis 3

#### Pattern of Natal Coat Loss

Both François' and Cat Ba langurs started to change pelage colouration on their heads and backs first, with limbs and tails being the last body parts to shift away from the orange natal colouration. In terms of understanding this pattern in relation to infanticidal pressures, these results suggest that the flamboyant natal pelage is not acting as a signal to group members – otherwise these areas that are visible while an infant is carried would retain orange longer (cf. Alley 1980). Instead, it suggests that paternity cloaking may be the selective pressure they are responding to; by masking areas that a male can use to identify his offspring (such as the ventrum, limbs, and tail), infants are protected from phenotypic-identification (Treves 1997).

### Implications

The faster shift to adult colouration for François' langurs suggests that they suffer higher infanticide pressure than Cat Ba langurs (cf. Bădescu et al. 2016); development may have been sped up so as to seemingly avoid a long period of dependence and, thus, vulnerability to infanticide. Interestingly, this visual indicator of dependence does not directly correspond to behavioural dependence: François' langurs do not appear to be fully weaned until 12-14 months (Hu Gang 2007), although their pelage shift is relatively complete by five months of age. Either way, this result suggests that François' langurs may have historically suffered higher infanticide pressure. Although the current François' langur populations are less fragmented and more populous than those of Cat Ba langurs – which means that takeovers are more likely, and infants would benefit from masking their maternal dependence (indeed, GH observed group splits, takeovers, and infanticide in the course of fieldwork) – it is unknown how long this difference may have been in place or when the differences in natal coat loss evolved. Interestingly, and in contradiction to the above implication, the paternity cloaking that seems to be happening among Cat Ba langurs suggests that *they* may experience higher threats of

infanticide from strange males than François' langurs; by retaining their natal coat longer, they are better able to confuse paternity.

These data and the hypotheses analysed thus present somewhat conflicting implications: developing into an adult coat may indicate that an individual is past the point of suckling (and thus not a target for infanticide), but retaining a natal coat may mask paternity (thus reducing infanticide threats). The key difference between the theories is that the former focuses on *timing* of natal coat loss, while the latter focuses on the *pattern* of body parts from which the natal coat is lost. The theory about increasing the speed of development (cf. Bădescu et al. 2016) suggests François' langurs are facing higher infanticidal pressures, while the theory about paternity cloaking (cf. Treves 1997) suggests Cat Ba langurs are under higher infanticidal threat. Ultimately, more detailed data and further research is needed in order to assess takeovers, infanticides, and infanticidal threats in these species.

Another implication of delayed maturation in Cat Ba langurs is that this island-living species may be exposed to poorer-quality habitat or resources than François' langurs (cf. Borries et al. 2008). However, this does not explain the differences in development between captive Cat Ba and Delacour's langurs, who were presumably supplied with similar foods at the Endangered Primate Rescue Center (Nadler & Ha Thang Long 2000; Agmen 2014), nor does it explain why the captive Cat Ba langurs are more similar to their free-living counterparts than other captive limestone langurs at the same facility. Research into comparative habitat quality would help address this possibility.

### Conclusion

In conclusion, both François' and Cat Ba langurs are born with flamboyant orange coats typical of *Trachypithecus* species, which are progressively lost as infants age (Hypothesis 1). By one month of age, both François' and Delacour langurs have predominantly black tails, whereas this does not occur in Cat Ba langurs until after they are a year old. At four months of age, François' and Cat Ba langurs have lost their bright coats, and have started to darken. By the time François' langurs are 9-11 months old they have their dark black coats; Cat Ba langurs gain adult colouration after one-two years of age. The loss of the natal coat is related to increased independence (in both species) and decreased interest in infants by group members (for Cat Ba langurs) (Hypothesis 2). The pattern to which areas of the body shifts colouration suggests that of the infanticide-avoidance hypotheses, the objective appears to be paternity cloaking (Hypothesis 3). Overall, Cat Ba langurs appear to lose their orange natal coat slower than François' langurs. This might be explained by differences in infanticidal pressure and habitat quality between the two species, although further research is necessary.

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