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, Côté, Festa-Bianchet, & Ouellet, 2008; Phayre's leaf monkey, *Trachypithecus 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; Bǎdescu, 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, *Trachypithecus 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') (Bǎdescu, 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, Bǎdescu, 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 (Cowlishaw, 1994), (b) to occur earlier for infants in unimale groups than for infants in multimale groups, as several males can offer greater predator defence (Cowlishaw, 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.