

# Interspecific variation in primate coat colour supports Gloger's rule

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## ABSTRACT

**Aim** In 1833, C.L. Gloger observed that bird populations living in warm and wet habitats were darker than those found in dry, cool areas. However, this hypothesis has seldom been evaluated, particularly for mammals. Here, we test Gloger's rule using a dataset consisting of more than 100 primate species representing all major primate clades.

**Location** Africa, Madagascar, Asia and the Neotropics.

**Methods** We used museum skins, digital photography, and colour correction software to quantify the brightness of the dorsal and ventral pelage surface of each species. We utilized the mean actual evapotranspiration (AET) within the geographic range of each species as a proxy for habitat conditions and accounted for additional variables that may influence coloration. To analyse the data, we used a generalized linear model that simultaneously accounts for the effects of phylogenetic and spatial autocorrelation.

**Results** We found that increasing levels of AET were significantly related to increasing pelage darkness on the dorsal surface of species, while accounting for other effects.

**Main conclusions** Our finding provides further support for the applicability of Gloger's rule to mammals, and is the first broad-scale evaluation for primates. The mechanism driving Gloger's rule is not easy to discern, but may include increased background matching for species living in relatively light or dark habitats, increased resistance to keratin-degrading micro-organisms in hair with large amounts of eumelanin, and/or thermoregulation.

## Keywords

Actual evapotranspiration, biogeography, coat colour, ecogeographical rules, hair, mammals, pelage, phylogenetic comparative methods, primates.

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## INTRODUCTION

Gloger's rule states that animals should be dark in warm and wet regions (Gloger, 1833; Caro, 2005). Although this hypothesis was formulated nearly 200 years ago, it has not been well tested for many animal groups. In addition, existing studies of birds and mammals at both the across- and within-species levels have yielded mixed results. In a broad comparative study, Zink & Remsen (1986) found that nearly all of the 52 North American bird species they examined followed Gloger's rule. Similarly, Hamilton (1958) found a positive correlation between pigmentation and humidity within geo-

graphically dispersed populations of passerine *Vireo* species, but did not detect an across-species effect. Further support for an environmental effect on brightness at the within-species level was provided by Burt & Ichida's (2004) study of song sparrows in Washington state and Arizona. In contrast, a recent study by Chui & Doucet (2009) found that golden crowned kinglets (*Regulus satrapa*) follow an opposite pattern to that predicted by Gloger's rule, with mantle coloration being lighter in more humid habitats.

For mammals, similarly variable results have been found, although some of these studies used latitude as a proxy for climate, which might confound results, as latitude does not

necessarily correlate with humidity. Stoner *et al.* (2003a) showed that tropical artiodactyls and bovids were darker than species living at higher latitudes. Ortolani & Caro's (1996) study of carnivores showed that members of some families (e.g. canids, herpestids, ursids) are more melanistic in tropical forests than in drier, more open habitats. However, species from other Carnivora families (e.g. mustelids, felids, viverrids) exhibited little relationship between pigmentation and habitat. This latter result is similar to Stoner *et al.*'s (2003b) study, where they did not detect a relationship between latitude and pelage brightness in lagomorphs when accounting for the phylogenetic history among species.

Some recent studies have investigated Gloger's rule in mammals at the within-species level. Lai *et al.* (2008) measured coat colour brightness in wild house mice (*Mus musculus*) across Asia. They found a strong negative relationship between rainfall and dorsal coat colour brightness using museum specimens with known localities. Interestingly, they did not find a strong relationship between dorsal and ventral coat colour. Two studies have examined coat colour variation in long-tailed macaques (*Macaca fascicularis*). Hamada *et al.* (2008) found that lighter coloured macaque populations existed at higher latitudes in Thailand. Villano *et al.* (2009) showed a similar pattern, with macaques in Indonesia displaying darker pelages than those at a higher latitude in Vietnam.

Aside from a few exceptions, most studies have focused on temperate taxa found at relatively high latitudes, especially in the case of birds. Of course, North American birds make excellent study systems to examine biogeographic questions considering the wealth of information available. We have less knowledge of taxonomic groups comprising species that are mostly distributed in the tropics, with only a minority of taxa found in subtropical and temperate regions. There may be several scenarios in which tropical clades may follow Gloger's rule due to elevational and regional climatic effects that lead to measurable differences in rainfall and temperature variation in areas at similar latitudinal levels. This in fact may be one reason for the mixed results of previous examinations of Gloger's rule that use latitude as a proxy for climate and habitat.

Our goal for this current study is to investigate whether Gloger's rule is supported across a large number of primate species, representing all major clades within the order. Compared to most other mammalian orders, primates are generally regarded as tropical forest species, yet some taxa do range into subtropical and even temperate environments. In addition, primate species vary in their habitat preference, with members of the order being found in woodland, savanna and desert habitat (Fleagle, 1999). Therefore, primates are distributed across a range of habitats varying markedly in average temperature and rainfall. This includes climatic variation across habitats that are found at similarly low latitudinal levels. We build on previous analyses by using objective colour measurements of museum specimens and implementing recently developed comparative methods that quantitatively account for potential confounding effects due to phylogenetic and spatial autocorrelation.

## MATERIALS AND METHODS

We measured 211 female museum skins representing 104 primate species. Only females were used to reduce the possible confounding effects of sexual selection that may impact male colour patterns (Bradley & Mundy, 2008). We only examined adult specimens that appeared in good condition and were not on display in museum exhibits.

We used a Canon Rebel XTi camera to obtain digital photographs and employed established methods to obtain objective colour measurements from these photos (Gerald *et al.*, 2001; Stevens *et al.*, 2007, 2009; Kamilar, 2009a; Kamilar & Bradley, 2011). The camera's colour mode was set to 'faithful' (i.e. true colour), with the white balance calibrated with an 18% grey card. An Xrite colorchecker card was placed in the frame of each specimen as a control. All images were originally recorded in RAW format. We used Digital Photo Professional to produce linearized 16-bit TIFF files from the RAW files. The Pictocolor plugin for Adobe Photoshop and the colorchecker card were used to colour-correct each TIFF image. We then used Adobe Photoshop to measure the luminance values (i.e. brightness) from two points on both the dorsal and ventral surface of each specimen's torso. On the dorsal surface, we measured the luminance at the midpoint of the torso, between the base of the tail (or the equivalent location on the apes) and the base of the neck at the midline of the body. We obtained the second luminance value from the upper part of the torso, just inferior to the articulation between the upper limb and the torso at the midline of the body. We also recorded the luminance values at analogous locations from the ventral side of the torso. The luminance value for each side of the specimen was obtained by averaging the values for the two sampling locations. In addition, some species were represented by more than one specimen; in these cases, we calculated the mean value for each species. Higher luminance values indicate brighter hair colour.

We used actual evapotranspiration (AET) values averaged across the geographic range of each species as a measure of the typical warmth and humidity of the species' habitat. This variable was obtained from the Pantheria database (Jones *et al.*, 2009) and was sourced from a GIS-based dataset. AET is the amount of atmospheric water resulting from both evaporation and transpiration. Evaporation increases when water availability, from rainfall and standing bodies of water, and temperature is high. Transpiration is due to water loss from plants, and therefore, should be higher in regions that are more densely vegetated. AET is an ideal metric to use when testing Gloger's rule and is an improvement over previous studies that used latitude as a proxy for climate and habitat characteristics.

We also included three additional predictor variables in the analysis because they may influence dorso-ventral brightness and produce confounding effects. These variables are as follows. 1. Female body mass. Results from our previous research indicate that counter-shading, with a ventral surface that is often light coloured, is more strongly pronounced in smaller-bodied primates (Kamilar, 2009a).

2. Frequency of adopting a vertical posture. Primates that adopt a quadrupedal, rather than suspensory, posture and locomotion are more likely to be countershaded (Kamilar & Bradley, 2011). For instance, species moving via brachiation or vertical clinging and leaping do not typically show countershaded pelages, and often exhibit a dark ventral surface (Kamilar & Bradley, 2011).

3. Number of years since the specimen was collected. The age of the specimen may be an additional factor to consider. A recent study of bird museum specimens (Armenta *et al.*, 2008) found that for some species, new specimens are brighter than old ones. Our preliminary assessments of this issue also suggested there may be a weak effect in the same direction with primate skins (J.M. Kamilar and B.J. Bradley, unpublished data).

We obtained body mass data from Smith & Jungers (1997) and supplemented it with additional sources (see Appendix S1 in Supporting Information). Positional behaviour data were quantified from descriptions of species biology (Fleagle, 1999; Campbell *et al.*, 2007). Briefly, taxa that are rarely found in vertical positions, such as baboons or macaques were given a score of zero; species that spend some time in a vertical position, such as spider monkeys or capuchin monkeys were given a score of one; and species that are known to frequently adopt a vertical position to feed or move, such as marmosets (*Callithrix*), gibbons (*Hylobates*) and bushbabies (*Galago*) were given a score of two. More details regarding this variable may be found in Kamilar & Bradley (2011).

The comparative nature of our analysis, incorporating both interspecific and spatially explicit data, requires a method that accounts for data non-independence due to phylogenetic relatedness and spatial autocorrelation (Felsenstein, 1985; Diniz-Filho *et al.*, 2003). A recently published generalized linear model by Freckleton & Jetz (2009) satisfies this requirement. In addition, this model contains three parameters that quantify the relative importance of phylogeny ( $\lambda'$ ), space ( $\Phi$ ), and variation independent of both phylogeny and space

( $\gamma$ ) in the explanatory model. Each parameter is measured on a continuous scale from zero to one, with larger values indicating that the particular parameter is more important in the model. The optimal value of each parameter is found via a maximum likelihood approach. The Freckleton & Jetz (2009) method requires a phylogenetic tree, as well as latitude and longitude values for each species. We obtained a phylogeny and branch lengths (estimated divergence times) from the species-level mammal supertree presented in Bininda-Emonds *et al.* (2007). We used the latitudinal and longitudinal midpoints of the geographic range of each species presented in the Pantheria database (Jones *et al.*, 2009). We conducted the analysis in R for Windows (R Development Core Team, 2007).

We conducted two analyses, one for the dorsal and one for the ventral surface. Our linear models consisted of the four previously mentioned predictor variables – AET, female body mass, the degree of vertical positional behaviour, and the age of the specimen – with the luminance of the pelage as the dependent variable.

All variables, except for the frequency of vertical positional behaviour, were natural log transformed prior to analysis.

## RESULTS

Our model of dorsal luminance was statistically significant at the  $P = 0.005$  level (Table 1). We found two variables that exhibited statistically significant effects on dorsal luminance, body mass ( $t = -2.147$ ,  $P = 0.034$ ) and AET ( $t = -2.139$ ,  $P = 0.034$ ). As body mass and AET increased across species, pelage luminance declined. In addition, there was a negative trend between time since collection and dorsal luminance ( $P = 0.060$ ). Positional behaviour was not related to dorsal luminance.

Our model of ventral luminance was also statistically significant ( $P < 0.001$ ), and our variables provided a better fit compared to dorsal luminance ( $r^2 = 0.252$  vs.  $r^2 = 0.137$ , respectively). Body mass and positional behaviour were

**Table 1** Generalized linear model examining the relationship between actual evapotranspiration and primate pelage brightness while accounting for potentially confounding variables. We used Freckleton & Jetz's (2009) method to control for phylogenetic and spatial effects.

Surface	Predictor	Estimate	SE	<i>t</i> -value	<i>P</i> -value
Dorsal	Actual evapotranspiration	-0.303	0.141	-2.139	0.034
	Mass	-0.052	0.024	-2.147	0.034
	Positional behaviour	0.017	0.035	0.493	0.623
	Time since collection	-0.190	0.099	-1.902	0.060
	Model parameters: Phylogenetic ( $\lambda'$ ) = 0.010, Spatial ( $\Phi$ ) = 0.010, Independent ( $\gamma$ ) = 0.980				
Full model: $r^2 = 0.137$ , $P = 0.005$ , d.f. = 4,99					
Ventral	Actual evapotranspiration	-0.292	0.184	-1.583	0.116
	Mass	-0.136	0.031	-4.262	< 0.001
	Positional behaviour	-0.202	0.046	-4.345	< 0.001
	Time since collection	-0.234	0.130	-1.798	0.075
	Model parameters: Phylogenetic ( $\lambda'$ ) = 0.010, Spatial ( $\Phi$ ) = 0.010, Independent ( $\gamma$ ) = 0.980				
Full model: $r^2 = 0.252$ , $P < 0.001$ , d.f. = 4,99					

excellent predictors of ventral luminance ( $P < 0.001$  for both), and the effect of AET was in the direction expected, yet exhibited a  $P$  value of 0.116. Similar to the model of dorsal luminance, we found a negative trend between time since collection and ventral luminance ( $P = 0.075$ ).

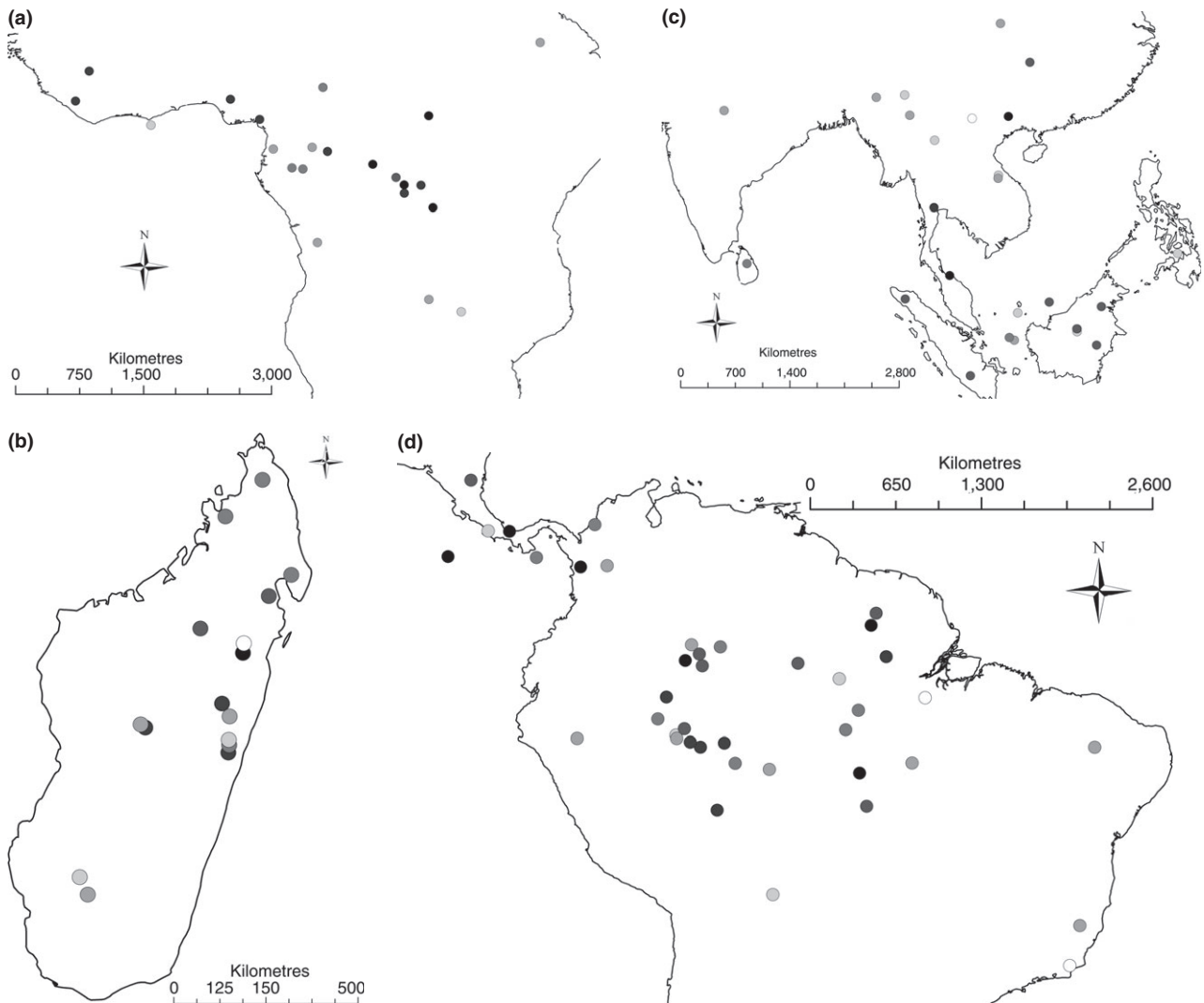
Neither phylogeny nor space played a significant role in our models, exhibiting lambda prime (quantifying the phylogenetic effect) and phi (quantifying the spatial effect) values of 0.01 (Figs 1–3). These values indicate that the relationship between our predictor variables and luminance are independent of phylogeny and space.

Although many of the primate species in our dataset are rain forest dwelling, there is variation in the type of habitat, and consequently AET, across species. In our dataset, AET varied from a minimum of 652 mm for *Semnopithecus entellus* to a maximum value of 1828 mm for *Presbytis melalophos*. Additional species with low AET values include *Rhinopithecus*

*roxellena*, *Propithecus verreauxi* and *Chlorocebus aethiops*. In contrast, leaf monkeys from the Sunda Shelf were found in high AET habitats, including *Presbytis rubicunda*, *Presbytis hosei* and *Nasalis larvatus*. In terms of pelage luminance, *Saimiri* and *Aotus* species displayed the brightest hair on the ventral portion of the torso and *Indri indri*, *Colobus angolensis* and *Trachypithecus francoisi* were among the darkest. On the dorsal surface, *Leontopithecus rosalia*, *Callithrix argentata*, and *Nomascus concolor* exhibited the brightest values, and *Indri indri*, *Colobus angolensis* and *Trachypithecus francoisi* were the darkest.

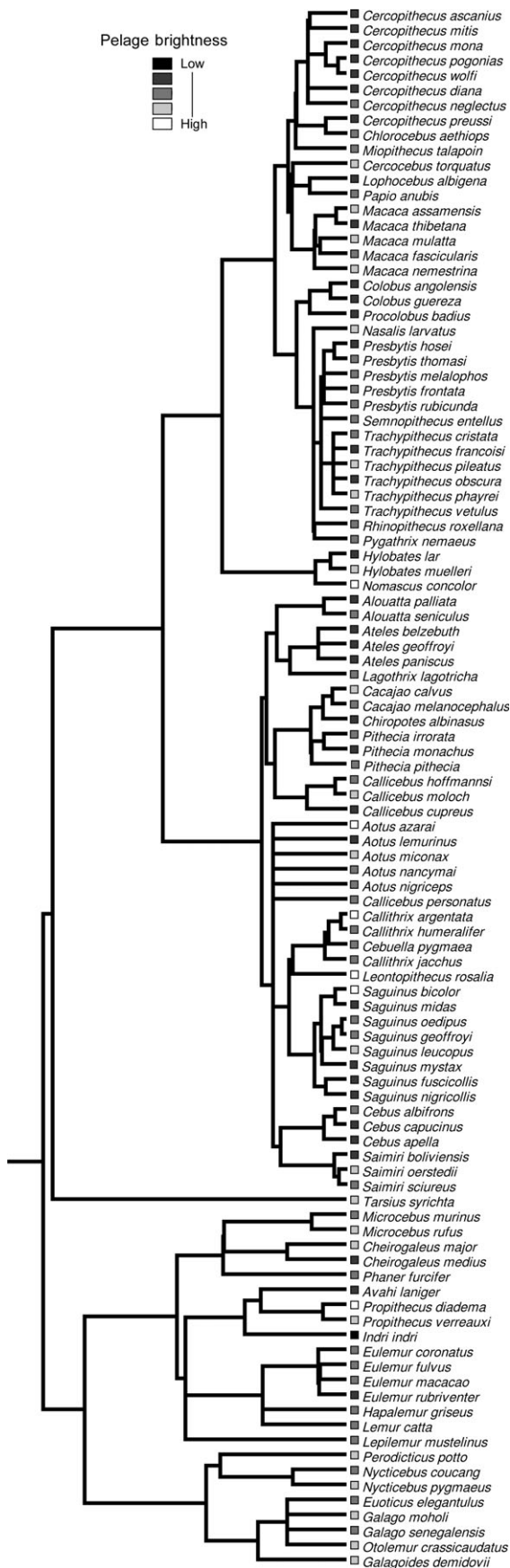
## DISCUSSION

Our study finds support for Gloger's rule (Gloger, 1833; Caro, 2005) in a large comparative dataset of primates. As the actual evapotranspiration (AET) in geographic ranges increases,



**Figure 1** Dorsal luminance of female primates in: (a) Africa, (b) Madagascar, (c) Asia, and (d) the Neotropics. Lighter circles indicate species with brighter dorsal pelages. Circles are placed at the midpoint of the geographic range of each species. As demonstrated from our statistical analyses, there is little relationship between geography and luminance values across species.



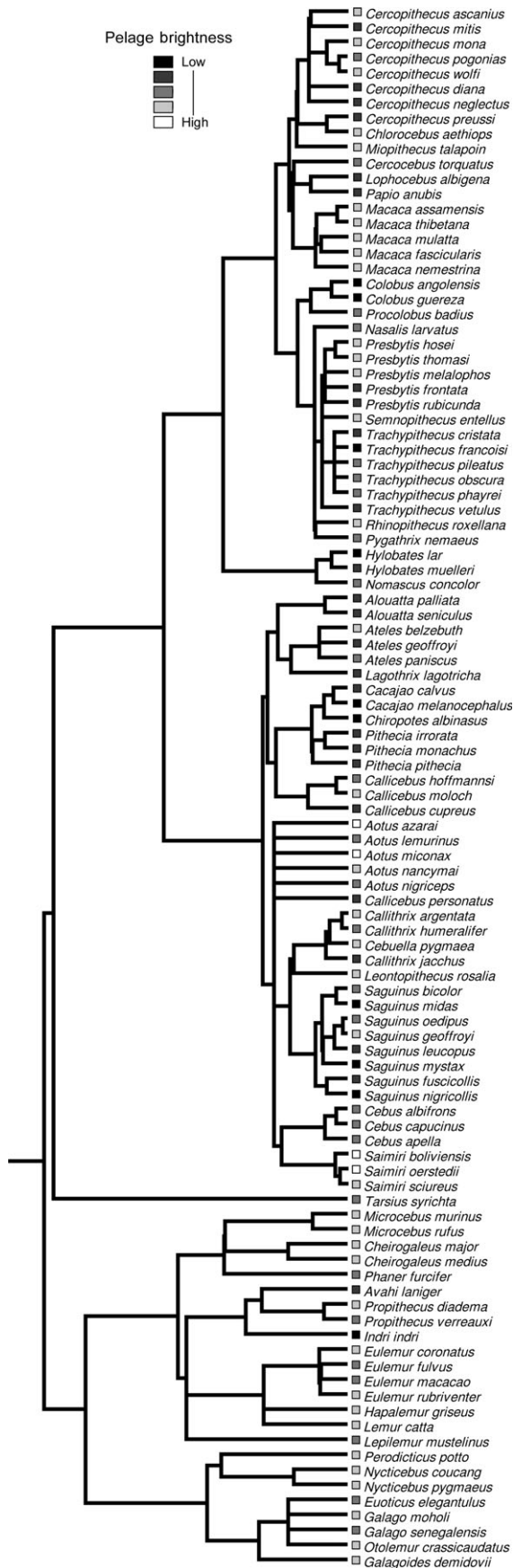


**Figure 2** Dorsal luminance of female primate coat colour in a phylogenetic context (phylogeny obtained from Bininda-Emonds *et al.*, 2007). Please note that the grey-scale shaded boxes do not represent the same luminance values for dorsal and ventral patterns. See Appendix S1 for the raw luminance data.

species exhibit darker hair on the dorsal surface of the torso. Our examination of the ventral surface exhibits a relationship in the same direction, yet is not statistically significant. In addition, the effect of AET on pelage luminance is independent of other factors, including body mass, positional behaviour, phylogeny and spatial location. Interestingly, phylogeny and space had little effect on the models for both the dorsal and ventral surfaces. Therefore, the association between pelage brightness and AET probably exists in several places along the primate phylogeny and in more than one geographic region. This is illustrated by several relatively dark-coloured species living in areas with high AET, such as *Trachypithecus obscura*, *Saguinus mystax* and *Ateles paniscus*. Similarly, several species exhibit relatively bright hair and typically live in habitats with low AET, such as *Propithecus verreauxi*, *Otolemur crassicaudatus* and *Macaca mulatta*. Our results contribute to a growing body of evidence showing evolutionary flexibility in mammalian coat colour, including a recent study demonstrating convergent evolution in the pelage patterns of felids (Allen *et al.*, 2011).

Our results support existing research on birds and some non-primate mammals (Zink & Remsen, 1986; Ortolani & Caro, 1996; Stoner *et al.*, 2003a; Burt & Ichida, 2004; Lai *et al.*, 2008). It is important to note that previous studies of Gloger's rule often used latitude as a proxy for environmental characteristics. For instance, Stoner *et al.* (2003a) found darker bovids and artiodactyls in the tropics (defined as 0–10° from the equator) and lighter species in deserts, with deserts not being defined by latitude. In contrast, Stoner *et al.* (2003b) did not find dark lagomorphs species in tropical latitudes when controlling for phylogeny. One possible reason for this inconsistent pattern may be the imperfect relationship between latitude and local environmental conditions. In general terms, low latitude habitats are tropical, yet there are many exceptions. Relatively high elevation areas may be one factor for lower than expected temperatures at low latitudes. In addition, the combination of topography, wind patterns, and proximity to large bodies of water may influence temperature and rainfall levels across regions that occupy similar latitudes, and subsequently affect animal distributions. This can be readily observed when comparing the climate, habitat, and primate communities of eastern versus western Madagascar, the Congo basin versus eastern Kenya, and the Deccan Plateau versus the Western Ghats of India (Kamilar, 2009b; Kamilar & Guidi, 2010; Kamilar & Muldoon, 2010). Only using latitude to quantify the climate and/or habitat of these pairs of locations would yield spurious results.

Although our models produced statistically significant results, they explained a relatively small portion of variation



**Figure 3** Ventral luminance of female primate coat colour in a phylogenetic context (phylogeny obtained from Bininda-Emonds *et al.*, 2007). Please note that the grey-scale shaded boxes do not represent the same luminance values for dorsal and ventral patterns. See Appendix S1 for the raw luminance data.

in pelage brightness. This is likely to be due to the several factors. Most importantly, we used species means for actual evapotranspiration, body mass and pelage brightness. Not accounting for geographic variation within species should not bias our results in any one direction, yet may yield models with increased error. In addition, we did not account for other factors that may influence animal coloration, such as species recognition (Cooper & Hosey, 2003; Bradley & Mundy, 2008).

Our results demonstrate that Gloger's rule is generally supported in primates, especially when considering their dorsal surface alone, yet the mechanisms driving this pattern are not clear. One factor may be increased crypsis via background matching (Zink & Remsen, 1986). Many primates are known prey for a wide range of predators, including birds of prey (Karpanty, 2006), carnivorous mammals (Isbell, 1990), and snakes (Tello *et al.*, 2002). Exhibiting dark hair in forested habitats that have relatively low light levels would probably reduce predation risk from visual predators. This may be especially helpful for reducing detection by aerial predators considering that we found a stronger relationship between AET and dorsal hair coloration than between AET and ventral coloration. From the perspective of an aerial predator, a dark primate back may match the dark ground below. In addition, primates living in drier, more open habitats (with more sunlight) may increase crypsis by exhibiting lighter coloured pelages.

Previous researchers have also argued that protection from ultraviolet radiation (Caro, 2005) or improved thermoregulation through absorption of solar radiation may be the mechanism leading to darker coloration in warm and wet habitats (Burt, 1981). Protection from ultraviolet radiation is unlikely to be a strong factor considering that many dark-coloured primates living in forests do not spend large amounts of time in the upper canopy (Fleagle, 1999) where ultraviolet radiation would be the strongest. In fact, exposure to ultraviolet radiation may be higher for many primates living in more xeric habitats, such as the spiny thicket areas of southern Madagascar. In addition, dark hair may help capture solar radiation and regulate the body temperature of primates in warm and wet habitats, but more research is needed to support this.

Finally, several recent studies provide evidence supporting the idea that melanin, as well as other colour pigments, have important pathogen-resistance functions (Mackintosh, 2001; Burt & Ichida, 2004; Gunderson, 2008; Burt *et al.*, 2011). Specifically, Burt & Ichida (2004) argued that melanin increases the resistance of darkly pigmented song sparrows to feather-degrading bacteria. They showed that dark feathers from populations living in wet environments degrade more

slowly than lighter feathers from populations living in dry regions. Consequently, increased melanin levels may preserve feather colour needed for communication, thermoregulation and/or flight. If a similar scenario is present for the hair of primates and other mammals, then melanin may have an important role for maintaining hair colour and structure through resistance to micro-organisms. This may be a strong selective pressure, considering that hair structure and colour may be especially critical for a mammal's ability to thermoregulate, communicate with conspecifics, and increase crypsis to reduce predation from visual predators (West & Packer, 2002; Bradley & Mundy, 2008). Further research is necessary to test the idea that pathogens affect mammal coloration.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

### Appendix S1 Data used in the analyses.

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