

Infanticide pressure accelerates infant development in a wild primate



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The rate at which infants develop can vary within species. This variation may be due to differences between infants in their nutritional intake and physiology, or the ability of females to adjust the amount and timing of maternal investment to maximize their lifetime reproductive success. This is the first primate study that uses a large sample size and multivariate analyses to investigate whether variation in early infant development (measured visually using durations of natal coat stages) is explained by differences in infanticide pressure, predation pressure or feeding competition among mothers. We recorded the number of days that infants took to transition through each of the two natal coat stages (white to grey: $N = 32$; grey to black-and-white: $N = 22$), as well as through their entire natal coats (white to black-and-white: $N = 38$) in a population of wild ursine colobus, *Colobus vellerosus*. Infant males, which are at greater risk of infanticidal attacks, transitioned coat colours earlier than females, and infants in multimale groups, where infanticide occurs more frequently, transitioned earlier than infants in unimale groups. Variation in group size did not affect natal coat durations, which suggests that the intensity of predation risk and feeding competition do not influence development. Instead of terminating investment in offspring before birth, as in the 'Bruce effect', females may invest more heavily in infants after birth in order to speed up infant development and reduce the time period during which offspring are the most vulnerable to infanticide. Mothers may therefore have flexible means of exerting choice over maternal investment in relation to infanticide risk. However, the extent to which mothers and infants are responsible for adjusting the speed of development is unknown.

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The rate at which infants develop can vary within species and lead to differences in life history characteristics of individuals later in life (Lindstrom, 1999). Infants may affect their own rates of development through their capacity to nurse and reach nutritional independence, and through their ability to influence lactation and caregiving behaviours of their mothers (Sellen, 2009; Winberg, 2005). Mothers can also influence the development rates of their infants by adjusting the amount and timing of maternal investment to minimize infant mortality and maximize their lifetime reproductive success (Lee, Majluf, & Gordon, 1991; Lindstrom, 1999). Within populations, specific factors, such as infanticide risk, predation pressure and feeding competition have been documented to impact infants' rates of development in terms of growth and timing in attaining nutritional independence. When infanticide pressure

from adult males is high, anecdotal reports suggest that mothers may accelerate the process of reaching nutritional independence by weaning infants sooner or more abruptly (rodents: Dobson, 1990; primates: Colmenares & Gomendio, 1988; Fairbanks & McGuire, 1987; Saj & Sicotte, 2005; Teichroeb & Sicotte, 2008a; Watts, 1989; Zhao, Tan, & Pan, 2008). Changing predation conditions can also affect maternal investment strategies and influence the development of offspring (birds: Coslovsky & Richner, 2011; Fontaine & Martin, 2006; lagomorphs: Sheriff, Krebs, & Boonstra, 2009; rodents: Mashoodh, Sinal, & Perrot-Sinal, 2009). For example, birds reared in conditions of high predation risk show accelerated growth rates that enable them to escape from predators at an earlier age (Bosque & Bosque, 1995; Coslovsky & Richner, 2011; Fontaine & Martin, 2006). Competition over food can decrease the foraging efficiency and net energetic gain of females (Chapman & Chapman, 2000; Chapman, Wrangham, & Chapman, 1995; Janson & Goldsmith, 1995; Koenig, 2002), which can compromise lactation and lead to slower infant development and delayed weaning

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(Australian sea lion, *Neophoca cinerea*: Lowther & Goldsworthy, 2011; white-tailed deer, *Odocoileus virginianus*: Therrien, Côte, Festa-Bianchet, & Ouellet, 2008; Phayre's leaf monkey, *Trachypitecus phayrei*: Borries, Larney, Lu, Ossi, & Koenig, 2008).

In some mammals, infants are born with a natal coat that is distinct from the pelage of adults. Although this paper does not focus on the functions of natal coats, it is useful to establish that their functions likely vary between taxa, and have yet to be determined in others. Among the functions that have been identified, natal coats can provide insulation against overheating (pinnipeds: Erdsack, Dehnhardt, & Hanke, 2013), provide protection against predation through background matching (felids, artiodactyls and pinnipeds: Booth, 1990; Caro, Stankowich, Mesnick, Costa, & Beeman, 2012), and trigger interest in infants to promote care or defence by individuals other than the mother (primates: Hrdy, 1976; Oates, 1977; Ross & Regan, 2000; Treves, 1997). The 'oddity effect' of having a different pelage, however, can be costly for infants if natal coats make them conspicuous and more vulnerable to attack by predators or conspecifics (Landeau & Terborgh, 1986). In conditions of high infanticide or predation risk, it might therefore be important for infants to attain the adult pelage more rapidly in order to avoid being killed by adult males or predators.

When marked transitions occur from one coat colour to the next (Altmann, Altmann, & Hausfater, 1981; Bădescu, Sicotte, Nelson, & Wikberg, 2015; Borries et al., 2008; Bowen, McMillan, & Mohn, 2003; Currier, 1983; McDonald, Goebel, Crocker, & Costa, 2012; Meyers, Bowen, & Stobo, 1997), coat colour transitions are a useful, noninvasive way to visually measure infant development (e.g. felids: Currier, 1983; pinnipeds: Bowen, Oftedal, Boness, & Iverson, 1994; Erdsack et al., 2013; Frisch & Oritsland, 1968; Goldsworthy, 1995; Lowther & Goldsworthy, 2011; McDonald et al., 2012; Meyers et al., 1997; primates: Treves, 1997). Transitioning early from the natal coat has been positively correlated with other markers of growth and development, such as weaning age and the attainment of physical and behavioural independence (e.g. Antarctic fur seal, *Arctocephalus gazella*, sub-Antarctic fur seal, *Arctocephalus tropicalis*: Arnould et al., 2003; McDonald et al., 2012; Verrier, Groscolas, Guinet, & Arnould, 2011; northern elephant seal, *Mirounga angustirostris*: Reiter et al., 1978; yellow baboon, *Papio cynocephalus*: Altmann et al., 1981; Nilgiri langur, *Trachypitecus johnii*: Poirier, 1968; *T. phayrei*: Borries et al., 2008). Variation in the timing of natal coat transitions may allow researchers to examine different maternal investment strategies and the varying capacities of infants to utilize resources to develop at different rates (Altmann et al., 1981; Borries et al., 2008; Bowen et al., 1994, 2003; McDonald et al., 2012). Specifically, in primates, a few studies suggest that there is variation in coat colour transitions between infants within populations in species where infants are born with a contrasting coat colour (Altmann et al., 1981; Borries et al., 2008), but sample sizes in these studies were limited and the range of potential factors influencing this variation has yet to be investigated.

The speed with which infants develop as newborns can have important consequences for their survival (Lindstrom, 1999). We take advantage of coat colour transitions, as a noninvasive way of measuring infant development, to investigate the variation in development during the life stage when infants are most vulnerable to infanticide (Teichroeb & Sicotte, 2008a,b), predation (Treves, 1997) and negative effects of feeding competition experienced by their mothers (Borries et al., 2008). This is the first study that uses the duration of natal coat colour as a proxy for infant development to evaluate whether infanticide pressure, predation pressure or the intensity of feeding competition can explain variation in development in a relatively large sample ($N = 92$ coat colour transitions in 48 infants). To investigate this question, we

used an arboreal primate, a member of the subfamily Colobinae, where the majority of species are characterized by contrasting natal coats (Treves, 1997). In our study species, the ursine or white-thighed colobus monkey, *Colobus vellerosus*, infants are born completely white and darken to grey and then to the adult black-and-white colour over several months (Brent, Teichroeb, & Sicotte, 2008). Our long-term observations at Boabeng-Fiema Monkey Sanctuary (BFMS) in central Ghana showed that the patterning of natal coat changes is uniform across infants but that variation occurs between infants in the speed with which the next coat colour is attained ('natal coat duration') (Bădescu, 2011; MacDonald, 2011). Infanticide attempts by extragroup males occur regularly during group take-overs and male incursions, accounting for 38.5% of infant mortality at BFMS between 2000 and 2005 (Teichroeb & Sicotte, 2008a). Large terrestrial predators were extirpated from the site in recent decades, but raptors, dogs and snakes still pose a threat to immature monkeys (MacIntosh & Sicotte, 2009; Teichroeb & Sicotte, 2012). Predation risk is greater in smaller groups, as individuals have fewer neighbours to help detect predators and dilute the chances of being preyed upon (MacIntosh & Sicotte, 2009; Teichroeb & Sicotte, 2012). Scramble feeding competition occurs in *C. vellerosus*, as females in larger groups spend more time feeding and range farther than females in smaller groups (Saj & Sicotte, 2007; Teichroeb & Sicotte, 2009).

We assessed interindividual variation in the development of *C. vellerosus* infants in relation to four hypotheses. First, if high infanticide pressure leads to faster infant development, we expected earlier colour transitions (a) for males than for females, because infant males have a higher risk of being targeted by infanticidal males in several primate species (Alvarez et al., 2015; Charpentier & Drea, 2013; Clarke, 1983; Hiraiwa-Hasegawa & Hasegawa, 1994; Sommer, 1987, 1994; Teichroeb & Sicotte, 2008a), (b) for infants in multimale groups than for infants in unimale groups, because multimale groups are more frequent targets of extragroup male incursions and male immigration attempts that increase infanticide risk (Teichroeb & Sicotte, 2010; Teichroeb, Wikberg, Bădescu, MacDonald, & Sicotte, 2012) and (c) for infants in larger groups, because larger groups have a higher number of females, making them more susceptible to male take-overs (Crockett & Janson, 2000; Steenbeek & van Schaik, 2001; Teichroeb et al., 2012).

Second, if the main factor behind variation in infant development is predation pressure, we expected the timing of colour transitions (a) not to be affected by the sex of infants (Cowlshaw, 1994), (b) to occur earlier for infants in unimale groups than for infants in multimale groups, as several males can offer greater predator defence (Cowlshaw, 1994; de Luna, Sanmiguel, Di Fiore, & Fernandez-Duque, 2010; Stanford, 1998) and (c) to occur earlier for infants living in smaller groups, as large group size decreases predation risk (Gillespie & Chapman, 2001; Hill & Dunbar, 1998; Lima, 1995).

Third, if the main factor influencing variation in infant development is feeding competition, we expected that the timing of colour transitions (a) would not be affected by the sex of infants, (b) would occur earlier in infants living in unimale groups than in infants living in multimale groups, as unimale groups are generally smaller and should experience less feeding competition and (c) would occur earlier in infants living in smaller groups, due to increased energetic gains and improved lactation of mothers residing with fewer feeding competitors (Borries et al., 2008; Koenig, 2002; Lee et al., 1991).

Fourth, if variation in infant development is random and nonadaptive ('null hypothesis'), we expected a combination of results regarding the effect of infant sex, group size and male group composition incompatible with the other hypotheses.

The predictions for predation pressure and feeding competition overlap completely, which means that if these predictions were met, we would only be able to reject the infanticide pressure and null hypotheses.

METHODS

Study Site and Species

This study was conducted at BFMS, a 1.92 km² semideciduous forest in central Ghana (7°43'N, 1°42'W). For more details on the ecology of BFMS see Teichroeb and Sicotte (2009) and Kankam and Sicotte (2013). *Colobus vellerosus* is an arboreal and mostly folivorous species (Saj & Sicotte, 2007) that lives in unimale/multifemale or multimale/multifemale groups of up to 38 individuals (Kankam & Sicotte, 2013; Wong & Sicotte, 2006). Males disperse from their natal groups at sexual maturity and may immigrate to a new group alone or as part of an all-male band (Saj & Sicotte, 2005; Sicotte & MacIntosh, 2004; Teichroeb, Wikberg, & Sicotte, 2011; Wikberg, Sicotte, Campos, & Ting, 2012). Females may remain in their natal group to breed, disperse alone, or disperse with unrelated or related females (Teichroeb, Wikberg, & Sicotte, 2009; Wikberg et al., 2012).

Female *C. vellerosus* give birth every 1.5–2 years, and infants are born throughout the year (Teichroeb & Sicotte, 2008b). Infant handling (i.e. when an individual other than the mother holds and carries an infant) occurs often (Brent et al., 2008), and nulliparous females and close maternal kin are the primary handlers (Bădescu et al., 2015). Infants with white natal coats receive the most infant handling, which suggests that natal coats attract interest and care from conspecifics (Bădescu et al., 2015; Treves, 1997). Group members sometimes try to defend infants against aggression from extragroup males (Saj & Sicotte, 2005).

Study Groups and Subjects

We (I.B., E.C.W., L.J.M., S.A.F., J.V.V. and A.C.) collected demographic data and information on natal coat transition between 2007 and 2014 in nine study groups. We individually recognized all individuals in our study groups, and monkeys were habituated to human presence (see Bădescu et al., 2015 for more details). Experienced and novice observers overlapped in the field every year to ensure consistency in identifying natal coat colour changes and in recognizing animals. We included 48 infants (22 females and 26 males) in this study (Table 1).

Data Collection

We recorded changes in the size and composition of the study groups every observation day. We determined infant sex from their genitalia. We observed the majority of infants from within 3 days of birth, and recorded the date when infants changed to grey or black-and-white within 3 days of their colour change. We visually identified whether infants had a white, grey or black-and-white coat colour using the following criteria.

White coat colour

Infants had a completely white face and no dark hair around the eyes or mouth (Fig. 1a). The body was completely white, and pink skin was visible through the hair. The tail was thin and white. Hands, feet and ears were slightly darker than the rest of the body.

Grey coat colour

Infants had some adult hair coloration such as the white band around the face (beginning of the face ruff; Fig. 1b). The end of the tail began to grow longer white hair. With the exception of the face ruff and the end of the tail, infants were fully grey in colour and had no white hair on the torso, face, back of head or limbs. The limbs and ears were a muted black that was darker than the rest of the body.

Black-and-white coat colour

Infants had the adult black-and-white coloration (Fig. 1c). The face ruff and tail were white, long and full. A white band was visible across the rump. The torso, limbs and head were black and showed no grey hair.

Data Analyses

We had the dates of both white to grey and grey to black-and-white coat colour changes for 22 infants. We had the dates of only the white to grey colour change for 10 infants and the dates of only the white to black-and-white colour change for 16 infants because of the absence of observers. Hence, some of our study infants contributed data to all natal coat transitions, while other infants only contributed data for one coat transition. To determine the durations of natal coats for each infant, we calculated the number of days that it took infants to transition from white to grey, grey to black-and-white, or white to black-and-white by subtracting the date of the colour change onset from the date of birth. During the natal coat transitions of each infant, we determined whether the group contained one adult male (unimale group) or more than one adult male (multimale group). We calculated group size during the natal coat transition of each infant as the total

Table 1
Study groups and subjects for the years of analysis

Group ID	Observation years ¹	Contact hours ²	No. infants ³	No. adult males ⁴	Group size ⁵
BO	2008–2009	403.5	5	1	14–15
BS	2008–2010	575.1	6	1–5	11–23
DA	2008–2009	495.7	5	5–6	18–20
NP	2008–2009	472.0	2	1	9
OD	2009–2010	443.8	4	1	15–16
RT	2008–2009, 2013–2014	1040.2	8	1–2	13–19
SP	2009–2013	2820.7	9	1–2	13–17
WT	2012, 2014	1693.9	2	1	4–5
WW	2007–2010, 2013	1178.7	7	1–4	7–22
Total	8 years	9123.6	48	1–6	4–23

¹ Includes only observation years used in analysis.

² Includes only contact hours when study infant was present.

³ Number of infants included in the analysis.

⁴ Number of adult males is a range due to immigration/emigration between study years.

⁵ The range of total number of individuals, excluding infants.



Figure 1. Natal coat colour transitions of *Colobus vellerosus* infants: (a) white; (b) grey; (c) black-and-white.

number of individuals in the group, excluding the number of infants (Wikberg, Teichroeb, Bădescu, & Sicotte, 2013).

We used three generalized estimating equation (GEE) models to examine the different coat colour transitions. First, we examined the influence of our independent variables on the white to grey colour change ($N = 32$; 18 females, 14 males). Second, we analysed the grey to black-and-white colour change ($N = 22$; 15 females, 7 males). Analysing the white to grey natal coat stage separately from the grey to black-and-white stage is useful because our independent variables may have the largest effect on the early coat colour transition. White infants are highly conspicuous and the most susceptible to infanticide and predation (Teichroeb & Sicotte, 2008a; Treves, 1997). These younger infants may also suffer the most from increased levels of feeding competition faced by their mothers (Borries et al., 2008). Third, we analysed overall duration of natal coats from white to black-and-white colour ($N = 38$; 19 females, 19 males), because it is important to know whether the factors associated with differences in early coat colour transition are also associated with differences in transition to adult coat colour.

In all three models, we included an interaction effect between infant sex and adult male group composition because, as male infants are most prone to infanticide (Teichroeb & Sicotte, 2008a), their natal coat development may be constrained by the number of adult males to a greater extent than female infants. We controlled for the identities of mothers in all models to account for repeated measurements of infants from the same mother. We used GEE models because they offered a more conservative analytical approach than generalized linear mixed models and allowed independent variables to be correlated (Ghisletta & Spini, 2004; Liang & Zeger, 1986; Zuur, Ieno, Walker, Saveliev, & Smith, 2009). We ran the GEEs in SPSS statistics software at $P = 0.05$ alpha level.

Ethical Note

These methods were approved by the University of Calgary's Animal Care Committee (Research Protocol Numbers: 2006-2008 BI 2006-28; 2009-2010 BI 2009-25; 2011-2012 BI09R-25; 2013 AC13-0050; 2014 AC13-0050_REN1), Ghana Wildlife Division, and management committee of Boabeng-Fiema Monkey Sanctuary.

RESULTS

Infants took a mean \pm SD of 48.94 ± 18.44 days to transition from white to grey ($N = 32$) and a mean of 44.36 ± 24.87 days to transition from grey to black-and-white ($N = 22$). The entire natal coat transition from white to black-and-white took 95.08 ± 21.77 days ($N = 38$). Of our study infants, 22 contributed data to all natal coat transitions, 10 contributed data only to the white to grey transition and 16 contributed data only to the white to black-and-white transition.

Differences in Durations of Each Coat Colour (White to Grey, Grey to Black-and-White)

Infant males transitioned from white to grey coats faster than females ($P = 0.002$; Fig. 2a) but not from grey to black-and-white coats ($P = 0.389$; Fig. 2b). Infants in multimale groups showed faster development from white to grey natal coat ($P = 0.012$) but not from grey to black-and-white coat ($P = 0.965$) compared to infants in unimale groups. Group size did not affect the duration of either coat colour change (white to grey: $P = 0.605$; grey to black-and-white: $P = 0.390$). The interaction effect showed that natal coat durations of male and female infants were differentially affected by male group composition for infants transitioning from white to grey ($P = 0.027$) but not for infants transitioning from grey to black-and-white ($P = 0.253$). To further depict the direction of this sex difference in the transition from white to grey, we present box and whisker plots for the natal coat durations of male and female infants in unimale and multimale groups (Fig. 3). These descriptive data suggest that male infants developed faster than female infants in unimale groups but less so in multimale groups.

Differences in Duration of Entire Natal Coat (White to Black-and-White)

Infant males transitioned through their natal coats faster than females ($P = 0.002$; Table 2). Infants in multimale groups showed faster natal coat development than infants in unimale groups ($P = 0.011$). Group size did not affect the duration of white to black-and-white colour change ($P = 0.684$). Again, the interaction effect revealed that the natal coat durations of male and female infants were differentially affected by male group composition ($P = 0.023$).

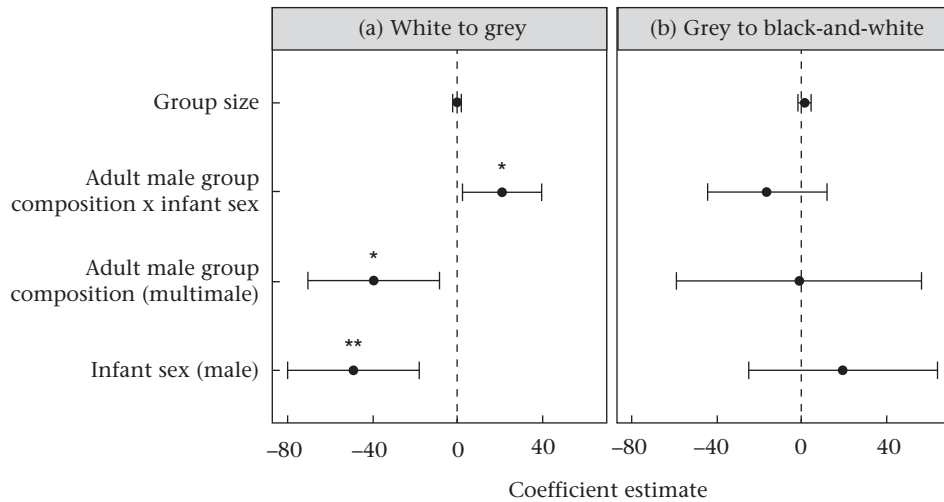


Figure 2. GEE β coefficient estimates and their 95% confidence intervals for the effects of each variable on the duration of the natal coat change (a) from white to grey and (b) from grey to black-and-white. Infant sex (male, female) and adult male group composition (unimale, multimale) were binary independent variables, while group size and the interaction effect between adult male group composition and infant sex were continuous independent variables. * $P < 0.05$; ** $P < 0.01$.

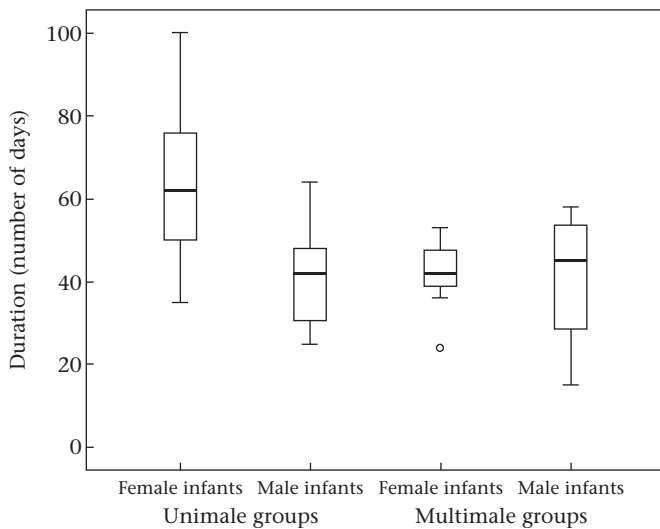


Figure 3. Durations of the white to grey coat transition for female and male infants in unimale versus multimale groups. Box plots show median values (solid horizontal lines), 25th and 75th percentile values (box boundaries), highest and lowest values (whiskers) and outliers (open circle).

Table 2

GEE for the effects of each independent variable on durations of natal coats (white to black-and-white transition)

Independent variables	β	Wald χ^2_1	SE	P
Group size	0.51	0.17	1.25	0.68
Adult male group composition * infant sex	28.43	5.20	12.47	0.02
Adult male group composition	-52.70	6.54	20.61	0.01
Infant sex	-58.21	9.90	18.51	0.00

Significant P values are shown in bold.

DISCUSSION

Our results conformed to the predictions of the infanticide pressure hypothesis but not to the predictions derived from the null, predation or feeding competition hypothesis. Newborn infants under higher infanticide pressure developed faster than infants under lower infanticide pressure. Although infanticide pressure did

not predict developmental rates during the latter half of the natal coat change, the accelerated start during the early stage of development appears to have allowed infants at high risk of infanticide to achieve adult pelage sooner than infants at low risk of infanticide. Thus, early developmental differences between infants may have lasting effects.

These results echo what has been previously described in our study population, namely that, infants displaying white or grey natal coats are more likely to be killed by immigrant males following male take-overs (4/5 infants with natal coats versus 1/6 unweaned infants with black-and-white coats were killed by immigrant males: Teichroeb & Sicotte, 2008a). Transitioning through their natal coats faster may thus decrease infants' risk of being targeted by infanticidal males, even though these infants are not weaned yet. Similarly, younger infants are more likely than older ones to be killed by infanticidal males in several species that do not exhibit contrasting natal coats, including red howler monkeys, *Alouatta seniculus* (Agoramoorthy & Rudran, 1995), mountain gorillas, *Gorilla gorilla beringei* (Watts, 1989), and lions, *Panthera leo* (Pusey & Packer, 1994). This suggests that it is important to contrast early and late infant development in relation to infanticide risk in other mammals, although it may be difficult to obtain reliable noninvasive measures of early infant development in species that do not display contrasting natal coats.

Infants transitioned from white to grey (but not from grey to black-and-white) faster if they lived in multimale groups rather than in unimale groups and if they were males rather than females. Similar differences as in the earliest coat colour transition were also apparent in the transition through their entire natal coats (white to black-and-white). As we indicated earlier, these findings support the infanticide pressure hypothesis. Infanticide rates at BFMS are significantly higher in multimale groups than in unimale groups (Teichroeb & Sicotte, 2010; Teichroeb et al., 2012). This difference in infanticide rates is likely caused by multimale groups having unstable male dominance relationships, often being displaced by unimale groups, and being the target of more male incursions and male immigration attempts than unimale groups (Teichroeb & Sicotte, 2010; Teichroeb et al., 2012). Male infants are two or more times more likely than females to be attacked by infanticidal males in this study population (Teichroeb & Sicotte, 2008a) and in several other primates, such as spider monkeys (*Ateles* spp.; Alvarez et al., 2015), chimpanzees, *Pan troglodytes* (Hamai, Nishida,

Takasaki, & Turner, 1992; Hiraiwa-Hasegawa & Hasegawa, 1994), northern plains grey langur, *Semnopithecus entellus* (Sommer, 1987; 1994; but see Borries, 1997), and howler monkeys (*Alouatta* spp.; Clarke, 1983). Infanticidal males may preferentially target male infants because in doing so, they eliminate future reproductive rivals for themselves and their own sons (Hiraiwa-Hasegawa & Hasegawa, 1994). In species where infanticidal males target male infants more often than female infants, it could be adaptive for males to develop more rapidly than females, thereby reducing their risk of mortality. In *Alouatta*, males also develop faster than females (Raguet-Schofield & Pavé, 2015), but the link between infant development and infanticide remains unexplored in this genus.

In our study, infant males appeared to develop quickly regardless of the adult male group composition, while infant females took longer to develop in unimale groups (which present lower infanticide pressure) than in multimale groups (which present higher infanticide pressure). This pattern could be due to infant males having more constrained development rates than females. Because of the generally greater infanticide risk that white infant males experience (Teichroeb & Sicotte, 2008a), changes in adult male composition may not lead to fluctuations (delays or accelerations) in natal coat transitions to the same extent as they do in infant females.

When it comes to predation, sex does not seem to influence vulnerability in infant primates (Cowlshaw, 1994), and it is thus unlikely that the sex difference in development that we found was due to predation risk. Detailed reports on the sex ratios of infant prey are still lacking (e.g. de Luna et al., 2010; Stanford, 1998), and more studies of primates might shed light on whether there is a sex bias in infant prey.

Group size was not a significant predictor of infant development rates. This contrasts with findings in *T. phayrei*, where infants in larger groups experience slower growth rates than infants in smaller groups, a finding that has been linked to the pressure of feeding competition (Borries et al., 2008), although predation pressure may also explain this result. Our finding that group size did not affect development in *C. vellerosus* may be due to multiple factors affecting natal coat changes simultaneously, as increased feeding competition and predation pressure may slow down infant development while infanticide threat may accelerate it. Thus, the relative strength of feeding competition, predation pressure and infanticide risk may explain the difference in results between our study and that of *T. phayrei*, as infanticide in *T. phayrei* has never been reported or suspected. Alternatively, the energetic constraints on mothers in larger groups may not influence infant development at our study site if natal coat changes are primarily driven by the physiology of the infants themselves, independently of maternal effects (Booth, 1990; Walker et al., 2004).

Mechanisms Leading to Variation in Infant Development

The exact mechanism by which natal coat transitions occur sooner in some situations than others is unknown. Recent work on the interactions between the environment and the physiology of lactation offers some interesting avenues, however. Lactation is a plastic trait, and the main mechanism underlying the differences in growth patterns in infant mammals is plausibly linked to lactation (Hinde & Milligan, 2011; Lee et al., 1991). For instance, rhesus macaque, *Macaca mulatta*, mothers who produce milk containing greater glucocorticoid concentrations have faster-growing infants (Hinde et al., 2015). In female baboons (*Papio hamadryas*), glucocorticoid levels surge when new immigrant males increase in dominance rank, which elevates infanticide risk (Alberts, Sapolsky, & Altmann, 1992; Beehner, Bergman, Cheney, Seyfarth, & Whitten, 2005; Engh et al., 2006). Varying degrees of stress can also affect

infant temperament and suckling stimulus, which also affect lactation and levels of maternal care (Walker et al., 2004). Thus, in addition to maternally mediated effects, varying infanticide pressure could lead to differences in stress levels that cause some infants to develop faster than others (Booth, 1990; Parker & Maestripieri, 2011). A combination of both physiological and behavioural mechanisms mediated by both mothers and infants may therefore be responsible for the accelerated rates of infant development that are sometimes observed in situations of high stress, such as when infanticide pressure is high (Palombit, 2012; Walker et al., 2004).

Mothers can also adjust the quality and quantity of milk transferred according to offspring sex (pinnipeds: Goldsworthy, 1995; primates: Hinde, 2007, 2009; ungulates: Cameron & Linklater, 2000; Hewison & Gaillard, 1999; White, Swaisgood, & Czekala, 2007). In Antarctic fur seals, for instance, infant sons receive more maternal milk than daughters, resulting in faster growth in males than in females (Goldsworthy, 1995). In rhesus macaques (Hinde, 2007, 2009) and red deer, *Cervus elaphus hispanicus* (Landete-Castillejos, Garcia, Lopez-Serrano, & Gallego, 2004), the milk that females produce for their sons is richer in protein and fat. Male infants in these species also grow faster than female infants (Hinde, 2009; Hinde, Power, & Oftedal, 2009; Landete-Castillejos et al., 2004).

The faster development of male infants may also be linked to infant handling. *Colobus vellerosus* nonmothers handle infant males more often than they do infant females (Bădescu et al., 2015). Infant handling may accelerate infant development and the attainment of nutritional independence (Maestripieri, 1994; Obie, Atkinson, Dunbar, & Shultz, 2013). More frequent infant handling could thus help explain the faster natal coat development of male infants in our study, although we lack the behavioural data on infant handling for most of the infants included in this study. There could also be a potential social cost of developing fast, as these infants would receive less infant handling once they have obtained the adult coat colour.

Future Directions and Conclusions

The coat colour changes exhibited by *C. vellerosus* provided a visually reliable, noninvasive measure of infant development that was easier to obtain in the wild than measurements of body mass or time to nutritional independence. It is possible that fast development early in life is reflected in later life stages if environmental and social conditions remain constant. Whether the rates of coat colour transitions positively correlate with nutritional independence or nursing cessation when conditions, such as group composition, remain the same is unknown in our study species and in other primates. It is possible that the rates of natal coat changes do not correlate with other measures of infant development, despite earlier studies that have found a correlation (e.g. Altmann et al., 1981; Arnould et al., 2003; Borries et al., 2008; McDonald et al., 2012; Poirier, 1968; Reiter et al., 1978; Verrier et al., 2011). If this is the case, differences in the duration of natal coat colours may not be an appropriate way to assess maternal investment or overall infant development. Thus, an important future research avenue will be to collect longitudinal demographic data to document how the duration of natal coat colours relates to other aspects of development that may be more energetically costly (for instance size or weight), and with developmental milestones such as the attainment of nutritional independence and sexual maturity.

In *C. vellerosus*, the recurring threat of male infanticide affects female reproductive strategies, dispersal patterns and group compositions (Teichroeb & Sicotte, 2008a; Teichroeb et al., 2012; Teichroeb et al., 2009). Here, we also suggest that the threat of

male infanticide accelerates infant development. Our finding is consistent with several anecdotal reports in primates showing more rapid infant development when infanticide pressure is high (Palombit, 2012). Thus, mothers or infants may accelerate or prolong infant growth, development and the timing of weaning in response to varying conditions (Palombit, 2012).

Previous studies documented that females exert choice over their degree of parental investment in relation to infanticide risk via the 'Bruce effect', in which females terminate pregnancies in response to new males (Berger, 1983; Roberts, Lu, Bergman, & Beehner, 2012). Our findings suggest an additional mechanism whereby females may be able to alter their investment in offspring depending on infanticide risk. Instead of terminating investment in offspring before birth, as in the Bruce effect, females may invest more in infants after birth to speed up infant development and thereby reduce the time period during which offspring are vulnerable to infanticide. If successful, this strategy can have a large positive effect on female fitness. Such an adaptive response to infant mortality risk is likely to occur in other species with infanticide. Our findings further highlight the importance of infanticide in the evolution of female reproductive strategies (Janson & van Schaik, 2000; Palombit, 2012).

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