Testing comparative predictions of primate natal coat function hypotheses using continuous coat conspicuousness quantification

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Abstract

Many species of primates have natal coats in infancy that can be lighter, darker, or an entirely different colour to that of adults. Sometimes these appear highly conspicuous, at least to humans, which is unusual for ontogenetic colour change for infants without any intrinsic defence. Previous comparative studies have tested various hypotheses as to what the benefit of a bright coat could be to the most vulnerable individuals in a group, and currently there is weak equivocal support for several different hypotheses. The main weakness of previous studies has been quantifying the great diversity of natal coat phenotypes in as little as two or three restrictive categories. In this study, primate natal coats are measured on a continuous scale of conspicuousness to more accurately represent the great interspecies variety of natal coats. In this hypothesis-driven study, phylogenetic comparative method were used to test comparative predictions about the function of primate natal coats. Results showed infanticidal behaviour, small relative testes mass, and ventral carriage of infants were all significantly associated with primate natal coat conspicuousness. The results suggest evidence to support the hypothesis that natal coats act as a signal to out-group, hostile males that the infant will be defended by other group members if the male attempts infanticide. This study furthers knowledge of an unusual form type of ontogenetic colour change that is currently unexplained and rarely seen in mammals and suggests that infanticide is a key selective pressure in many primate societies.

Lay summary

Many animals change colour as they develop from babies into adults. Colouration can change for many different reasons. Animals like lions and antelopes have spotted infants to hide from predators but then lose these spots and as they grow older, use different habitats and become better at avoiding predation due to their increased size, speed, or survival experience. Colour change can also signal sexual maturity in animals, such as the development of a silver-grey back in male gorillas. Lots of species of primates have a natal coat: a pelage that they are born with that is distinctly different from an adult pelage. These coats are present from birth and are lost around the time of weaning. There is a lot of variation of natal coats between primate species: Some are only slightly different from adults, others can be much lighter, much darker, or even a different colour altogether. What makes primate natal coats unique within mammals and so puzzling to understand is that they can cause the infants, who are the most vulnerable individuals in the group, to be the most conspicuous, seemingly increasing the likelihood of being spotted by predators. The function of primate natal coats is unknown but current ideas include promoting infant care and infanticide defence.

I asked people to classify how distinct primate natal coats are in different species and related this to lifestyle data collected from scientific articles and books to test predictions of five ideas about why some species of primate have conspicuous natal coats. The only hypothesis for which supporting evidence was found was the anti-infanticide hypothesis, suggesting that primate natal coats act as a signal to hostile males from outside the social group that if they attempt infanticide on the infant, other group members will defend it. Primate natal coats are proposed to function as aposematic visual cues to potentially aggressive conspecifics which is a function rarely, if ever, documented in mammalian infants.

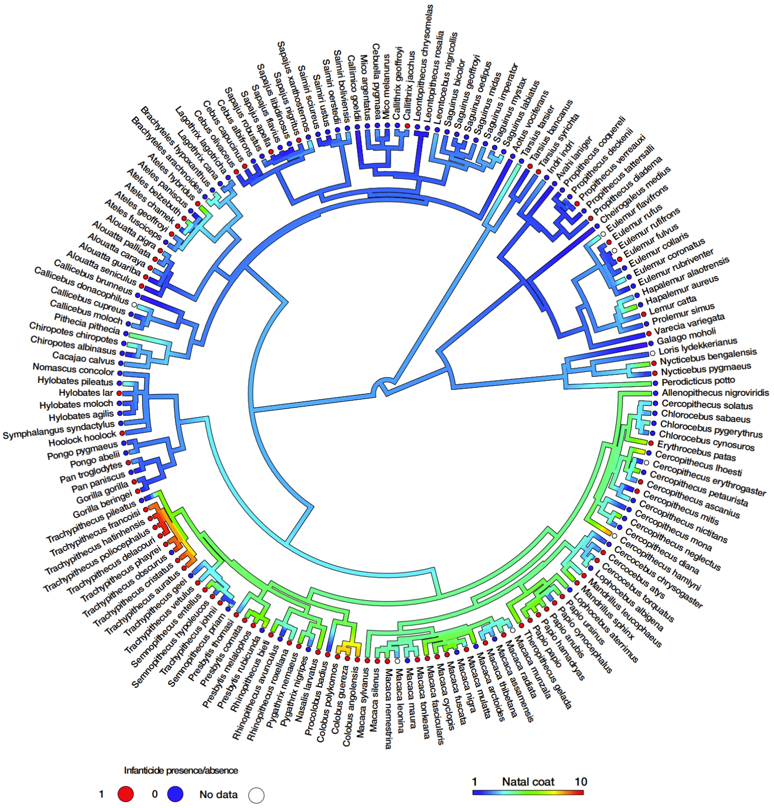

Figure 1. Natal coat conspicuousness (colour of node tips) and infanticide presence/absence (dots at the end of tips) of the 168 primate species in the study.

Declarations

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

Signed..Ewan Suttie...

Date..02/11/2022...

This thesis is the result of my own investigations, except where otherwise stated. Other sources are acknowledged by footnotes giving explicit references. A bibliography is appended.

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I hereby give consent for my thesis, if accepted, to be available for photocopying and for inter-library loan, and for the title and summary to be made available to outside organisations.

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Signed..Ewan Suttie...

Date..02/11/2022...

MRes Biosciences Statement of Expenditure

Student name: Ewan Suttie

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Project title: Testing comparative predictions of primate natal coat function hypotheses using continuous coat conspicuousness quantification.

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I hereby certify that the above information is true and correct to the best of my knowledge.

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Investigation	ES
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Supervision	WA, AK
Validation	N/A
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Ethics approval

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Definitions of Abbreviations

OCC = Ontogenetic colour change

CNC = Conspicuous natal coats

PCM = Phylogenetic comparative method

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Introduction

In many taxa species undergo ontogenetic colour change (OCC), that being colour change as an individual develops from an infant to an adult. OCC can result from selection for a variety of different functions. Often, it facilitates changes in defensive colouration as an organism goes through developmental phases, causing changes in body size, vulnerability, and/or habitat usage (Booth, 1990). For example, Juvenile snappers have been hypothesised to mimic and school with damselfish, where they can predate upon them from within the school, but adult snappers lose this mimicry, potentially because they are better predators and no longer need to rely on mimicry (Booth, 1990). Another common form of OCC involves the acquisition of secondary sexual traits such as male gorillas gaining a silver/grey lower back as they mature which functions as a sign of sexual maturity (Schaller, 1963). In most instances in which infants of a species are differently coloured to the adults, infant colour is believed to function as a defence against predators. Infants are often smaller in size, weaker, slower, and less experienced in evaluating dangerous scenarios compared to fully grown individuals, making them an easier target for predators as well as viable prey to a greater range of predators (Caro et al., 2022).

Ontogenetic colour change is observed in many primate species in the form of conspicuous natal coats (CNCs): in some species the pelage of infants can be distinctly different to adult pelages. Natal coats differ among primate species; some are a lighter shade compared to parents, some are darker, and some are a different colour altogether (Fig. 2). They are unlike most other mammalian natal coats which tend to facilitate crypsis in specific microhabitats where infants spend time whereas more mobile and less vulnerable adults tend to have camouflage for another microhabitat or general-purpose camouflage which offers less protection but works against a variety of backgrounds. Examples of this include the spotted pattern of infant antelopes and lions, or the white natal coats of pinnipeds that give birth on pack ice (Caro et al., 2022; Stoner et al., 2003) . Another function of natal coats in mammals is mimicry of a defended animal, such as infant cheetahs mimicking ratels (Eaton, 1976) . What is interesting about primate natal coats is that infants that can be highly conspicuous and OCC is a transition to become apparently more cryptic as they develop their adult coat, which is seemingly the opposite to the cryptic infant-to-differently cryptic adult pattern that is followed by most mammalian species with natal coats. Furthermore, the function of primate natal coats is still relatively unknown. None of the explanations for OCC in other mammals such as microhabitat camouflage or acquisition of secondary sexual characteristics fit. The conspicuous nature of primate coats suggests crypsis is not the function. Coats do not function as sign of sexual maturity since the coat is lost before weaning, let alone sexual maturation. There is no evidence that primates with natal coats are mimicking an animal better defended than themselves. My project aims to work towards understanding the phenomenon of primate CNCs by identifying their function.

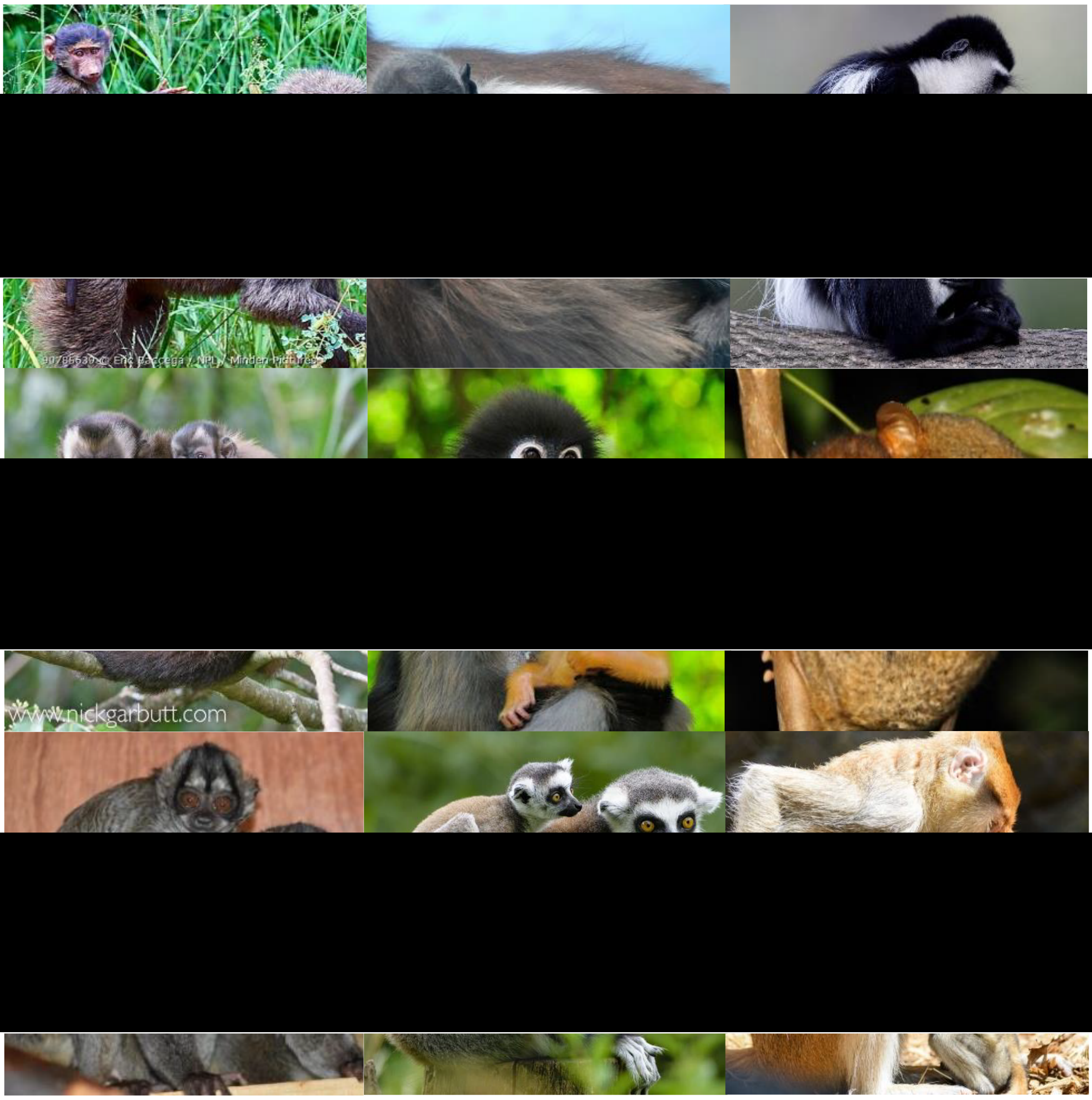

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Figure 2. Examples of natal coat diversity across primates. Species shown are *Papio anubis* (top left)*, Ateles hybridus* (top middle)*,* and *Colobus guereza* (top right), *Sapajus apella* (centre left), *Trachypithecus obscurus* (centre middle), *Tarsius syrichta* (centre right), *Aotus vociferans* (bottom left), *Lemur catta* (bottom middle), *Erythrocebus patas* (bottom right). Examples of variation of natal coats between species. They can be darker shades, lighter shades, or a different colour to the mother altogether.

In beginning to consider the function of natal coats, understanding important aspects of primate socio-ecology is informative. Primates are heavily predated upon by many different types of predators, with more arboreal primates being particularly vulnerable to raptors and terrestrial primates vulnerable to mammalian carnivores (Boinski et al., 2000). The high level of sociality and group-living behaviour generally observed in primates can be beneficial when considering the risk of predation (van Schaik & van Hooff, 1983) . Primates living in social groups have less individual vulnerability, increased effectiveness of deterring threats, opportunity for group confusion, and better chance of identifying and warning of incoming threats (Boinski et al., 2000). In some species infanticide, often by hostile, out-group males is relatively common (Hrdy, 1974). Frequency of infanticidal behaviour varies between species but has been recorded in every major primate group.

It is prevalent in catarrhines like langurs and colobus monkeys (Hrdy, 1974; Oates, 1977), and also well documented in some platyrrhines such as red howler monkeys (Agoramoorthy & Rudran, 2010). The common threat of predation or infanticide for primates makes it seem counterintuitive for the individuals most vulnerable to predation to be the most conspicuous. However, the benefit of conspicuous natal coats must outweigh the apparent risk that comes from being more conspicuous to predators or hostile out-group males.

Primates rely heavily on visual cues and signals to give and receive information between conspecifics. Body language and facial expressions convey emotional information, such as a relaxed face indicating intentions of play (de Waal, 2003), and colouration of skin and pelage convey status information (e.g. health and hierarchical position) (Bergman et al., 2009). Of primate species that have conspicuous natal coats, there have never been recordings of neonates not having these natal coats, suggesting that the trait has rapidly fixated within its populations and alludes to strong selection pressure for natal coats. Due to this, a functional explanation is being strongly suspected rather than natal coats being a non-functional trait arising through random mutation, drift or genetic developmental constraint (Treves, 1997). The visual nature of primate communication and conspicuous colouration of many primate natal coats has lead researchers to propose that the coats are a signal to conspecifics.

Explanations for the evolution of primate conspicuous natal coats relate to infant caregiving and/or protection towards infants. The mothering hypothesis (Caro et al., 2022; West-Eberhard, 1983) suggests the conspicuous colour acts as a visual cue to mothers to promote maternal care, such as carrying or feeding, to the infant. Whilst the allomothering hypothesis suggests primate conspicuous natal coats act to encourage care-giving from all group members (Hrdy, 1976; Treves, 1997). Rather than promoting caregiving in a general sense, it has also been proposed that primate conspicuous natal coats have evolved in response to the specific risk of infanticide. This anti-infanticide hypothesis suggests primate conspicuous natal coats work to either promote nonmothers to provide defence against infanticidal males, or as a signal to the potentially infanticidal male that the group will defend the infant (Treves, 1997). The infant tracking hypothesis instead proposes conspicuous natal coats act as a signal for group members to keep track of the infant so that risk of being lost, dropped, or isolated is reduced. Finally, another hypothesis related to infanticide - the paternity cloak hypothesis (Treves, 1997) suggests primate conspicuous natal coats make it more difficult for adult males to use visual cues regarding relatedness, and this uncertainty could reduce likelihood of infanticide (Treves, 1997). Below, I provide more detailed information regarding each hypothesis and any empirical support for each.

Allomothering hypothesis

In every mammalian species, mothers are the primary caregivers to their offspring (Rymer & Pillay, 2018), with paternal care only substantial in the few monogamous mammals. However, in certain taxa, it is common for other individuals to aid in caregiving (Isler & van Schaik, 2012). Allocare is particularly common in canids and primates. Within primates there is a wide variety in amount of allocare between species though. For instance, there is almost no opportunity for allocare among orangutans due to their solitary nature. Conversely, other primate species provide lots of care to infants that are not theirs at great energetic cost such as feeding by lactation in Nilgiri langurs (Ross & MacLarnon, 2000). Allomothering costs time and energy from the allocarer and so it is unlikely that this behaviour has evolved with no benefit to the carer’s fitness. Many benefits of allocare for the alloparent have been proposed, for example, direct fitness benefits such as gaining practice and experience in caring for an infant to increase ones’ own future reproductive success. There may also be indirect fitness benefits like the increased chance of survival of a closely related infant (Ross &

MacLarnon, 2000). Oates (1977) put forward the allomothering hypothesis for primate conspicuous natal coats which was based on conjecture from Hrdy (1976) that flamboyant coats of some Colobinae elicit a care response from group members towards the flamboyant infant. It proposes that primate natal coats act as a signal to promote allocare from group members, specifically that motivation to care for the infant is released by the visual cue of the coat rather than created by it.

Evidence both for and against the allomothering hypothesis has been found in observational and comparative studies. Observational studies of *Colobus vellerosus* and *Trachypithecus auratus* have recorded that infants with natal coats accrue the most allomaternal care (Bădescu et al., 2015; Trisilo et al., 2021). However, it is difficult to conclude that natal coats are the traits that promote allocare when natal coat presence is confounded with infant age. The comparative study of Ross and Regan (2000) found evidence associating allocare with natal coat reflectance, whereas Treves (1997) and Caro et al (2022) found no association between allocare and natal coats.

Mothering hypothesis

Caro (2022) proposed a hypothesis similar to the allomothering hypothesis but with the target of signal being the mother rather than other group members. The coat functions to garner more maternal care to increase growth rate allowing the infants to progress out of the highly vulnerable phase sooner. The proposed evidence for this hypothesis comes from ~~results~~ Caro et al (2022) in which shorter interbirth intervals, earlier weaning ages, and infanticide were all associated with distinct natal coats. It was suggested that distinctly coated infants receive higher quality or quantity care so that they grow quickly out of the phase in which they are particularly vulnerable to infanticide. As no association was found between allomothering and distinct natal coats, it was hypothesised that it is maternal care that natal coats promote (Caro et al., 2022).

Anti-infanticide hypotheses:

Infanticide is observed in a wide range of taxa in the animal kingdom. Functions of infanticide include exploitation of the infant as a resource, eliminating the infant as a competitor for resources, parental infanticide to increase maternal survival or lifetime reproductive success, and to increase reproductive access to females (Hrdy, 1979). The latter is theorised to be the most common reason for infanticide in primates. Males of catarrhine, platyrrhine, and great ape species have been observed killing infants when they enter a new breeding situation such as when they take over a group after ousting the previous dominant male (Hrdy, 1979). Killing unrelated infants brings mothers out of lactational amenorrhea so that the mother will be ready to mate and give birth to the infanticidal male's offspring sooner. For example, Hrdy (1974) observed three troops of Hanuman langurs in which 70% of females whose infants had been killed gave birth just over one gestation period later. This is particularly apparent in species with short breeding seasons where the male will have a time limit for successful reproduction. Due to the severity of infanticide on populations as well as how widespread it is among primates, infanticide should be considered as strong selection pressure for anti-infanticide adaptations (Treves, 1997). Adaptations of primates to lessen the chance of infanticide can include concealed ovulation, reproduction suppression (Bruce effect), and physical defence (Heistermann et al., 2001; Roberts et al., 2012). The anti-infanticide hypothesis, or infant defence hypothesis, is a modified version of the alloparental hypothesis and was proposed by Treves (1997). It stems from Oates' (1977) work on black and white colobus monkeys in which Oates put forward that the white natal coat was a signal to promote care of the infant from nonmothers and that this, in turn, would provide defence against infanticidal males. Treves' modification of this is that the natal coat is a signal to the potentially infanticidal male that the group will defend the infant (Treves, 1997). Treves (1997) found some evidence to support this hypothesis through a significant association between “flamboyant” natal coats and relative testes mass, which is a predictor of promiscuity. Caro et al (2022) also found supporting evidence through phylogenetic generalised mixed models where infanticide was significantly associated with distinct natal coats.

Paternity cloak hypothesis

In several mammalian groups, inherited appearance such as coat colour and markings is a clue that fathers and non-fathers might use to determine the paternity of an infant. (Clarke, 1983). This is seen in primates. For example, a male mantled howler monkey that had an uncommon foot colouration was seen to kill all infants except one infant who had a similar foot colouration (Clarke, 1983). The paternity cloak hypothesis is that the function of primate natal coats is to look markedly different from any adult male pelage so that no male can use visual cues to determine if an infant either is or is not related, possibly reducing likelihood of infanticide (Treves, 1997). Support for this hypothesis was found by Treves (1997) in that the head and dorsum were the first parts of infant pelage to lose the natal coat. The head and dorsum are the least likely areas to present inherited marking and so are the least likely to be usable to determine paternity certainty.

Infant tracking hypothesis

As previously discussed, infant primates are highly vulnerable to predation and infanticide. Since they rely heavily on the adults in the group to protect them, infants are most vulnerable when they are separated from the group. This may occur due to the infant getting separated due to exploration behaviour or potentially accidentally being dropped when being carried. In such situations where there is a potential threat to an infant’s fitness, it may be advantageous for conspecifics, most likely the mother, to be able to identify the location of the infant and focus on protecting it. The infant tracking hypothesis suggests that a conspicuous natal coat makes it easier for conspecifics to find an infant among the environment to protect it from nearby threats.

There are a few comparative studies that have already attempted to investigate the function of primate natal coats and have returned mixed results due to different sample sizes, colour scoring methods, and hypothesis tested. In summary, Treves (1997) tested three hypotheses of primate natal coat function (allomothering, anti-infanticide, and paternity cloak), categorising infant coat conspicuousness into three groups (none, inconspicuous, and flamboyant) for 138 species. Using non-phylogenetic methods, weak support was found for the anti-infanticide hypothesis. Regan (1998) used phylogenetic independent contrasts on an expanded sample of 158 species and found no support for any hypothesis. Most of the tests between natal coats and allocare conducted by Ross & Regan (2000) showed no association. Some tests, with p values between 0.1 and 0.05, suggested allocare is associated with increased natal coat reflectance. Ross & Regan (2002) also found a significant association between natal coat contrast and terrestriality. The latest comparative study of primate natal coat function is Caro et al (2022) which revised the data on which primate species did and did not present natal coats as well as updated the socio-ecological data on primates, increasing the sample size to 242 species. Support was found relating natal coat presence with infanticidal behaviour and short interbirth intervals. Overall, these mixed results can be attributed to weak comparative predictions and analyses, sample size, and issues with how natal coat appearance was quantified.

Aspects of the methodologies of these studies do raise some questions and could be labelled as shortcomings. This current study aims to address and improve on those weaknesses. The lack of control for phylogenetic non-independence in Treves (1997) study must be noted since it is a necessity when comparing traits between species. As with the comparative studies that have come after Treves (1997), I account for phylogeny by using phylogenetic comparative methods in the statistical analyses. One main shortcoming present in all previous comparative studies is the restrictive categorisation of natal coats. Primate natal coat conspicuousness of primates has been reduced to just two or three categories which do not correspond well to observed trait variation across species. There is a huge variety in natal coat conspicuousness and ignoring/minimising it could result in the loss of important detail in the results. This study measures natal coats of primate species on a continuous scale of how different the infant pelage is relative to the mother's pelage and foliage as ranked by human participants comparing images of infants and mothers from the internet. This method of natal coat conspicuousness quantification allows for species' conspicuousness to be ranked quite quickly and the number of species is only restricted by the availability and quality of images on the internet. This was a favourable method over spectrometry or digital photography as both methods require a sample of the primate pelage or the presence of the animal itself which would need a lot of travel and/or external help (Stevens et al., 2007). In the interest of time and resources, a classification task using human judgements was preferred.

The final weakness of previous comparative work in this area is that comparative analyses have been more exploratory rather than focussed on testing specific a priori hypotheses. In this hypothesis driven study I aim to test comparative predictions to see if the results offer support for any of the five hypotheses of the function of primate natal coats that have been previously outlined (Table 1). Phylogenetic comparative methods will be used to estimate the relationships between natal coats and socio-ecological traits of primate species. The phylogenetic comparative method (PCM) is a collective of statistical methods for inferring the evolutionary history of traits. There are two main goals with using PCMs: the first is estimating the how the value of a trait changes through time, and the second goal, the one that this study focuses on, is estimating how traits are evolutionarily linked both to other traits and to the environment (Cornwell & Nakagawa, 2017).

Table 1. Comparative hypotheses, predictions, statistical tests and variables involved.

Hypothesis	Comparative prediction	Test	Response variable	Explanatory variable
Anti-infanticide aposematism	Natal coat conspicuousness is positively associated with high paternity certainty.	PGLS	Primate natal coat (PNC) conspicuousness against mother	Relative testes mass (proportion of total mass)
	Natal coat conspicuousness is positively associated with polygynous mating systems.	Phylogenetic ANOVA	PNC conspicuousness against mother	Mating system (spatial polygyny/ monogamy/polyandry/ harem polygyny/ polygynandry)
	Natal coats are more conspicuous when risk of infanticide is high.	PGLS	PNC conspicuousness against mother	Infanticide (presence/absence)
Paternity cloak	Natal coat conspicuous is positively associated with polygynandrous mating systems.	Phylogenetic ANOVA	PNC conspicuousness against mother	Mating system
	Natal coat conspicuousness is negatively associated with low paternity certainty.	PGLS	PNC conspicuousness against mother	Relative testes mass
Allomothering	Natal coats are positively associated with allomothering behaviour.	PGLS	PNC conspicuousness against mother	Allomothering (presence/absence)
	Natal coats are relatively more conspicuous against an adult female pelage than against foliage.	Phylogenetic paired t	PNC conspicuousness against mother	PNC conspicuousness against foliage
Mothering	Natal coats are more conspicuous with earlier weaning.	PGLS	PNC conspicuousness against mother	Weaning age (days)
Infant tracking	Natal coat conspicuousness is positively associated with risk of being dropped.	PGLS	PNC conspicuousness against mother	Infant carrying method (ventral/dorsal/both)
	Natal coats are more conspicuous against foliage when at high risk of being dropped.	PGLS	PNC conspicuousness against foliage	Infant carrying method
	Natal coat conspicuousness is positively associated with arboreality.	PGLS	PNC conspicuousness against mother	Arboreality (arboreal/terrestrial/both)
	Natal coats are relatively more conspicuous against foliage than an against an adult female pelage.	Phylogenetic paired t	PNC conspicuousness against mother	PNC conspicuousness against foliage

Methods

The phylogenetic comparative analyses required data on phylogenetic relatedness, the conspicuousness of primate natal coats, and socio-ecological data. The phylogenetic relatedness data was taken from Upham et al (2019). A classification task was created and undertaken by five participants to collect data on natal coat conspicuousness. A database of socio-ecological trait information for all primate species was collated from the literature.

Phylogeny and taxonomy

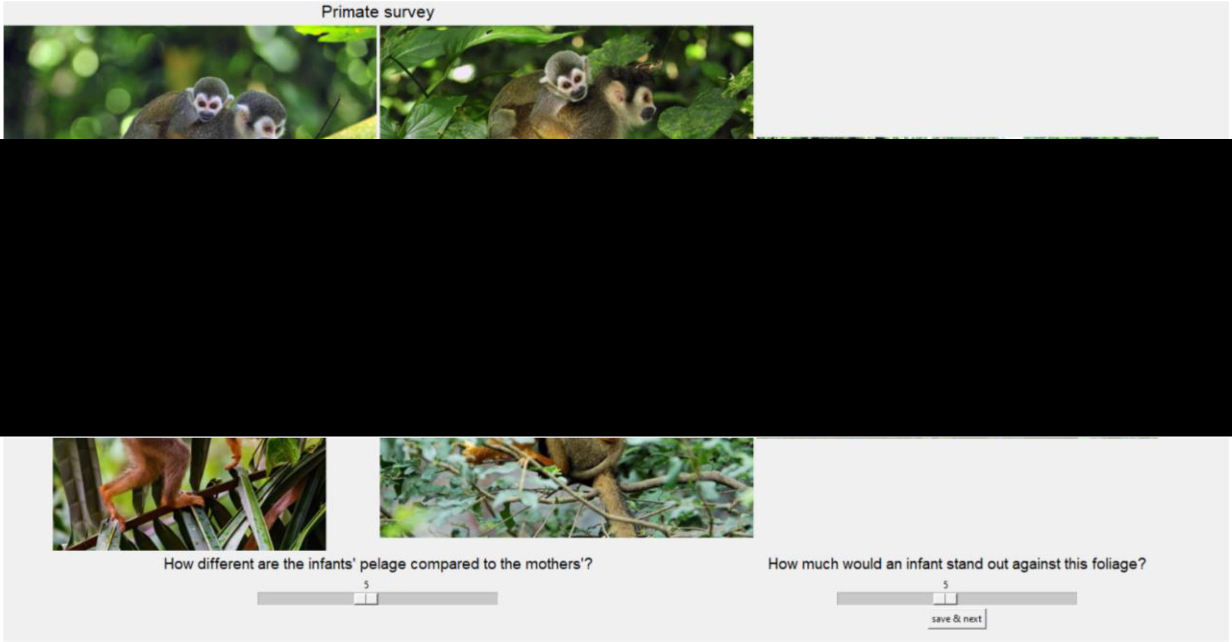
The phylogenetic relatedness data was obtained from the mammalian phylogeny of Upham et al. (2019). I used the DNA-only maximum-clade credibility tree of 4098 species available on Github. The phylogeny was pruned so that only primate species were present. Extinct primate species were pruned as this study is focused on extant species. Humans (*Homo sapiens*) was also pruned as is often the case in primate comparative studies since they are often an outlier when comparing life history traits (DeCasien et al., 2017). After pruning, the phylogeny contained 327 extant primate species.

Primate infant image database

For the classification task, multiple images showing both an infant primate and its mother for each species were collected as well as an image of the approximate habitat that the species resided. Primate images were found using google images. Searches for each species included a combination of either common name or scientific name and one of “infant” or “baby”. The images had to be of both an infant and its presumed mother, although maternity could not be confirmed since most images had limited information. Images of the adult carrying the infant were prioritised as the carrier is likely to be the mother. The images also needed to show enough of both individuals’ pelage so that the participants could easily compare them. To further ensure ease of comparison, images of high resolution and least amount of blur were preferred. The webpages and titles of the images were read to verify that the images found indeed depicted the species intended. Very few web pages or image descriptions offered information on the age of the infants in the images so the size of the infant and behaviour (e.g., being carried by mother) were used as visual aids to estimate age. The intention was to collect four images per species, but due to the selection criteria, four images could only be found for 70 species. Images ranged from 1 to 4 per species in the survey and the average number of images used per species was 2.77. Of the 327 primate species with molecular phylogenetic information, images deemed adequate for the purpose of the classification task could be found for 168 species and so only those species were used in both the survey and statistical analyses.

Quantifying natal coat conspicuousness

The two continuous response variables to be used in the phylogenetic comparative analysis were the difference between infant and mother pelage, and the difference between infant pelage and approximate foliage colour of the specific species’ habitat. To collect this response data, a graphical user interface (GUI) survey was created using python 3.10.3 and the tkinter package (Figure 3). Every species had its own page on the survey. On each page there were images of the species’ infants with their mothers as well as the habitat image. For each species, there were two questions on the page with a slider under each question. The first question was “How different are the infants' pelage compared to the mothers'?” and the second question which is under the habitat image reads “How much would an infant stand out against this foliage?”. The sliders for each question ranged from 1 to 10 and increased in increments of 1.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Primate survey

How different are the infants' pelage compared to the mothers'?

5

How much would an infant stand out against this foliage?

5

Figure 3. Example page of the classification task Species shown is the common squirrel monkey *Saimiri sciureus*.

The participants were four of my family members as well as myself. There were two female and three male participants ranging in age from 19 to 56 years old. Each participant signed a consent form and were briefed on the task via a slideshow presentation before completing the survey. The pre-task presentation explained the purpose of the task and showed examples of how the task would be displayed. The participants were shown example images of species that were predetermined by myself to be at the extreme ends of the value scales (e.g. infants that looked identical in pelage to their mothers and infants that looked very different to their mothers). After being shown examples of the extreme ends of the value scale, participants were told that it was up to them to decide where each species fit along that scale. All participants completed the survey in the same room and used the same computer and screen (Dell Inspiron 16 7610, diagonal: 16 inch, resolution: 3072 x 1920) when completing the survey. Although the survey was done at different times of the day, an effort was made to keep lighting consistent by having the same interior light on. Four of the participants took between 90 and 120 minutes to complete the survey. One participant completed it in only 40 minutes.

Once all five participants had completed the survey, intraclass correlation coefficients were calculated for both natal coat ratings against maternal pelage and foliage to test the interrater reliability. The values given for each species were averaged by calculating the arithmetic means to get a continuous measure from 1 to 10 as opposed to just integer values from 1 to 10. This was done using the average function in Excel. To assess the reliability of rating between participants, the intraclass correlation coefficient was calculated.

Socio-ecological data collection

All socio-ecological data was compiled from scientific studies and were found either from the articles themselves or the supplementary data from the articles. Data collected from the scientific articles was usually primary research and the supplementary data was often secondary, sourced from other studies as well as books. The methodology of each source was read to understand and assess the quality and content of the data. The data was compiled into one Excel spreadsheet and formatted to import into R.

Data on which species were infanticidal was collected from the supplementary data from Caro (2022) which had been compiled from four different sources (Lukas & Clutton-Brock, 2014; Opie et al., 2013). The data spanned all major groups of primates, with a final sample size of 258 species. In the primary research, infanticide events were only recorded if they had been directly observed or if all other possibilities were ruled out. In this current study, infanticide presence was classified as 1 and absence as 0. Presence and absence of allomothering was also collected from the Caro (2022) supplementary data, compiled from multiple sources (Treves, 1997), containing data on 223 species. Allomothering presence was classified as 1 and absence as 0. Data on the method of carrying infants was acquired from Nakamichi & Yamada (2009) who had compiled information from previous primate literature as well as from researchers and zookeepers. The data spanned 77 simian species. Nakamichi & Yamada (2009) measured dorsal and ventral carriage as two separate variables. These variables had 3 categories: category 0, the carriage method (dorsal or ventral) is not used by the species; category 1, the carriage method in question is either rarely used or there is mixed evidence among sources; category 2, the carriage method in question is commonly used. I transformed this data from two measurements of dorsal and ventral carriage frequency into one measurement of most common carrying method. My measurement also had 3 categories: category 1, dorsal carriage is the only common carrying method; category 2, both dorsal and ventral carriage are common; category 3, ventral carriage is the only common carrying method. Information on arboreal/terrestrial lifestyle comes from the primate ecological trait database made by Galán-acedo et al (2019). The database includes the locomotion type (arboreal/terrestrial/both) of 497 primate species and was compiled from a range of sources. The species that were labelled as arboreal are described as rarely going to the ground in an undisturbed forest. Terrestrial species spend most of their daily activity on the ground. Species labelled as “both” are commonly active on the ground and in trees. In my database, I transferred this into a scale of 1 being arboreal, 2 as both, and 3 as terrestrial. Data on the mating systems of primate species was gathered from DeCasien et al’s (2017) supplementary data. Mating system data was compiled from several previously published literature sources and includes 142 species spanning all major primate groups. The mating systems included were spatial polygyny, monogamy, polyandry, harem polygyny and polygynandry. The supplementary data of Lupold (2019) contained male body mass as well as combined testes mass. Data included 64 simian and lemur species but no tarsier, loris, or galago species. To get the relative testes mass as a proportion of male body mass I divided the combined testes mass by the male body mass. Weaning age data was collected from supplementary data of Opie et al (2013) which was compiled from books about primate life history (Campbell et al., 2011; Smuts et al., 1987). Weaning age was recorded in units of days from birth until weaned and covered 119 species including all major primate groups.

Analysis

To test the hypothesis about which visual background natal coats were more conspicuous against, a phylogenetic paired t test was used (Revell, 2012). The phylogenetic paired t test tested the difference between the means of the natal coat consciousness vs. the mother’s coat and the conspicuousness of natal coats against foliage.

Phylogenetic generalised least squares (PGLS) was used to test relationships between the continuous response variables and the continuous, binary, or ordinal explanatory variables. PGLS fits a linear regression model whilst accounting for phylogenetic non-independence (Revell, 2012). Individual models were run for each comparative prediction (see table 1) to maximise the sample size. Multi-predictor models were also run, and variance inflation factors calculated to investigate whether any significant effects were robust to potential multicollinearity between predictors.

Because the mating system data is nominal and cannot be ordered, it was analysed using a phylogenetic analysis of variance (ANOVA) (Garland et al., 1993).

All tests were carried out using the maximum possible sample size possible for that specific test which was dependent on the number of species that had data on the socio-ecological trait in question.

Statistical analyses were carried out in R 4.1.2 (R Core Team, 2021) using packages: Phytools (Revell, 2012), Caper (Orme et al., 2018), and Car (Fox & Weisberg, 2019).

Results

The intraclass correlation coefficient was calculated between the results of the participants in the classification task to test the reliability of ratings. A high degree of reliability was found between ratings of how different the infant pelages were compared to the mothers' (ICC = 0.96, F(167,672) = 27, P = 8.1 x 10^{-215}). There was also high reliability among ratings of how different infant pelages were against foliage (ICC = 0.89, F(167, 672) = 9.2, P = 3.8 x 10^{-98}).

The anti-infanticide hypothesis predicts that natal coat conspicuousness is negatively correlated with relative testes mass. Alternatively, the paternity cloak hypothesis predicts a positive correlation between coat conspicuousness and relative testes mass. A significant negative correlation was found between natal coat conspicuousness and relative testes mass (β =-243.1, N = 54, λ = 0.867, t = 4.392, P = 0.041, Figure 4), indicating that natal coats are more conspicuous when paternity certainty is high.

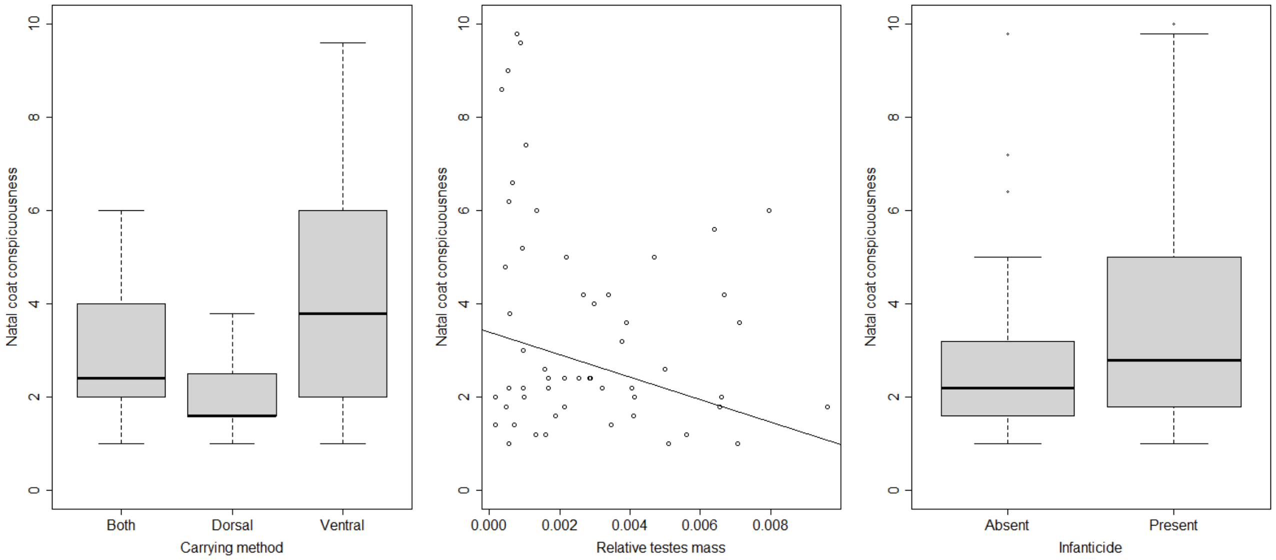

Figure 4. Relationships between natal coat conspicuousness and a.) carrying method, b.) relative testes mass, and c.) infanticide.

The anti-infanticide hypothesis also predicts natal coat conspicuousness to be positively associated with polygynous mating systems whereas the paternity cloak hypothesis predicts a positive association with polygynandrous mating systems. The phylogenetic ANOVA found no significant effect of natal coat conspicuousness on mating systems (F(4,101) = 6.956, P = 0.242). No association between coat conspicuousness and any mating system means this test does not support the anti-infanticide hypothesis or the paternity cloak hypothesis.

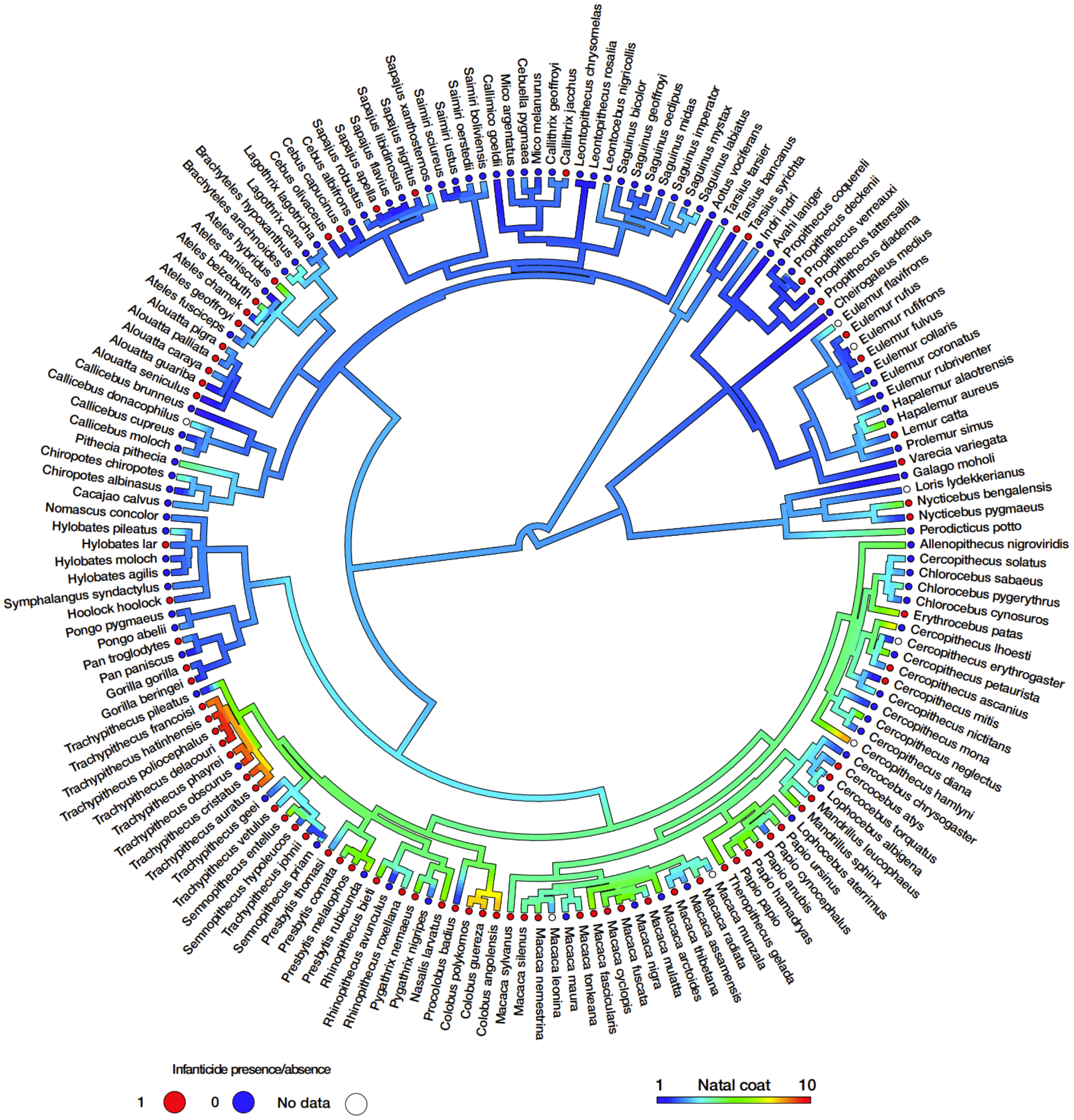

Figure 5. Natal coat conspicuousness (colour of node tips) and infanticide presence/absence (dots at the end of tips) of the 168 primate species in the study.

Another prediction of the anti-infanticide hypotheses is that natal coat conspicuousness should be positively correlated with presence of infanticidal behaviour (Figures 4 & 5). The results of this study strongly support this prediction ($\beta = 1.42$, $N = 160$, $\lambda = 1$, $t = 18.24$, $P = 3.352 \times 10^{-5}$). This suggests that natal coat conspicuousness is higher in species that experience infanticide.

A positive correlation between infant coat conspicuousness and ventral carriage is predicted by the infant tracking hypothesis, and this is also supported by the current study's results ($\beta = 1.15$, $N = 69$, $\lambda = 0$, $t = 15.35$, $P = 0.0002$, Figure 4), implying that infants have more conspicuous coats in species that carry infants ventrally rather than dorsally. The infant tracking hypothesis also predicts a positive association between natal coat conspicuousness and arboreality, however results suggest instead that natal coat conspicuousness is positively associated with terrestriality ($\beta = 0.66$, $N = 167$, $\lambda = 0.313$, $t = 8.502$, $P = 0.004$). Further, the infant tracking hypothesis predicts a positive correlation between natal coat conspicuousness against foliage and ventral carriage. This was not supported in the results. No significant association was found between infant coat conspicuousness against foliage and mode of infant carriage (β = -0.033, N = 69, λ = 0, t = 0.0145, P = 0.9045).

Under the infant tracking hypothesis, natal coats are predicted to be more conspicuous against foliage than against the mother's pelage. Alternatively, the allomothering hypothesis predicts the opposite; that natal coats are more conspicuous against the mother's pelage rather than against foliage. Through the phylogenetic paired t test, infant pelage was found to be significantly more conspicuous against foliage than against the pelage of the mother (t = -2.978, P = 0.003), supporting the infant tracking hypothesis. The other prediction of the allomothering hypothesis tested in this study is that NCC is positively correlated with presence of allomothering behaviour. There was no significant association between natal coat conspicuousness and presence of allomothering (β = 0.105, N = 145, λ = 0.564, t = 0.07147, P = 0.7896).

The maternal care hypothesis would suggest that natal coats are associated with earlier weaning ages. However, the results show no association between natal coat conspicuousness and weaning age (β = -7.364 x 10^{-6}, N = 78, λ = 0.205, t = 7.187 x 10^{-5}, P = 0.993).

Multi-predictor PGLS models were run to test all four of the significant variables (infanticide presence/absence, relative testes mass, infant carrying method, arboreality/terrestriality) in one model against natal coat conspicuousness. Since the variables relative testes mass and carrying method reduced the sample size greatly, two other multi-predictor models were created, one without testes mass and one without carrying method.

The results of the multi-predictor model that included all four significant variables shows only carrying behaviour as having a significant association with natal coat conspicuousness (β = 1.71584, N = 37, λ = 0, t = 5.12, P = 0.0016). When the multi-predictor model did not include carrying method as an explanatory variable, both the infanticide and relative testes mass variables had significant associations with natal coat conspicuousness (N = 54, λ = 0.898, t = 3.289, infanticide: β = 1.241741, P = 0.03423, relative testes mass: β = - 230.568, P = 0.04459).

The multi-predictor model without relative testes mass resulted in carrying method as the only variable significantly associated with natal coat conspicuousness (β = 0.914641, N = 69, λ = 0, t = 8.102, P = 0.00298).

Variance inflation factors (VIF) were calculated between the significant variables used in the multi-predictor model to assess multicollinearity: variables not providing independent information because they are highly correlated. All VIF values were below 2 (Infanticide presence/absence = 1.196440, Carrying method = 1.129567, Arboreality = 1.091877, Relative testes mass = 1.026849), which suggests that each variable is relatively independent and provides unique information.

Table 2. Results of each test and whether the hypotheses are supported or not.

Hypothesis	Comparative prediction	Test	Results	Supported?
Anti-infanticide aposematism	Natal coat conspicuousness is positively associated with high paternity certainty.	PGLS	(β =-243.1, N = 54, λ = 0.867, t = 4.392, P = 0.041)	Yes. Significantly supported.
	Natal coat conspicuousness is positively associated with polygynous mating systems.	Phylogenetic ANOVA	(F(4,101) = 6.956, P = 0.242)	Not supported. No significant trend.
	Natal coats are more conspicuous when risk of infanticide is high.	PGLS	(β = 1.42, N = 160, λ = 1, t = 18.24, P = 3.352 x 10^{-5})	Yes. Significantly supported.
Paternity cloak	Natal coat conspicuous is positively associated with polygynandrous mating systems.	Phylogenetic ANOVA	(F(4,101) = 6.956, P = 0.242)	Not supported. No significant trend.
	Natal coat conspicuousness is negatively associated with low paternity certainty.	PGLS	(β =-243.1, N = 54, λ = 0.867, t = 4.392, P = 0.041)	Not supported. Significant trend in the opposite direction.
Allomothering	Natal coats are positively associated with allomothering behaviour.	PGLS	(β = 0.105, N = 145, λ = 0.564, t = 0.07147, P = 0.7896)	Not supported. No significant trend.
	Natal coats are relatively more conspicuous against an adult female pelage than against foliage.	Phylogenetic paired t	(t = -2.978, P = 0.003)	Not supported. Significant trend in the opposite direction.
Mothering	Natal coats are more conspicuous with earlier weaning.	PGLS	(β = -7.364 x 10^{-6}, N = 78, λ = 0.205, t = 7.187 x 10^{-5}, P = 0.993)	Not supported. No significant trend.
Infant tracking	Natal coat conspicuousness is positively associated with risk of being dropped.	PGLS	(β = 1.15, N = 69, λ = 0, t = 15.35, P = 0.0002)	Yes. Significantly supported.
	Natal coats are more conspicuous against foliage when at high risk of being dropped.	PGLS	(β = -0.033, N = 69, λ = 0, t = 0.0145, P = 0.9045)	Not supported. No significant trend.
	Natal coat conspicuousness is positively associated with arboreality.	PGLS	(β = 0.66, N = 167, λ = 0.313, t = 8.502, P = 0.004)	Not supported. Significant trend in the opposite direction.
	Natal coats are relatively more conspicuous against foliage than an against an adult female pelage.	Phylogenetic paired t	(t = -2.978, P = 0.003)	Yes. Significantly supported.

Discussion

The intriguing phenomenon of primate natal coats has been studied sporadically for decades yet there is no clear evidence for their function or functions. Multiple hypotheses have been proposed, however, previous studies have found little clear support for any of them. The overall results of this study found strong support for the anti-infanticide hypothesis, that being the idea that primate natal coats are a signal to out-group males that the infant will be defended by the group if the male tries to harm it (Oates, 1977; Treves, 1997). Three predictions of this hypothesis were tested: i) Natal coats are more conspicuous when paternity certainty is high, ii) natal coats are more conspicuous when infanticide risk is high, and iii) natal coats are positively associated with polygynous mating systems. Both predictions i and ii were supported by the results of this study. No consistent support was found for any of the other hypotheses (allomothering, mothering, infant tracking, paternity cloak), however in the course of testing predictions I also found that ventral carriage of infants and terrestrial lifestyles were positively associated with natal coat conspicuousness, associations that I did not predict that were in the opposite direction to those made by different functional hypotheses.

Presence of infanticide and small relative testes mass (suggesting high paternity certainty) were both significantly associated with natal coat conspicuousness and support the anti-infanticide hypothesis. These results are reinforced by previous studies as the association between small relative testes mass and coat conspicuousness was found by Treves (1997) and the relationship between infanticide and coat conspicuousness was significant in the results of Caro et al (2022). These results are also supported by examples of the primates with the most conspicuous natal coats. Leaf monkeys (*Trachypithecus*) generally scored the highest for natal coat conspicuousness in the classification task; the babies are bright orange and the adults are greys and blacks (Zhao et al., 2011). Infanticide is common in eight out of the eleven leaf monkey species analysed in this study, two of the species absent of infanticide have natal coats very similar to adults. Leaf monkeys also commonly have polygynous mating systems resulting in high paternity certainty and carry their infants ventrally. In the data, almost all *Trachypithecus* are strictly arboreal, none are strictly terrestrial. When comparing the variables that have significant associations to natal coat conspicuousness, the genus with the most highly conspicuous natal coats shows evidence for three (infanticide, small relative testes mass, ventral carriage) out of the four significant relationships. Significant relationships were not driven by this genus alone, the genus *Colobus* and *Erythrocebus patas* are two convergent examples of species with distinct natal coats, infanticidal behaviour, and relatively small testes mass.

Caro et al (2022) found a significant association between natal coats and infanticide in two out of five natal coat conspicuousness measures tested. The two measures of coat conspicuousness that found significant relationships were the two most conservative measurements in which only very highly conspicuous coats were scored not incorporating variation in natal coats limited the reliability of their results. Earlier comparative investigations into primate natal coats found weak support for the anti-infanticide hypothesis (Treves, 1997), though analysis did not account for phylogenetic dependence among species. Regan (1998) used phylogenetic independent contrast to analyse primate natal coats and found no support for any hypotheses then Ross & Regan (2000) found weak evidence to support the allomothering hypothesis. Although past studies have not found strong support for the anti-infanticide hypothesis and in some cases found support for other hypotheses, by scoring primate natal conspicuousness on a continuous scale I found strong and consistent support for the predictions made by the anti-infanticide hypothesis.

The fact that ventral carrying behaviour was significantly associated with natal coat conspicuousness in the multi-predictor model suggests that of the significant variables (infanticide presence/absence, relative testes mass, infant carrying method, arboreality/terrestriality), the method of infant carriage explains the most variation in coat conspicuousness. The association between ventral carriage and natal conspicuousness is opposite to the prediction made by the infant tracking hypothesis, as infants are under less close control by the caregiver when dorsally carried. The infant tracking hypothesis also cannot account for the significant associations of infanticide and relative testes mass. The association between carrying infants ventrally and natal coat conspicuousness could be explained by carrying behaviour also being a strategy to protect infants from infanticide (Nakamichi & Yamada, 2009). Maybe distinct natal coats act as an aposematic signal to infanticidal males and ventral carriage makes it easier for the adult carrier to defend the infant if the male decides to attack. However, there might be a methodological reason for this significant association. Carrying method may be the better predictor because there is more information in the data for carrying method (three levels) than there was for infanticide (binary) (Batini et al., 2009). If infanticide was measured as continuous data, ideally the probability of infanticide per birth, maybe carrying method would not have been preferred in the model (Batini et al., 2009). However VIFs were low, indicating that potential multicollinearity between carrying behaviour and infanticide is not the explanation for the association between carrying behaviour and infanticide. This relationship between ventral carriage and natal coat conspicuousness is undocumented by past comparative studies due to the way that they have been conducted (Caro et al., 2022; Ross & Regan, 2000; Treves, 1997), which is interesting in itself. Further research should be conducted to discover if ventral carriage of infants in primates is potentially linked with infant protection and, if so, is also an anti-infanticide defence tactic.

Terrestriality being significantly associated with natal coat conspicuous was not predicted by any of the hypotheses. This association was also found by Ross & Regan (2000). Terrestrial primates like *Papio* and *Macaca* present more subtle natal coats which have arisen multiple times in conjunction with shifts towards terrestriality. From that perspective, brightly coated, arboreal langurs are the exception. The reasoning behind the association between terrestriality and natal coat conspicuousness cannot be explained by current understanding of the anti-infanticide hypothesis and should be explored further in other work. It may be that different natal coat phenotypes have different or multiple functions.

It has been noted that the presence of distinct primate natal coats is most frequent in Cercopithecoidea clade (Caro et al., 2022). This is supported and expanded upon in this study as figure 5 shows the conspicuousness of natal coats across primates. On top of displaying that the highest conspicuousness values are witnessed within the colobine clade, it shows that the majority of infant catarrhine species are somewhat distinct from their mothers, whereas the majority of platyrrhine and prosimians do not have distinct natal coats. The life histories of the platyrrhine and prosimian species that have independently evolved even slightly distinct natal coats should be assessed to see if they have any particular similarities with conspicuous catarrhines since traits shared between these species and less so with the less conspicuously coated primates may be the key to explaining natal coat function.

Images of primate infants and their mothers were only available for a third of primate species. Lorises, galagoes, and tarsiers were particularly underrepresented as images for each species were very limited or non-existent. This could be because these primates are small and often nocturnal, making them difficult to find and photograph in the wild. Many of these species are nocturnal. Therefore, there are some taxonomic and ecological biases in the species sample which may affect results.

The results of this study are the most compelling support for any hypothesised function of primate natal coats of any comparative study. The method of quantifying natal coat conspicuousness by using multiple participants to determine how different infants looked to their mothers on a continuous scale allowed this study to have the most detailed and realistic measurement of primate natal coats. It far better depicts the variation in natal coats between species compared to the binary, presence/absence or ordinal (none/inconspicuous/flamboyant) measurements of previous comparative studies. My classification task was independently completed by five participants, one of which was the researcher, and arithmetic means were calculated to address discrepancies between individuals and create a measurement for how the "average" human perceives natal coats. This is advantageous over Caro et al's (2022) classification task which used two participants, both were researchers, and discrepancies in answers resolved through discussion. Both this study and Caro et al (2022) found support for the anti-infanticide hypothesis but Caro et al (2022) rejected this hypothesis due to certain assumptions of the hypothesis, instead suggesting the mothering hypothesis. It was stated that of the assumptions that lead to the anti-infanticide hypotheses being rejected was that a conspicuous coat would not unduly draw attention an infanticidal male's attention to the conspicuous infant. This is a peculiar reason to discount the hypothesis since drawing the male's attention is the exact function proposed by the anti-infanticide hypothesis (Treves, 1997).

Past comparative studies of primate natal coat function have measured primate natal coats as a binary presence or absence trait, or categorically with very few categories such as none, inconspicuous, and flamboyant (Caro et al., 2022; Ross & Regan, 2000; Treves, 1997). This masks great deal of variation of natal coats among primate species and the significance of the variation is greatly minimised when it is reduced to only a few categories. This study treats natal coats as a continuous scale of dissimilarity to the mother's pelage so that the hypothesised key perceptual attribute of natal coats is quantified while still allowing for diverse adult and infant phenotypes (e.g. both the black mothers and white infants of *Colobus guereza*, and grey mothers and orange infants of *Trachypithecus obscurus* received similar high scores, despite having very different appearances). My results showed that quantifying variation across the range of natal coat phenotypes is important to revealing the function of primate natal coats.

The use of human observers and Likert scales in a colour-based classification task does involve risk of collecting results with low interrater reliability as values along the Likert scale can be inconsistent between participants (O'Neill, 2017). In this case, the intraclass correlation coefficients suggested high interrater reliability. This is probably due to the pre-task presentation in which guidance was given in the form of example images of species that should be scored at each end of the Likert scales. Using human observers to measure infant coat conspicuousness through this method is liable to result in subjective responses due to variation in how individuals perceive colour as well as the possible difference in lighting at the time of surveying. A more objective approach would have been the use of standardised digital photography (Stevens et al., 2007) or spectrophotometry, which was used by Ross & Regan (2000). However, only a few species of primate have spectral reflectance data of their pelages publicly available, and even less for infants. The time and resources needed to acquire such data was not available, so the classification task was deemed the next best method. As primate species ourselves, the human visual system is very similar to that of other catarrhines who are all trichromatic. In platyrrhines there is colour vision polymorphism where all males are dichromatic and two thirds of females are trichromatic (Jacobs, 2008). A human observer survey was also employed by Caro et al (2022) but the only observers were two of researchers, risking researcher bias. Although I participated in the classification task in this study, four out of the five observers were not researchers, so researcher bias was reduced both by the fact that most observers were not researchers and also the higher number of observers meant that there is a better chance of the results being closer to that of the average human perception of infant primate conspicuousness. Future studies should build upon the method of measuring natal coats as a continuous trait to account for the variation in conspicuousness that is seen among neonatal primates. For the most objective and high-quality natal coat colour quantification, standardised colour photographs should be collected for infants of all primate species as well as adults (Stevens et al., 2007). Through spectral image analysis, just noticeable differences (JND) could be calculated between infants and adults. Using spectral sensitivity data for each species, quantitative and objective measurements of how conspicuous/different infant pelages are to the visual system of that species can be calculated. This method would give more objective and more detailed data on natal coat contrasts which could allow for relationships to be found with less bias.

The continuous scale on which natal coat conspicuousness was been measured in this study sets it apart from those that came before in terms of the quality of coat colour quantification. However, the measure of infanticide is still that of presence or absence of the behaviour meaning that variation in the frequency of infanticide between species is not accounted for in this study. If the frequency of infanticide was measured this may give a better understanding of whether and how infanticide is the primary selection pressure on primate natal coats.

Considering that male platyrrhines are dichromatic(Jacobs, 2008), this could suggest why conspicuous coats which are often orangey are not present in these species. If the anti-infanticide hypothesis is true, and bright orange natal coats are evolved to stand out to males, would make sense why this has not been selected in platyrrhines because the males would not find them conspicuous.

What is still unclear about the anti-infanticide hypothesis is at what level of a hostile takeover the aposematic signal functions. It may be that an out-group male will see the group from afar and spotting a conspicuous infant will deter the male from attacking in the first place. Alternatively, once a male is in the process of aggressing the group, that may be when the coat functions to deter the male from attacking the infant. Alternatively, the natal coat may signal presence to in-group members to facilitate their defence. To better understand the anti-infanticide hypothesis, the level at which the aposematic coat functions should be investigated through field research.

A hypothesis that was not tested in this study is that conspicuous primate natal coats function as aposematic signals to predators. Conspicuous natal coats in primates could be an aposematic signal to potential predators that an infant will be defended by others in the social group and that the possible injury or energy required is not worth the potential reward. This is similar to the anti-infanticide hypothesis but with the difference that the signal receivers are potential predator species rather than male conspecifics. Where OCC in mammals usually results in cryptic infants due to vulnerability to predators and may become conspicuous as they grow and become better defended (Caro et al., 2022; Stoner et al., 2003), it is not unknown for other species to be aposematic in infancy and become cryptic as adults. For instance, some moth caterpillar species have aposematic warning colours and then, once they pupate, are cryptic (Grant, 2007). Perhaps due to the extremely social nature of primates and their ability to defend from predators as a group (Smuts et al., 1987; Tello et al., 2002), and the ability of their predators to learn that attacking primates can have negative consequences (Zuberbühler et al., 1999), primate infants can benefit from being aposematic since the benefit of predator deterrence outweighs the negative of being highly conspicuous to uneducated predators (Ruxton et al,. 2018). Furthermore, results from my undergraduate dissertation suggest that amongst a foliage background, bright orange infants are more conspicuous to trichromats (catarrhines and most female platyrrhines) than to dichromats and tetrachromats. From this, the increased risk of being easily spotted by predators due to conspicuous natal coats may not be as high as it initially appears to us as trichromatic primates (Suttie, 2021).

Conclusion

In summary, of the five hypotheses of the function of primate natal coats tested in this study, only evidence to support the anti-infanticide hypothesis was found. Infanticidal behaviour and small relative testes size were both found to be significantly associated with natal coat conspicuousness. Ventral carriage of infants was strongly associated with coat conspicuousness, which has resulted in a new proposition that ventral carrying could be a predictor of the anti-infanticide hypothesis by being a strategy of anti-infanticide defence. All hypotheses of primate natal coat function tested in this study involve infant care. With only evidence being found in support of the anti-infanticide hypothesis, it is specifically infant care in the form of infant defence from infanticidal out-group males that is alluded to here. Future experimental studies could observe how different potential signal targets (mothers, allomothers, out-group males) behave when presented with a natal coat stimulus to further test the anti-infanticide hypothesis.

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